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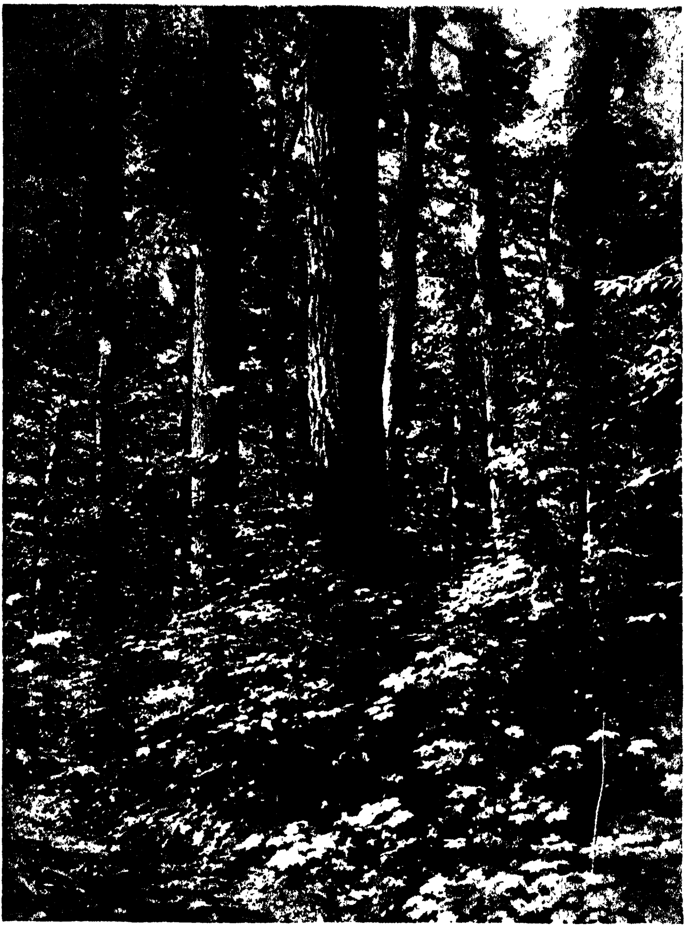

Frontispiece.—Climax deciduous forest of *Acer saccharum*, *Tsuga canadensis*, and *Fagus grandifolia*. Bay View, Michigan. (*Photo by Fuller.*)

PLANT SOCIOLOGY

THE STUDY OF PLANT COMMUNITIES

AUTHORIZED ENGLISH TRANSLATION OF

PFLANZENSOZIOLOGIE

BY

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PREFACE TO THE GERMAN EDITION

Phytosociology, the study of vegetation, has had a very rapid development. A few years ago it lacked aim or limitations, appearing merely as an offshoot of ecology, an appendix to geobotany. The immediate past has wrought a great change. The rapidly accumulating mass of phytosociological data demanded arranging, testing, and orienting in the system of sciences. It was further necessary to test the findings of phytosociology philosophically, to reconsider its conclusions, and to synthesize these into broad general principles. From these exacting tests this new branch of science emerges with a well-defined individuality.

Meanwhile we have lacked any unified and comprehensive survey of the scope, aims, and limits of plant sociology. The purpose of this book is to meet this need and to supply a brief handbook to those who are studying vegetation.

This work, matured by many years of intimate contact with nature, has grown out of my lectures at the Federal College of Technology (Technischen Hochschule), Zürich, and out of ecological field trips in Switzerland, Germany, and France. The leading principles and the viewpoints are naturally those which I have persistently held for many years—whether for better or for worse, time alone can tell.

In the foreground of all my effort stands the plant community as a social unit. Every natural aggregation of plants is the product of definite conditions, present and past, and can exist only when these conditions are fulfilled. The whole structure of plant sociology rests upon this idea of sociological determination. Its definite objective, however remote its accomplishment, is to catalogue and describe the plant communities of the earth, to discover their causal explanation, to study their development and geographic distribution, and to arrange them according to a natural system of classification.

In order to keep within the assigned limits of the book the text has had to be severely restricted. The choice of suitable citations from the voluminous literature required still greater restrictions. An attempt has been made to include as far as possible the more important contributions of North American, English, and Russian scholars.

To all who have aided my work by counsel or by the loan of photographs I extend my most cordial thanks. I am especially indebted to Dr. H. Burger, Dr. W. Koch, and Dipl. rer. nat. H. Pallmann of Zürich, who were kind enough to read portions of the manuscript. To the editor of the "Biologische Studienbücher," Professor Dr. W. Schoenichen, I owe sincere thanks for sympathetic interest in my work. I also wish to thank the publisher for his appreciative cooperation in making the book.

J. BRAUN-BLANQUET.

MONTPELLIER, FRANCE,
Cabinet de Géobotanique Méditerranéenne
(now Station Internationale de Géobotanique
Méditerranéenne et Alpine).
October, 1927.

PREFACE TO THE ENGLISH EDITION

Believing that Dr. Braun-Blanquet's "Pflanzensoziologie" will long serve as a milestone and guidepost on the road to an adequate knowledge of vegetation, the translators have undertaken to make it more easily available to the English-speaking world. They have already proved its value as a textbook in the teaching of field botany and ecology.

In the preparation of the English edition one of them (Conard) has had the greater part of the task of translating the German text, while the editing and revising have been done mostly by the other (Fuller), who has also inserted, with the approval of the author, some of the results of American investigators. In certain portions of the text the opinions of the author have prevailed rather than those of the editors.

In their work the editors have had the full cooperation of the author, who has made many changes in the original and has added the results of investigations that have been reported since the appearance of the German edition. He has also approved the insertion of certain topics not appearing in the earlier edition. The present book is, therefore, not only a translation but also a revised and enlarged edition of the original.

The translators and editors are indebted to the author for permission to translate his book and for his assistance in the revision of this English edition; to Dr. Frank Thone of Science Service, who read the entire manuscript; to Prof. Hans Jenny of the University of Missouri and to Prof. Paul Emerson of Iowa State College, who read the chapters on soils; to Dr. Clare F. Cox, who read portions of the manuscript; and to other friends who have assisted in various ways. To all of these they tender their sincere thanks. They will welcome criticisms, corrections, and suggestions by which a second edition may become better than the present one.

George D. Fuller.
Henry S. Conard.

The University of Chicago, Chicago, Illinois,
Grinnell College, Grinnell, Iowa,
July, 1932.

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PLANT SOCIOLOGY

INTRODUCTION

When a decade ago on both sides of the Atlantic the term "plant sociology" emerged and took its place on the records of science—the name was coined much earlier by Krylov and by Paczoski (1896)—the foundation and framework of this new branch of knowledge had already been laid down in broad outlines. Based upon Warming's "oecology" and Schröter's "synecology," strengthened by increments from neighbor sciences, and vitalized by the suggestive power of new and fruitful ideas, plant sociology has made in a few brief years astounding progress and now looks hopefully forward to the solution of its future problems.

The term plant sociology (or phytosociology) has been much criticized, especially on etymological grounds. Nevertheless it has quickly become internationally accepted, because it is so expressive and understandable. It may be admitted that there is no close parallelism between plant sociology and the sociology of August Comte. The two have one important point of contact: they are concerned not with the life expression of the individual organism as such but with groups or communities of organisms having more or less equivalent reactions, bound together in mutual dependence. The communal values resulting from the mutual relations of organisms are the social phenomena; the cooperation of organisms is the social process. The community has an existence altogether independent of the individual.

Starting from this philosophic foundation, we may divide all biology into (1) idiobiology: the science of individual organisms; and (2) sociology: the science of organic communities.

The latter is divided into the social science of man (sociology in the usual sense), zoosociology, and phytosociology or plant sociology.

Plant sociology, the science of plant communities or the knowledge of vegetation in the widest sense, includes all phenomena which touch upon the life of plants in social units.

The present range of sociological investigations in plant science includes five major problems involving the investigation of the following fundamental communal and environmental relationships, ever present in the plant community:

1. The organization or structure of the community; the investigation of the composition of plant communities.
2. Synecology: the study of the dependence of plant communities upon one another and upon the environment.
3. Syngenetics (development of communities, closely related to synecology): the discovery of the laws of the rise, development, and decline of plant communities.
4. Synchorology (geographic distribution of communities): the investigation of the arrangement of the plant communities in space, their occurrence and distribution.
5. Sociological classification (systematics): the delimitation of the social units, their grouping into higher units, and the systematic arrangement of these units. This grows out of the preceding as a synthesis of the first four problems.

The first problem—the investigation of the composition of communities—stands at present at the focus of phytosociological effort. It furnishes the indispensable foundation for an unbiased treatment of all the other partial problems. On the other hand, classification, like every natural systematization, has as its prerequisite the most accurate possible knowledge of all the partial problems. From the nature of the case, therefore, this part of sociological science, at present lacking the necessary broad basis, is quite undeveloped.

PART I

THE BASIS OF SOCIAL LIFE AMONG PLANTS

CHAPTER I

SOCIAL LIFE AMONG PLANTS

The kinds of communal relationships among plants are manifold, but not all have socialistic value. They are fundamentally different from the relationships among animals as described by Deegener (1918) (following Espinas, 1875). A division into "accidental," without advantage to the individual organisms, and "essential," for the benefit of all the individuals or of some of them (Deegener), cannot be considered in the case of plants. The principles of usefulness, of division of labor, of conscious support, of marshaling all resources for the accomplishment of a common purpose do not exist in the plant world. The struggle for existence rules here undisturbed. It regulates directly or indirectly all the unconscious expressions of the social life of plants. Herein lies the deep and fundamental difference between the vital relations of plant and those of animal communities.

Inanimate nature furnishes to most plant communities the necessities of life, whereas most animal communities are conditioned by the vegetation and therefore are dependent upon it.

According to their nature we distinguish two principal types of social relation of plants: dependent unions and commensal unions.

Dependent Unions.—As dependent unions we designate all communal relations of plants in which the members are in any way dependent upon one another; parasites, epiphytes, humus plants, and plants requiring mechanical support or protection must be regarded as dependent.

The most intimate form of communal life of plants is parasitism, a nutritive symbiosis in the sense of McDougall (1918). In one-sided parasitism the parasite is dependent upon the host, while the latter suffers only harm. The grim "destroyers in the plant world" from the families Loranthaceae, Rafflesiaceae, Orobanchaceae, etc., are well-known examples of one-sided plant parasitism. And there are all transitions from complete independence to obligate parasitism (Fig. 1).

In mutual parasitism each of the united organisms furnishes food or food material for the other. As examples of mutual parasitism McDougall cites ectotrophic mycorhiza, the nodule bacteria of Leguminosae, and the union of algae and fungi in lichens.

Warming-Graebner (1918), on the other hand, considers the relation of alga and lichen fungus as "helotism." The alga by its chlorophyll provides carbohydrate nutrients; the fungus, the rest. The alga does not need the fungus at all but is held in slavery by it. And yet by this union there is formed a new organism wholly self-sufficient, from the standpoint of competition, and one with a specific ecology. The original individualities of fungus and alga are lost and merged in a new and more aggressive organism, so that the term helotism does not seem any more fortunate than the term mutual parasitism.

FIG. 1.—Symbiosis in the *Tamarix* coastal forest at Oum er Rebia, Morocco. *Cynomorium coccineum*, a root parasite, *Lonicera biflora*, a liana, and *Ephedra*. (*Photo by Hoffmann-Grobéty.*)

Mycorhizal fungi present undoubted cases of mutual symbiosis (Melin, 1923), wherein the higher plant serves as host and the root fungus as feeder. The union benefits both symbionts, and in spite of their antagonistic relation they form a double organism which thrives better as a unit than either symbiont does by itself alone.

Epiphytes are less closely related to the host plant. They receive no nourishment from the latter and use it solely as a substratum. By their abundance they may, however, injure the host. In cold and temperate climates epiphytes are without exception algae, mosses, and lichens, but in warm, moist regions ferns and seed plants also grow epiphytically and form sharply circumscribed communities (dependent communities). As leaf epiphytes (epiphylls) a number of lichens and liverworts gather on the leaf surfaces of tropical plants.

Parasites and epiphytes, more especially the former, often show a specific selection of hosts and are frequently confined to one particular species.

Much feebler is the relationship which binds together the representatives of the third group of dependents: humus plants, climbers, and plants requiring protection. The term "humus plant" is here used broadly and includes not only the true non-chlorophyll saprophytes and green hemisaprophytes but also those humicolous species which are clearly dependent upon raw humus.

As with parasitism and epiphytism, there is a whole series of gradations in the adjustment to saprophytism and more or less strict dependence of species. All plant groups from bacteria, algae, and fungi to ferns and seed plants include saprophytic species. There are saprophytes which seem adapted to the utilization of specific organic plant wastes and therefore are dependent in this way upon certain plant species (*cf.* Romell, 1921, p. 207).

Humus plants are often confined to the decomposition products of certain plant communities or groups of communities (deciduous forest litter, coniferous forest litter). They participate in high degree in the development of community life.

Climbers (lianas in the broadest sense) are more independent of their supporting plants, since they respond only to the need for support or for better illumination, by attaching themselves to taller growing plants. So also with plants requiring protection. Under this head may be included all plants which are benefited by the protection of other plants or plant communities. They are not a few; sometimes they unite into ecologic units. Protection from light is a requirement of the shade vegetation of the lower layers of forests. If the tree layer is removed, many species succumb to the increased intensity of the light. Upper layers also furnish protection from cold, since they reduce the radiation by night and thus keep the minima above those of the surrounding open country. On exposed ridges every little shrub or tussock gives protection from wind; patches of shrubs or trees are evidently much more protective. On the wind-swept slopes of the Colorado Rockies, at 3,500 m., deformed specimens of *Pinus aristata* shelter colonies of delicate mesophytes like *Polemonium pulcherrimum* (Fig. 2). The sugar-loaf dunes of *Argania sideroxylon* of the wind-swept coast of West Africa south of Agadir harbor many wind-shy companions which without the shielding of the larger plants could not

Fig. 2.—*Polemonium pulcherrimum* thriving and flowering under the shelter of deformed *Pinus aristata*, at 3,500 m., James Peak, Colorado. (*Photo by Cooprider.*)

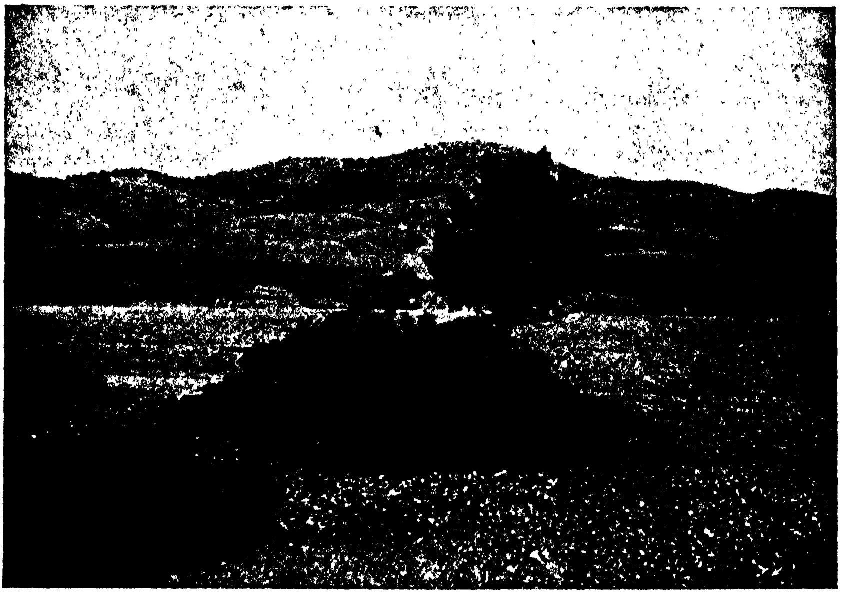

Fig. 3.—Shrub dunes of *Pistacia lentiscus* in the plains near Kasbah Fokohine, Morocco, with *Callitris articulata*. (*Photo by Daguin.*)

exist there (Fig. 3). Most efficient is the protection afforded, unconsciously of course, by spiny shrubs for their companion plants. In open pastures individuals or clumps of *Crataegus* often shelter seedlings of oak and maple that are entirely absent from adjacent grazed woodlands. In closely grazed mountain valleys there are often young spruces, pines and larches surrounded by a protective circle of *Juniperus*. It is striking that in the plains between Ujda and Taourirt (eastern Morocco), populated by thousands of sheep, the last remnant of a tree is the *Pistacia atlantica*, confined to the protection of the impenetrable spiny armor of the Jew's-thorn.

The list of plants requiring protection might easily be extended. They represent the least intimate stages of dependence; but even among them there may be mutual relations of protected and protector. Such a list might include protected plants changing the soil conditions to the advantage or disadvantage of the protector; forests smothered by invasion of peat moss; raw humus of the forest floor hindering natural reproduction; more favorable moisture conditions for seedlings provided by a layer of moss; or the exhaustion of the soil moisture by the more deeply rooted protected tree to the detriment of the protecting shrub. Sukatschev ("Esquisses phytosociologiques," vol. I, 1921) states that in the *Pinus cembra* region of Lake Baikal *Hypnum schreberi* and *Hylocomium splendens* in places become so luxuriant that natural reproduction of the pine is prevented, and the forest degenerates into a mossy scrub community of *Ledum palustre*.

From these considerations it is evident that dependency plays an important but secondary rôle in the life of plant communities; the really decisive rôle is taken by the second type of social life, commensalism.

Commensal Unions.—According to Van Beneden, we understand by commensal organisms those which enter into competition separately, and their common relation consists in the fact that they simultaneously utilize the various life conditions of a given habitat. *Le commensal est simplement un compagnon de table.* The relation between the commensals rests upon the struggle for space, light, and nutrients. The struggle for existence goes on between similar commensals when different species have the same or nearly the same requirements and becomes most intense between individuals of one and the same species. But the "table companions" may have different needs, either because they use different nutrients or because their organs use different layers of soil or air. In such cases we have to do with unequal commensals.

The most simply organized plant communities, such as plankton and many lichen and moss communities, form a round table of equal commensals. All highly organized communities, on the other hand, are composed of unequal commensals: only such are able to utilize to the fullest extent the possibilities of the habitat. The low shrub, moss, or lichen cover of a forest draws its nourishment from the upper and middle horizons of soil; the trees, from deeper layers.

Commensalism begets competition, which becomes the more intense the more nearly the life adjustments of the individual commensals coincide and the more favorable the external inorganic conditions are for plant life. Under unfavorable conditions of climate and soil the competition even between species with similar requirements takes on a milder form (Fig. 4). That competition is not wholly absent even among the open communities of deserts and high alpine rock clefts and gravel slides is shown by many observations.

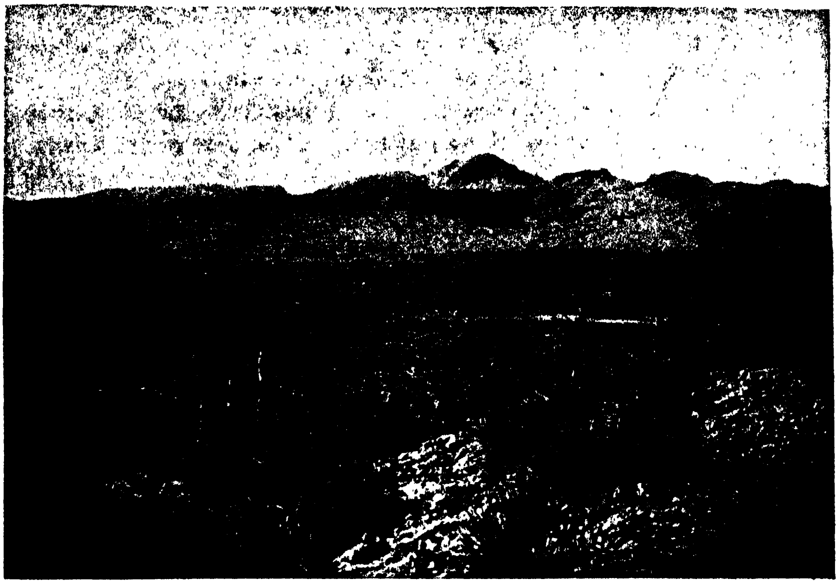

FIG. 4.—Open *Stipa* steppe in the northern limits of the Sahara, Djebel bou Arfa, with root competition. (*Photo by Daguin.*)

Jenny-Lips (1930) found that there was active competition in a gravel slide association, although the vegetation covered only 5 to 15 per cent of the surface. At a depth of 25 cm. the fine fibrous roots of the herbaceous *Thlaspi rotundifolium* plant were intimately interwoven with those of an *Athamanta* plant standing 130 cm. away. In a very open *Stipa calamagrostis* association on the gravel slide there was a horizon of very fine soil, only 5 cm. thick, lying under 15 cm. of coarse gravel. This horizon of fine soil was filled with a mat of roots from plants standing widely apart. Thus the competition of plants appears to be effective over a much wider area than has been supposed (Fig. 24).

Competition.—The community life of plants rests upon relations of dependency and commensalism; its universal and ever present expression is competition. Wherever the struggle for a place in which to germinate and to grow, or to obtain light or food, can be demonstrated, there is competition, there is relationship.

Competition may be purely mechanical, as in crowding out or growing over or stifling of the weaker by the stronger. It is, in its simplest form, the competition between individuals of one and the same species. But local conditions of climate and soil may be more or less profoundly modified by the vegetation itself, thus affecting the aggressiveness of the combatants. This often happens in the competition between different species or between different plant communities.

Competition within the Species.—The intensity of the competition between individuals of the same species is greatest in dense stands with high sociability.

The individuals of a species that are widely apart (soc.[1] 1) rarely conflict for space. The first colonizers have the advantage over later arrivals, in having well-rooted individuals established and multiplying by seedlings or by vegetative offspring, before their competitors arrive (Fig. 5). In the competition between individuals, and still more in that between species, the outcome is greatly influenced by the vigor, or rather by the rapidity of the germination of the seeds. The greater the difference in time of sprouting and the denser the seeding the better is the prospect for those first germinating to preempt the space. First comes the conflict for space only, then the struggle for light, and lastly that for nutrients.

One square meter of the *Suaeda martima-Kochia hirsuta* association on the shell dunes, along the lagoons of Vic in Southern France, contains on the first of May about 2,000 seedlings of the annual *Suaeda* 1 to 3 cm. tall. In late autumn their number is reduced to six or eight fruiting plants.

The progressive intensification of the "struggle for existence" is most impressive in many-layered communities. As one of its most striking expressions the natural elimination in a forest may be considered. Morosow (1920) counted on one hectare 1,048,660 ten-year-old beeches. In a fifty-year-old pure stand of the same area there were 4,460; in a stand one hundred and twenty years old only 509. The completely closed crowded growth permitted, therefore, only 1 out of

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[1] Sociability.

about 2,000 young beeches to come to maturity. According to Cajander (1925), a fifty-year-old pine requires an area of 2 sq. m.; at the age of seventy-five years it requires 3.8 sq. m.; at one hundred and twenty-five years, 11 sq. m.; at one hundred and fifty years, 15 sq. m. On a given area, therefore, only a definite maximum number of well-developed individuals of one species can find a place in the sun.

Competition between Individuals of Different Species.—Within the bounds of a social unit that is in equilibrium, very rarely does one single species gain control to the exclusion of all others. Usually a plant community exhibits a motley mixture of the most varied plant forms. The reason for this lies in the fact that the locality includes many ecologically different habitats due to layering in air and in soil, rather than to a great variety of edaphic conditions within a very limited space. Within a homogeneous plant community the edaphic conditions are often extremely uniform, although the opposite has been claimed by many investigators. The example of the beech forest with its successive waves of flowers and assimilation in the ground and herb layers is well known (*cf.* p. 47). Many such examples could be cited. Many communities of the subtropics begin their annual development

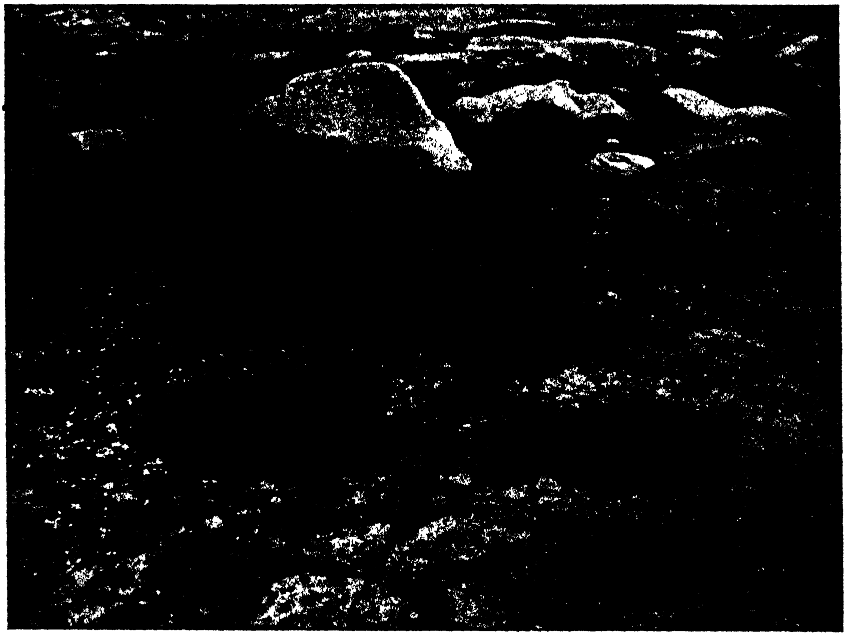


FIG. 5.—Tufts of *Carex rufina* with peripheral spreading (Soc. 3) as pioneers upon snow soil in the Norwegian mountains near Voss at 1,300 m. (*Photo by Lid.*)

with a therophyte aspect, which later is replaced by a bulb geophyte, hemicryptophyte, or chamaephyte aspect, following each other in the course of the year on the same limited area.

That the competition between the species of a community is the more intense the more closely these species agree in their requirements, life forms, and seasonable development may be accepted as a general principle.

The more manifold the structural units of a community are the better will all the space be utilized and the greater, as Darwin has said, will be the sum of life per unit area.

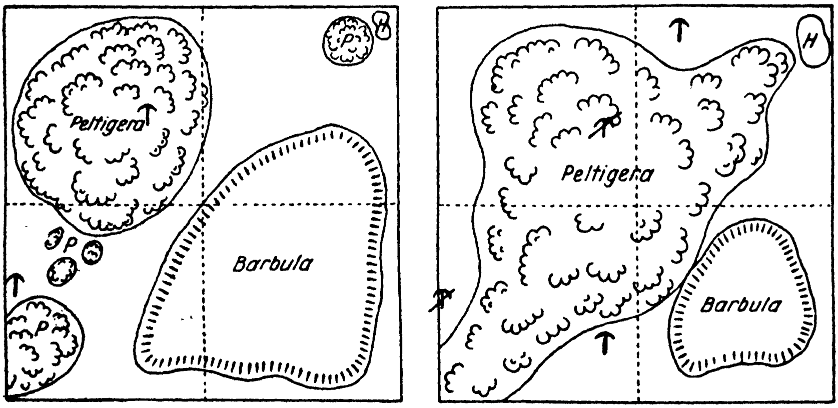
Aggressiveness of Species.—The possibility of numerous species living together in limited space is largely affected by the aggressiveness of the dominant species. The aggressiveness of a species depends upon its fecundity, its rapidity of reproduction and spread (formation of clumps or masses), and its capacity to occupy its place permanently. *Carex curvula*, an alpine tussock plant of a high degree of sociability, hinders by its dense stands the invasion of companion plants into the Curvuletum. In the nearly related Festucetum halleri, on the contrary, there are no dominant species of such overwhelming aggressiveness, and the density of stand, and the diversity of species of companion plants on the same area, is much greater (*cf.* p. 55).

Morphoecologic plasticity favors a plant in the struggle of life (*Polygonum amphibium*, *Hedera helix*, *Calluna*, etc.). The cosmopolitan *Phragmites communis*, which is ecologically (but not morphologically) extremely plastic, thrives equally well in the brackish marshes of the southern European coasts, in central Asia, in the United States of America, and in South Africa, in the cold meadow moors of the lower Alps, and under the continually humid skies of the Atlantic coast of Europe.

The aggressiveness of species must be empirically determined, but the morphobiologic framework of the species—the life form—gives a basis for an estimate. In the temperate zones the tree form is superior to the shrub, and this to the chamaephyte. Annuals are here far inferior to all other life forms; nevertheless in the arid regions of the subtropics they dominate wide areas. The aggressiveness of a definite life form is therefore connected with the climatic region. It is also related to the type of habitat. Every climatic region and every type of habitat favor certain classes of life forms. From these are recruited the species most efficient in competition (*cf.* chapter on Life Forms).

Determination of Aggressiveness.—Experimental investigations of aggressiveness in pure cultures of one species and in mixed cultures of several species, under controlled conditions of soil and climate, have been carried out by Clements and his associates (1929). Long before this Bonnier had studied the spread of lichens at the expense of mosses, a theme which has recently been revived by McWhorter. Y. Bogdanowskaia (Leningrad, 1926) approached the problem from another side. She followed minutely the increase by seedlings in different associations and arrived at very interesting conclusions that prove the significance of phytosocial structure for the rising generation of plants.

Under natural conditions the aggressiveness of species is shown in every permanent quadrat used in the study of the development of communities (Fig. 6).



A. B.

Fig. 6.—Permanent quadrats showing the results of competition between *Peltigera spuria* and *Barbula convoluta* on an old charcoal kiln near Praspol, 1,680 m., Swiss National Park. *H* = *Helianthemum grandiflorum*; T = *Pinus silvestris* seedling (T dead). The same quadrat, 1 sq. m., in 1922 (*A*) and in 1927 (*B*.)

In order to determine experimentally the aggressiveness of the species of a given group it is necessary to observe their reaction to the varying intensity of a single factor such as salinity, acidity, or grazing. Everyone has noticed with what readiness *Polygonum aviculare*, *Plantago major*, and *Lolium perenne* spread over little-trodden footpaths. When the paths are more frequented these species lose their luxuriance and finally disappear, but they also disappear when the paths are too little used, being crowded out by other species. Their optimum growth, therefore, is maintained within very narrow limits.

The mutual displacements of position on the ground are measured on small areas; on extended areas one must be content to estimate the abundance, cover, and sociability of each species. On small permanent quadrats the number of seedlings can be counted (Fig. 7). Ochsner (1928) for years followed the competition of bark mosses and lichens by means of annual sketches showing displacements of the tussocks and thallus borders and the periods of inactivity (Fig. 8). Sometimes photographs give excellent data.

Overestimation of the Factors of Competition.—When a new and important viewpoint enters a science, its significance is often overvalued, not rarely leading to error. For instance, it has been claimed that the occurrence of nearly all plants is rather independent of soil conditions but depends on competition and the competitors (Warming-Graebner, 1918, p. 126; Cajander, 1926). It is pointed out that in botanic gardens plants from the most diverse climates and soils grow harmoniously side by side. The thing that is not mentioned, and mostly not investigated, is whether they continue to produce viable offspring and maintain themselves without renewed planting. In many cases they certainly do not.

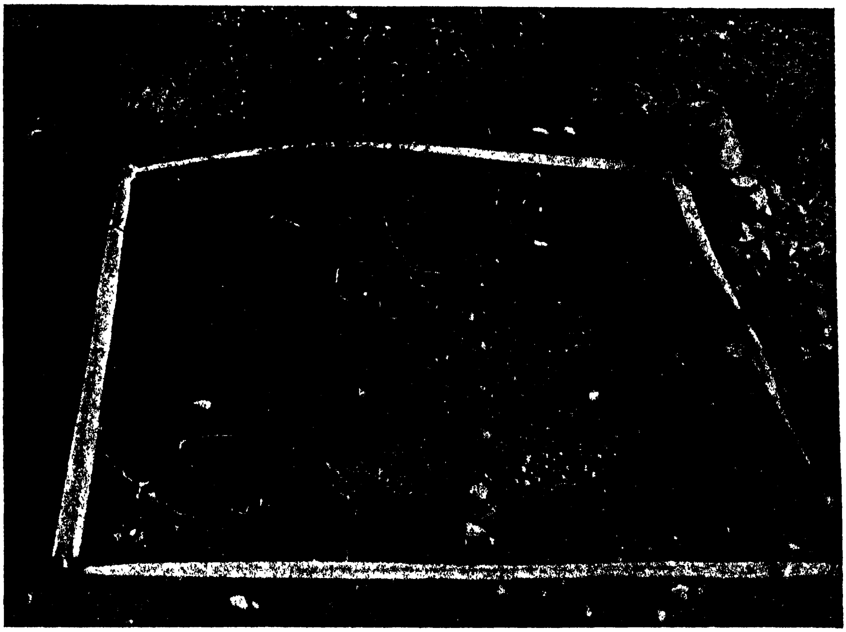


FIG. 7.—Permanent quadrat (1 sq. m.) for seedling counts on an open area in the *Rosmarinus-Lithospermum fruticosum* association near Montpellier, France. (*Photo by Braun-Blanquet and Keller.*)

It has further been said that certain species are in general confined to certain soils, but when they come into competition one wins on calcareous soil, the other on siliceous soil. K. Nägeli cites *Achillea* *atrata* and *A. moschata, Rhododendron hirsutum,* and *R. ferrugineum.* In fact the pronouncedly basophilous and calcicolous *A. atrata* and *R. hirsutum* never survive long on acid soils, whereas *A. moschata* and *R. ferrugineum* being acidophiles do not appear on calcareous basic soils. The life requirements of these pairs of species are so different that the question of competition cannot arise. Unfortunately this long-recognized error (*cf.* Braun-Blanquet 1913, p. 141) still crops up as an example in the latest textbooks like Lundegårdh's (1925, p. 299) and also in the book of Clements, Weaver, and Hanson (1929). Indeed, it is constantly extended by new and equally untenable examples (Rübel, 1912, p. 417; Vierhapper 1922, p. 41).

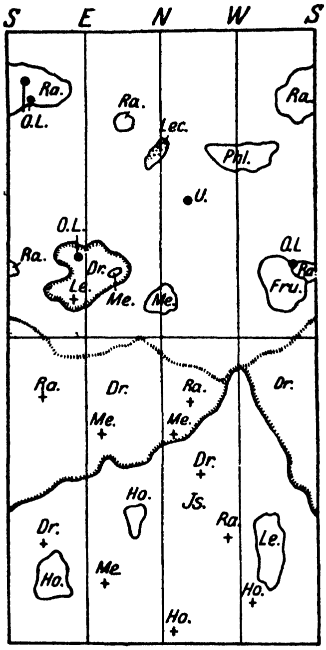


FIG. 8.—Bark surface of a beech trunk 122 cm. in diameter, unrolled to show competition among epiphytes. (*After Ochsner.*) *Lec.* = *Lecanora subfusca; Phl.* = *Phlyctis argena; Le.* = *Lepraria glauca; Ra.* = *Radula complanata; Fru.* = *Frullania dilatata; Me.* = *Metzgeria furcata; O. L.* = *Orthotrichum lyellii; U.* = *Ulota crispa; Dr.* = *Drepanium filiforme; Is.* = *Isothecium myurum; Ho.* = *Homalia trichomanoides;* + = *sparse.*

Competition between Plant Communities. In the competition between plant communities the aggressive domineering species of great dynamic and genetic significance play the rôle of advance guard and main army; the more or less constant companions furnish the reserves.

Most conspicuous is the conquering march of communities of few species or the advance of swarms of foreign immigrants with great powers of expansion. The spread of *Elodea* and of *Jussieua* at the expense of the European aquatic flora came with the suddenness of an explosion, as also did the spread of the river-bank societies of American *Solidago, Aster,* and *Stenactis* species in central Europe; *Diplotaxis erucoides* and *Xanthium macrocarpum* in the vineyards of southern France; and *Spartina townsendi* in the tide basins of the canals, where it dispossessed the native *S. stricta.* Similarly in North America the rivers of Florida were rapidly invaded and navigation obstructed by the water hyacinth, *Eichornia crassipes,* from Brazil, while the European moneywort, *Lysimachia nummularia,* is found abundantly on many flood plains in the United States. The seed and sprout production of these foreigners is so overwhelming, and the distribution follows so suddenly, that a change of the local climatic or edaphic factors, if it occurs at all, must be a consequence of the change in vegetation but not its cause. We have here a direct effect upon vegetation through the newly immigrating swarms of plants.

There is also a very rapid succession of communities in the early stages on neglected arable land, ruderal habitats, and burned areas, where often several short-lived plant communities may succeed one another, although no immediate change in the soil can be demonstrated.

This fleeting conquest and the rapid succession of artificially induced pioneer stages are in contrast with the slow, tense struggle of the later stages of primary succession. The numerical superiority of shoots and disseminules of certain species is certainly important here; but it is not the cause of the changes in vegetation. The vegetation itself affects and gradually changes the physicochemical factors of the habitat and therefore favors the development of certain competitors at the expense of their neighbors.

In any case one must not expect a common and uniform reaction on the part of all the species of an association. Each species has its own reaction to each factoral change in the habitat.

If the light factor suffers a change because of the vegetation (development of the tree layer), certain species disappear earlier; others, later. From a mixed stand of deciduous and needle-leaf trees in Finland *Alnus incana* is the first to be eliminated. In fifty years it is everywhere overshadowed and leads a precarious existence. Later *Populus tremula* and *Betula* disappear. After three hundred years there is left only the original old pines together with *Picea excelsa* and its progeny, since the pine cannot reproduce in the shade of the spruces (Cajander, 1926).

If the character of the soil is gradually changed by accumulation of humus, the individual species, both dominant and subordinate, react to this. Scarcely perceptible changes in the acidity of the soil solution may favor the scattered and apparently weaker competitors in their struggle with the dominant plants. By means of changes in acidity due to vegetation it may happen that a community literally poisons the soil for itself. Thereby it becomes possible for species of another association better adapted to the new conditions of the habitat to win places for themselves and finally to drive the formerly dominant community out of the field. A succession on calcareous talus in the Central Alps due to the influence of soil acidification may make this clear.

Sesleria coerulea and *Festuca violacea*, tussock plants furnishing large amounts of humus, are highly acidifying. They prepare the soil for the successive penetration of the acidophilous species of the Curvuletum,

TABLE 1.—SOIL ACIDITY AND THE SUCCESSION OF PLANT COMMUNITIES

Association	Soil reaction, pH	Number of species	
		Acidophilous[1]	Basophilous, neutrophilous
Curvuletum	5.4 to 4.2	Dominant	0
↑			
Festuca violacea-Trifolium thalii	6.6 to 5.4	21	15 to 20
↑			
Seslerieto-Semperviretum	7.1 to 6.2	10	Dominant
↑			
Dryas-Globularia cordifolia mats	7.5 to 6.8	0	Dominant

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[1] Words such as acidophilous, xerophilous, etc., are used throughout this book without any suggestion of emotion on the part of the plants, and should be understood as having no teleological implications.

while poisoning it for themselves. Within the individual stands of the Seslerieto-Semperviretum and the *Festuca violacea-Trifolium thalii* association the number of acidophilous species and the number of individuals vary with the pH of the soil and increase with the rising soil acidity.

PART II

THE ORGANIZATION OF PLANT COMMUNITIES

CHAPTER II

THE SMALLER SOCIAL UNITS

The ultimate "atomistic" particles of any community are the individual plants. The combination of these creates the social organism. The countless individuals may be grouped in two distinct ways: under the concept of the taxonomic species or under the concept of the growth forms or life forms (*cf.* chapter on Life Forms). The Brussels Congress (1910) rightly decided in favor of the species as the fundamental unit of the plant community. The concept of "life form" is indefinite, has not been adequately defined, and cannot be considered as a sufficient basis for a science of vegetation. Species, however, are groups of individuals with uniform inheritance and have been for many years the objects of careful investigation.

In the species are embodied certain definite adjustments to and demands upon the environment. Hence the species have come to be regarded as conspicuous indicators of certain conditions of life. The most exact indicators are often, indeed, not the "good Linnaean species" but rather the elementary species or races, the "ecotypes" of Turesson (1925). These forms require more narrowly circumscribed life conditions and therefore are socially more sharply specialized. A knowledge of the species usually gives at once an idea of the life form in which it falls.

Precise recognition of species is therefore the first and indispensable requirement for the phytosociologist. Studies of the structure of vegetation without accurate knowledge of the species concerned are scientifically worthless. The goal of these studies is to establish precisely the significance of the species in the organization of the community and to discover the order which prevails in the grouping of the species into communities.

Habitat and Plant Community.—By the term "habitat" we mean, following Yapp (1922), the dwelling place of a species or of a community including all of the operative factors, except competition, that influence the plants themselves. The exact place of occurrence is called the locality or "station."

A given plant community may occur in many localities. But it exists usually in only one well-defined and ecologically characteristic habitat. From this concept have come the long-continued efforts to delimit and sharply define the habitat. The hope was to arrive thus at a classification of the plant communities themselves—a hope which has not been realized.

The more sharply we have sought to delimit the problem of the habitat the more complicated and involved its definition has become. The effective external factors are so numerous and so variable, the possible combinations so manifold, the overlappings so frequent that a clear and unequivocal delimitation of habitats according to operative external factors appears quite unattainable. It may be added that the relation of habitat to plant community is not a simple and reversible function. In the first place, the flora of a region is historically the result of a long process of natural selection.

On account of this difficulty it is becoming more and more necessary, in investigating the communities, to go directly to the vegetation itself. We then arrive at the point from which we should logically have started out: the natural grouping of plants. The natural units of vegetation come thus into the foreground of our study, and, temporarily ignoring the habitat, we seek to recognize and define the floristic individuality of the communities.

From the exact floristic analysis of individual communities of vegetation we proceed to the synthesis of plant communities. This analysis and synthesis should afford the basis for conclusions regarding the combination of species, the numerical relations of the individual species, and the significance of each species in the origin, development, maintenance, and decline of plant communities, especially of those fundamental units of vegetation: the associations.

Fundamental Unit of Plant Sociology.—"An association is a plant community of definite floristic composition" (Flahault and Schröter, 1910). In this statement the Third International Botanical Congress at Brussels recognized as fundamental the floristically uniform character of this unit of vegetation. The definition is at once too narrow and too broad: too broad, because not only the association but all the lower and higher units, variants, facies, societies, alliances, etc., are characterized to a greater or lesser extent by definite floristic composition; too narrow, because, with few exceptions, no two bits of vegetation have precisely identical floristic composition.

The possible combinations of plant species are indeed endless. To attribute to every actual combination in nature the value of a type would result in a chaotic splitting up of the units of vegetation. On such a basis every quarter of a square meter of a meadow community would form a separate unit. We are obliged, therefore, to institute comparisons between the various bits of vegetation. Pieces of vegetation with similar combinations of species are united into abstract types. These types are the "associations," the separate pieces being called the individuals or examples of the association or more simply the "stands."

Individual Association or Stand.—The more or less similar bits of vegetation or "stands" found in nature are the concrete realities with which the plant sociologist has to do. An association usually includes many spatially separated stands. They correspond in a general way to the individual plants in taxonomy, although the anthropocentric assumption of individuality applies to them in a lesser degree than to individuals of a species.

The larger the number of stands investigated the more truthful will be the resulting picture of the association. From the more or less perfect agreement in the composition of these stands comes the greater or lesser uniformity of the association and the range of its variation.

The concept of the association includes a true reality, namely, the characters common to the individuals of the associations. The association as such, however, is, like all systematic categories, a group concept, intended to deepen and organize our knowledge of vegetation.

Alechin (1925) regards this group concept itself as an indivisible unit and likens the stands to the pieces of a cut apple.[1] He overlooks the fact that the piece of apple can no more regenerate itself than can a quartered ox, whereas each stand arises independently of the rest of the association and can continue to develop and reproduce itself independently.

Each stand has in itself a distinct individuality, with its own life history, and embodies in itself the distinctive marks of the association. The practical and theoretical value of the association concept depends upon the greater or lesser external and internal resemblances of the several individuals of the association. An important phase of the study of vegetation is the distinguishing of these resemblances. This leads to sharper individualizing and delimiting of the association from the floristic, ecologic, genetic, and geographic viewpoints.

The stand embodies the association as one house embodies the concept *house*. This prolonged discussion seems to be necessary for a better understanding of many sociological treatises. It is to be hoped that the proposal of Nichols (1923) will continue to gain ground and that the word "association" will be used both in a concrete (an associa-

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[1] The same error is made by Vierhapper (*Verh. Zool.-Bot. Ges.*, Wien, 74–75: 1924–1925), who likens the *Einzelbestand* to a granite block. On this account his proposal of the *Assoziationselement* cannot hold.

tion, *Assoziationsindividuum* or *Einzelbestand*) and in an abstract sense (the association).

Smaller Units.—The fundamental unit of vegetation, the association, is not identical with the smallest unit; it stands to the latter rather in the relation of the species to the variety or form. But as in systematic botany a knowledge of the species must be acquired before the smaller units (varieties, forms) have any meaning, so should the recognition and definition of the association, which requires skill, sociological training, and wide experience, precede the simpler, more purely mechanical study of quadrats. A subsequent arrangement of the data of this mechanized "inductive" method under the head of the larger natural association is indeed in many cases impossible. Moreover, the synthesis of quadrat samples into larger and more convenient units often fails from the lack of tangible social characteristics. Moreover, when using this method there is always danger of stopping with the purely superficial features and losing sight of the more far-reaching "genotypic" features which are the significant marks for characterizing and understanding the association (Wangerin, 1922, p. 10).

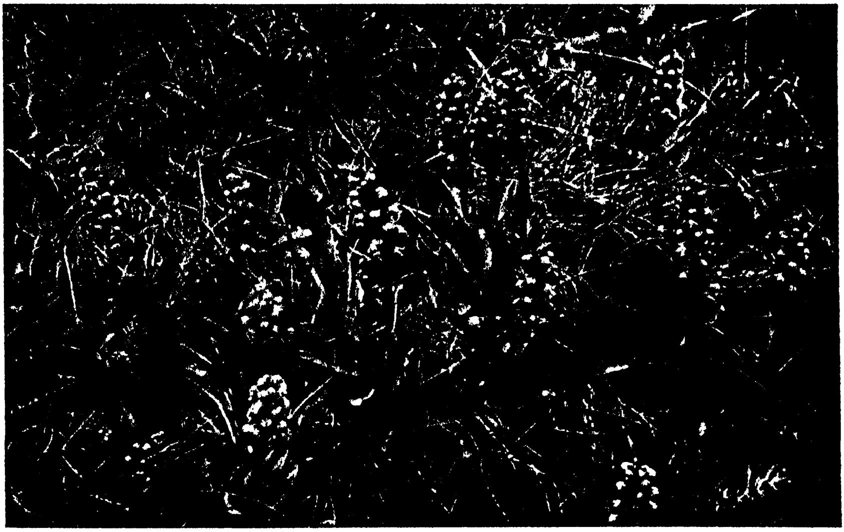

FIG. 9.—Association fragment of the Nardetum upon Alp La Schera (2,000 m.), Swiss National Park. *Nardus, Nigritella, Coeloglossum viride, Botrychium lunaria.* (*Photo by Heller and Braun-Blanquet.*)

The smallest distinguishable units of vegetation are of course not to be neglected. But they should be classified as sub-associations or facies, subordinate to the association in the larger sense.

The sub-association is comparable to the subspecies and rarely has its own indicator or characteristic species. Rather it is characterized by "differential species" which, in other expressions of the association, are absent, occur more sparingly, or are more poorly developed. Naturally there cannot be a sharp distinction between the association and the sub-association.

The facies is distinguished wholly by differences in the quantity or distribution of species, especially by the predominance of certain companion species of the association.

Facies and sub-associations are occasionally called elementary associations, following Drude (1919). This expression it seems better to avoid.

Fragmentary Associations.—Every individual association, every stand, must include the essential characteristics of the association, if it is to rank as fully representative. Especially the normal characteristic combination of species must be present. Bits of vegetation whose membership in a definite association is beyond doubt, but which for any cause have been hindered in their development or disturbed by external agencies such as lack of space, unfavorable habitat, human or animal intervention and therefore give only an incomplete picture of the association, are called "fragmentary associations." A *Carex curvula* sod with *Phyteuma pedemontanum*, *Avena versicolor*, *Sesleria disticha* or a beech wood near a large city with only a few companion species of the beech is a fragmentary association (Fig. 9). There are associations which today occur solely as fragments or mere remnants.

Settlement.—By the term settlement (*Siedlung*, *Vegetationsfleck*) we may designate any small combination whatsoever of individual plants, without regard to taxonomic value or sociological status. A stone overgrown with lichens or algae, a moor or a group of trees, are all settlements.

CHAPTER III

THE STRUCTURAL CHARACTERISTICS OF THE COMMUNITY

The analysis of plant communities may follow the purely practical lines of forestry and agriculture or the more theoretical lines of plant sociology. For the phytosociologist, the first task is to carve out and delimit the association, in order to lay the most indispensable foundation for synecological, synchorological, and syngenetical investigations. Investigations of the laws of the internal structure of plant communities as well as of purely syngenetical matters comprise a narrower field.

Problems of the structure of communities, as presented by agriculture and forestry, form in themselves a very comprehensive complex. These can be considered here only in so far as they are related to the structural studies of general plant sociology.

Analytic Characters.—Immediately available for phytosociologic analysis, and accessible in every sample of vegetation, in every stand, are the following characteristics of the community, based upon the species present:

a. Quantitative characters:
  Number of individuals (abundance) and density.
  Cover, space, and weight (*Dominanz, Deckungsgrad*).
  Gregariousness (*Soziabilität*) and distribution.
  Frequency.
b. Qualitative characters:
  Layering (stratification).
  Vitality, vigor (*Gedeihen*).
  Periodicity.

The apparent simplicity of the analysis of the concept of vegetation is directly in contrast with the difficulty of making any universal rules. Sometimes it is entirely impossible to submit different vegetation types to similar methods of treatment. All too often the attempts to combine the most exact counts and measurements of sample communities (stands) into an abstract unit (a plant association) results in nothing but vague averages. "Measure what can be measured, and count what can be counted, but always be conscious that the figures obtained are purely relative." Not infrequently mere estimation gives better results than counting and measuring. In each case, the judgment of the investigator must decide how the minute analysis of a given piece of vegetation can best be carried out and what characteristics of the community will, under the given conditions, give promising results.

In the analysis of vegetation few methods have developed for application to other than the higher plants. The following directions have to do with the rooted and clinging communities. The analysis of floating communities (plankton), a field that is very specialized and as yet but little worked, is relegated to a brief concluding section.

Kind of Sample Plot.—The analysis of a plant community may be an end in itself. Mostly, however, it is done for the purpose of evaluating the sample sociologically and of establishing its place in the association. In the latter case the choice of the sample plot is of utmost importance.

As a general rule, every sample plot, whether large or small, precisely delimited or not, should show the greatest possible uniformity, not only in regard to its floristic composition, which determines the appearance or physiognomy of the community, but also in regard to soil and relief as far as these can be observed. Areas without uniformity should be withheld from the beginner. The demand for uniformity in the sample plots leads in itself to distinguishing the communities from one another and to a fragmentation of the plant covering of the earth. Every unit portion that is distinguished must first be studied by itself. The defining of the unit areas of vegetation (which not infrequently are individual associations) is not always easy, since mixtures are abundant, and between two different uniformly organized pieces of vegetation we very often find narrow or broad transition strips. Here the boundaries should be so chosen as to omit the heterogeneous transition zones.

Furthermore, an apparently uniform area may consist of components of two or more different associations such as occur on steep grassland with regular terraces (Seslerieto-Semperviretum, Varietum tatricum, Fig. 10). on stone-covered pasture, or on rock wall with crevices. In this case each component of the uniform mosaic must be studied separately.

Size of Sample Plots.—A complete record requires the study of the uniform community throughout its entire area. In small communities, like the epiphytic communities on trees or high alpine grassland communities, this is simple and obvious, but it is very difficult in the case of extensive forest, shrub, or grassland communities. If the uniform community is too extensive, the investigator must be satisfied with samples of vegetation. If, as only rarely happens in practice, a more or less homogeneous stand extends unchanged over an area too large to inspect, the area may be divided for sociological investigation into as many portions as complete and mutually exclusive association samples (containing the normal combination of species) can be made from it. For diagnostic purposes and for many ecological and syngenetical studies it is necessary to investigate the largest possible portions of the uniform area. To give just one example: The Seslerieto-Semperviretum of the Central Alps originates on alkaline or neutral soils, but the accumulation of humus, combined with leaching, transforms these to a very acid condition. Unmistakable indicators of this acidifying process are the acidophilous companion species which come in and gradually increase during the course of the acidification (Braun-Blanquet and Jenny, 1926). This transformation of vegetation can be recognized and understood only when the uniform stand is studied floristically in every part. Portions of 10, 20, or 50 sq. m. do not suffice to include, especially in the earlier stages of development, the very sparsely scattered acidophilous indicators, much less to discover their sociologic significance (*cf.* Alechin, 1925). The larger the number of species and the more mixed the community the less satisfactory is a limited number of small and arbitrarily bounded samples (meter quadrats).

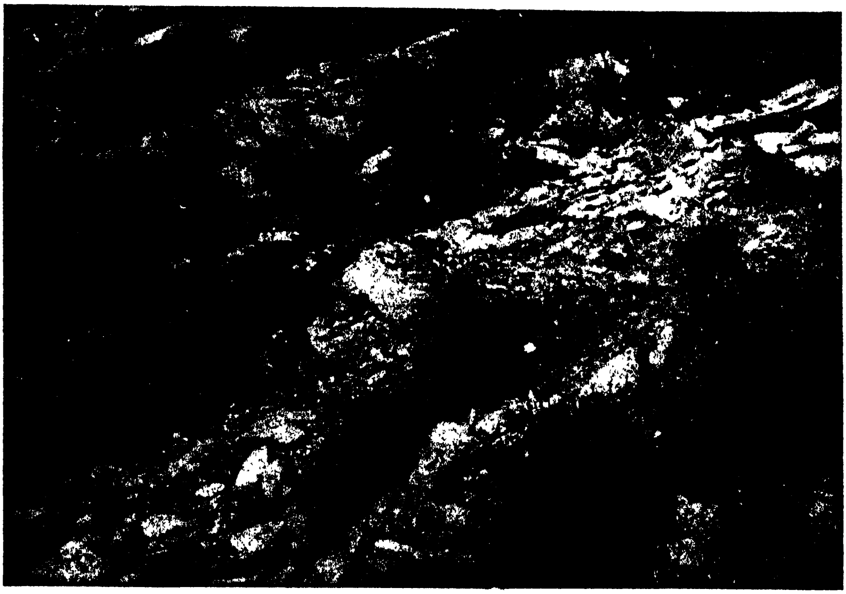

FIG. 10.—An open terraced stand of the Seslerieto-Semperviretum, var. tatricum upon steep limestone rubble in the Tatra, at 1,830 m. (*Photo by Zlatnik.*)

To give the data accuracy and completeness, the following procedure is suggested: Begin with the record of a small sample plot (in meadow communities 1 or 4 sq. m.). Let all the species be noted with quantity or coverage, sociability, etc. Then double the size of the sample plot and add to the first list the additional species included. Then within the same type of uniform vegetation select a larger area (16, 32, 50, or 100 sq. m.) so as to include the previous sample plots. The study of this area will be found relatively simple, since usually but few species will be added to the list. Any variations in the quantity, sociability, etc., of any species of the first small sample plot should be noted. It finally remains to note the species present in the stand outside the sample area. By this procedure two or more exactly delimited areas of different sizes have been analyzed in the shortest possible time, and at the same time a complete list of the species of the uniform community has been obtained. The sample plots are best square, or at least rectangular (Fig. 35). Communities arranged in mosaic fashion, as in mountains and moors, must be worked by means of a measuring line (Fig. 11). The shape of the sample plot will often be irregular. If the sample areas are dotted with fragments of "foreign" vegetation, or if a terrace-like structure prevails, or if the vegetation is interrupted by scattered rocks or by breaks in the sod, an approximate estimate of the extent of the homogeneous sample plots must suffice. In any case the total area of the uniform stand and the

FIG. 11.—A sharply delimited stand of the *Polytrichum sexangulare* association on a snow pocket in the Bernina Alps at 2,450 m. (*Photo by Klika.*)

percentage of the surface occupied by foreign vegetation or bare ground must be determined.

Number of Individuals (Abundance) and the Spacing of the Species.—Abundance is intended to express the plentifulness (number of individuals) of each species. The density on a definite area expresses the average spacing of the individuals and hence the average area occupied by each individual of a certain species.

Often the quantity and density of a species will differ widely in both space and time in different samples of one and the same community. This hinders an exact determination and in many cases greatly reduces the usefulness of averages.

Determination of Abundance.—In practice it is found that a series of five figures suffices to express the relative plentifulness of the individual species.

1 = very sparse (very rare).
2 = sparse (rare).
3 = not numerous (infrequent).
4 = numerous (abundant).
5 = very numerous (very abundant).

Whatever is lost by this method of estimating as compared with that of counting exactly the species on very small sample areas is gained in the survey of a larger area that has not been arbitrarily chosen and in the saving of time. To give an exact quantitative value to results from one or more very small sample areas, arbitrarily chosen, in spite of all effort to the contrary, is to give the appearance of exact reliability to accidental data, by using precise methods on material of uncertain and diverse quality. It is very important, however, that the estimate be made on a uniform stand.

Determination of Spacing and Density.—In order to get accurate numerical results sample plots of definite size must be investigated. If all the individuals of a species were evenly distributed over the entire surface, it would be sufficient to measure the area of the plot A and count the number of individuals n in order to determine the area a occupied by each individual: $a = A/n$. Similarly, the average distance apart (*distance moyenne*) of the individuals d may be determined: $d = \sqrt{A/n}$. If the distance apart of the individuals d be first determined, then from it the area occupied by each individual a may be determined: $a = d^2$.

In natural plant communities, however, the distribution of individuals is mostly irregular, and the density must be obtained by indirect methods. Sample plots of equal size are taken in various parts of a uniform community, and the number of individuals or shoots of each species on each sample plot is recorded. The density (distance between individuals) of a species is equal to the number of square units of the total area divided by the sum of the individuals (*cf.* Martinet, 1898). The exactness of the result obtained increases with the number of sample areas examined and with the evenness of the distribution of the species throughout the entire community.[1] The size of the sample plot chosen may vary within wide limits and naturally depends upon the kind of vegetation. In a Mediterranean therophyte community areas of 0.5 or 1 sq. m. are appropriate; in the beech or spruce woods at least 500 sq. m. must be taken for the tree layer. This counting method is especially indicated in mature timber of uniform age, in bush steppe, and in rock-slide communities. Much more difficult is its application in grassland communities, with tussock or sod-forming plants, where it is further complicated by the difficulty of distinguishing the individuals and counting the shoots. If density can be determined, the determination of abundance would obviously be superfluous.

Cover, Space, Weight (*Deckungsgrad, Dominanz*).—The question of the space demands of a species is a wholly different concept from that of the number or density of the individuals. In close connection with the former stands the question of the cover (*Deckungsgrad*) of the species. In clinging communities (algae, lichens, mosses) the degree of dominance is identical with the relative participation of the species in the covering of the surface (cover, areal percentage). In several-layered tree and shrub communities the degree of dominance of a species is given by its share in the different layers of the vegetation.

Determination of Cover.—The degree of dominance of clinging and rooted species is expressed in all field work by the cover, that is, the area covered by the individuals of one species. The entire shoot system of all the individuals of a species is thought of as projected on the ground, and the area covered thereby is estimated. In distinctly layered communities each layer must be estimated separately. The significance of cover was recognized by Von Post (1867), but it was first clearly distinguished as "areal percentage" in 1914 by Lagerberg. For the determination of cover, Lagerberg (1915) used small quadrats of 0.5 or 0.1 sq. m. which were arranged in straight lines regularly spaced over the area studied. The estimate of the surface covered by each species in the quadrats was indicated by means of the fractions 4/4, 3/4, 2/4, 1/4, and each species received the number nearest to the fraction of the area actually covered by it. Species with very small

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[1] It should therefore be noted whether the mode of distribution is regular (hypodisperse) or irregular and crowded in places (hyperdisperse) (*cf.* Schustler, 1923, and p. 36).

cover were left out of consideration. This method, designed for use in forestry, is suitable only for large uniform bodies of vegetation.

A five-parted scale is better for the study of most communities. In Scandinavia the so-called Hult-Sernander scale is most used. The limits of the cover classes are as follows:

1 = covering less than 1/16 of the ground.
2 = covering 1/16 to 1/8 (6.25 to 12.5 per cent).
3 = covering 1/8 to 1/4 (12.5 to 25 per cent).
4 = covering 1/4 to 1/2 (25 to 50 per cent).
5 = covering 1/2 to 1 (50 to 100 per cent).

The values of these cover classes are easily memorized. But on account of the very wide range of the upper grades they give in many cases no true idea of the degree of cover. Whereas the figures 1, 2, 3 are confined to the narrow limits of one-quarter of the surface, there are available for the important larger classes—one-fourth to four-fourths of the surface—only the two figures 4, 5 (Fig. 12*a*).

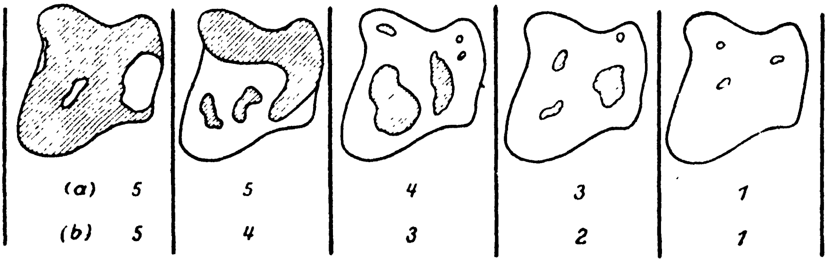

Fig. 12.—Degrees of cover (hatched); (*a*) according to Hult-Sernander; (*b*) according to Braun-Blanquet.

In actual field work the following scale has proved more satisfactory (Fig. 12*b*):

1 = very scant (covering less than 1/20 of the ground surface).
2 = covering 1/20 to 1/4 of the ground surface.
3 = covering 1/4 to 1/2 of the ground surface.
4 = covering 1/2 to 3/4 of the ground surface.
5 = covering 3/4 to 4/4 of the ground surface.

The exactness of the estimate is entirely satisfactory in small test areas (up to 10 sq. m.). With large areas, however, the estimate is difficult to carry out, especially when there is a mixture of many species.

When dealing with communities whose cover shows great seasonal variations, the estimate must be made repeatedly at different seasons of the year. Under some circumstances it may be done at the culmination of the seasonal development, but many communities, especially in regions with a dry resting period, necessarily demand several examinations per year. Between dry and wet years there will often be (particularly in steppes and deserts) very great differences in the cover of the species on the same area.

Determination of Space.—The degree of dominance of the species in plankton communities is given by the number of individuals of a species in a unit volume (1 cc.) of water, multiplied by the volume of one individual. In rooted communities the estimate of cover always gives an approximate idea of the space occupied by the species.

Del Villar (1925) has attempted a determination of the space occupied by shrubby species in the Spanish meseta. He assumed the volume of the shrubs to be ellipsoidal and calculated the cubic contents from the vertical and horizontal diameters. For *Salsola vermiculata* he found 208 cu. m. per hectare; for *Thymus zygis*, 197 cu. m. The frequency percentage (according to Raunkiaer) gave for *Salsola* only 7.2 per cent; but for *Thymus*, 55 per cent. In a certain sense the measurement of the cubic volume of standing timber by the forester may be considered as a determination of dominance. According to Hausrath, *Pinus silvestris* on an average soil produces in 100 years 404 cu. m. of wood; in 120 years 430 cu. m., whereas *Picea excelsa* in the same time produces 739 and 806 cu. m. respectively.

Weighing.—The method of weighing the shoots has hitherto been applied almost exclusively to pasture studies. The grass of a small measured piece of ground is sheared off, the shoots of each species are sorted out, and the amount of each species is given in percentage by weight. Or 1 sq. ft. of turf is dug out and the percentage by weight is determined for both aerial and buried parts (*cf.* Stebler and Schröter, 1892).

Kultiassoff (1927) in Central Asia investigated the decrease in weight of the root mass with increasing depth.

TABLE 2.—DECREASE OF ROOT MASS WITH DEPTH IN SOIL IN THE THEROPHYTE STEPPE NEAR TASCHKENT

Depth, centimeters	Root mass, grams
0 to 10	1,400.2
10 to 20	84
20 to 30	20.6
30 to 40	3.0
40 to 50	2.2
50 to 60	3.0
60 to 70	1.5

In the therophyte steppes of Taschkent the weight of roots exceeds the weight of tops fifteen times (tops per cubic meter about 100 g., roots 1,515.3 g.). The principal part of the root mass is supplied by *Carex hostii*.

Total Estimate.—For the minute monographic study of a definite community, for studies of succession, or for the solution of a variety of questions of more practical nature good results are obtained by considering cover and density together. The question of whether the results are likely to be commensurate with the labor involved must always be considered, for the determination of density is usually very troublesome and not always feasible.

FIG. 13.—*Gentiana costei* (Soc. 1) and *Daphne cneorum* (Soc. 3). Causse Noir 950 m. (*Photo by Keller.*)

A material reduction of the field work is attained by combining the estimate of abundance and cover, ignoring density. For this a conventional six-part scale is used. The meaning of the signs and figures is as follows:

\+ = sparsely or very sparsely present; cover very small.
1 = plentiful but of small cover value.
2 = very numerous, or covering at least $\frac{1}{20}$ of the area.
3 = any number of individuals covering $\frac{1}{4}$ to $\frac{1}{2}$ of the area.
4 = any number of individuals covering $\frac{1}{2}$ to $\frac{3}{4}$ of the area.
5 = covering more than $\frac{3}{4}$ of the area.

It is plain that the smaller numbers have more to do with abundance, the larger with the cover.

Each well-defined layer of vegetation must be estimated separately. In the closed beech woods the beeches in the tree layer and *Asperula* *odorata* or *Carex pilosa* in the herb layer may each reach a cover of 5.

When this combined estimate is used, the gregariousness (sociability) should also be given.

Whereas in small areas (1 to 2 sq. m. or less) the estimate of cover is often sufficient, in larger areas, and especially in less homogeneous areas, the combined estimate can be used to advantage. Besides, from the combined estimate the cover can mostly be deduced, since the figures + and 1 taken together correspond to cover 1, and number 2 of the combined estimate corresponds with cover except in case of a species with many very small individuals which covers less than one-twentieth of the area (many therophytes of the Mediterranean communities).

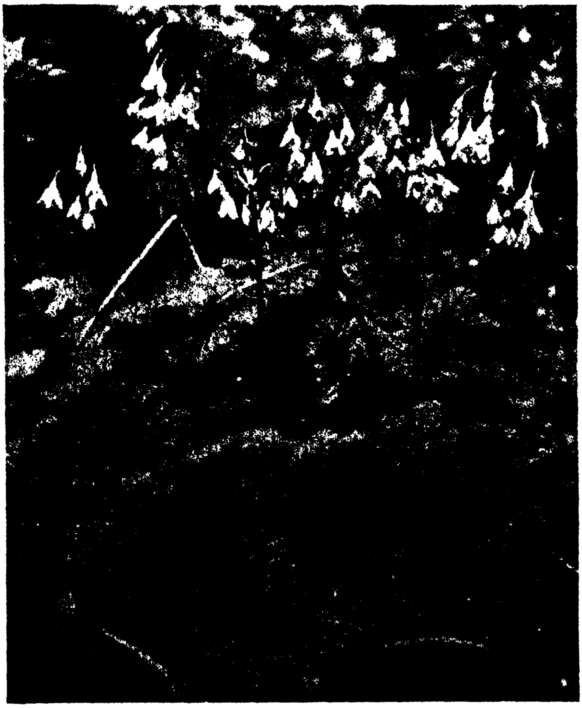

FIG. 14.—*Cortusa matthioli* (Soc. 2) between *Alnus viridis* shrubs Lower Engadin, Swiss Alps. (*Photo by Hoffmann-Grobéty.*)

Sociability, Gregariousness (*Soziabilität*), **and Dispersion.**—After Willdenow (1798) first took notice of the difference in the gregariousness of plants, Heer (1835, p. 49) directed attention to the grouping of species, "whether the species stand close together in mass formation and thus cover the ground in patches or are wholly isolated and stand scattered among each other in motley mixture." Heer expressed the degree of association by the figures 1 to 10. Lecoq (1854) (who, however, used the term "sociability" with a somewhat different meaning) and Lorenz (1858, p. 227) also concerned themselves with the gregariousness of species.

FIG. 15.—*Chrysosplenium alternifolium* (Soc. 4) Frankfurt-on-Oder. (*Photo by Hueck.*)

Gregariousness or "sociability" expresses a space relationship of individual plants, answering the question, How are the individuals or shoots of a species grouped?

To describe the grouping we use the following scale:

Soc. 1 = growing one in a place, singly.
Soc. 2 = grouped or tufted.
Soc. 3 = in troops, small patches, or cushions.
Soc. 4 = in small colonies, in extensive patches, or forming carpets.
Soc. 5 = in great crowds (pure populations).

The density of the stand of individuals or shoots is indicated by a dotted or solid line under the figure. Thus *Typha minima* (Soc. $\underset{\cdots}{5}$) means an open but large patch of *Typha minima*, and *Calluna* (Soc. $\underline{5}$) indicates a large, dense, closed stand of heather (Figs. 13 to 15).

Only a few plants have a predetermined unchangeable degree of aggregation of individuals or shoots (sociability) based upon the manner of growth. The degree of gregariousness of most species is greatly influenced by conditions of habitat and by competition (see also Jenny, 1930, p. 152). Even such cushion and tussock plants as *Carex elata* and *Silene acaulis* show a difference in the crowding of shoots according to the community in which they occur and their state of development. From the gregariousness of the species conclusions may often be drawn as to the nearness of approach to optimum conditions. In the typical Molinietum the individual plants of *Phragmites* are always isolated (Soc. 1), but in the adjacent Scirpeto-Phragmitetum they occur in troops and crowds (Soc. 3 to 5). *Stipa capillata, Iris sibirica, Veratrum album, Viola tricolor,* and countless other species which in general are not considered "social" plants may enter into competition in almost any degree of gregariousness, according to the more or less favorable conditions of the habitat. In general, vegetative reproduction leads to crowding, that is, to increased sociability (*cf.* Kujala, 1925).

Because it is so easily modified, the gregariousness of many species changes materially during the course of a succession, as on newly formed land or on neglected cut-over woodland.

The estimate of sociability is easily made, and on large sample areas it enables us to form a picture of the plant mosaic in much sharper outlines than would be possible from mere density and dominance estimates.

Statements of sociability are especially desirable where species occur in groups or colonies, whether the organisms are rooted, clinging, or free floating. As Alechin (1926) has pointed out, increased sociability is of great service to plants in competition with other species. The sociability of pioneer species on talus is almost always great and may be considered a characteristic of such vegetation (Jenny-Lips, 1930).

The specific number of individuals or shoots or, for attached lichens, mosses, and algae the size or diameter of colonies, may be indicated by definite class numbers (*cf.* Häyrén, 1914).

Statistically speaking, species and individuals may be distributed either with normal dispersion, or they may have hypo- or hyperdispersion. In hyperdispersion the individuals are crowded (*Oxalis* in beech woods); hypodispersion occurs when the individuals are more regularly arranged than would be expected to result by chance (*Solanum tuberosum* in a potato field, *Juniperus* in the Lüneburg heath, Fig. 16). In nature normal as well as hypo- and hyperdispersion occurs. The more pronounced the hypodispersion in regard to species and individuals the more homogeneous is the vegetation of the area under

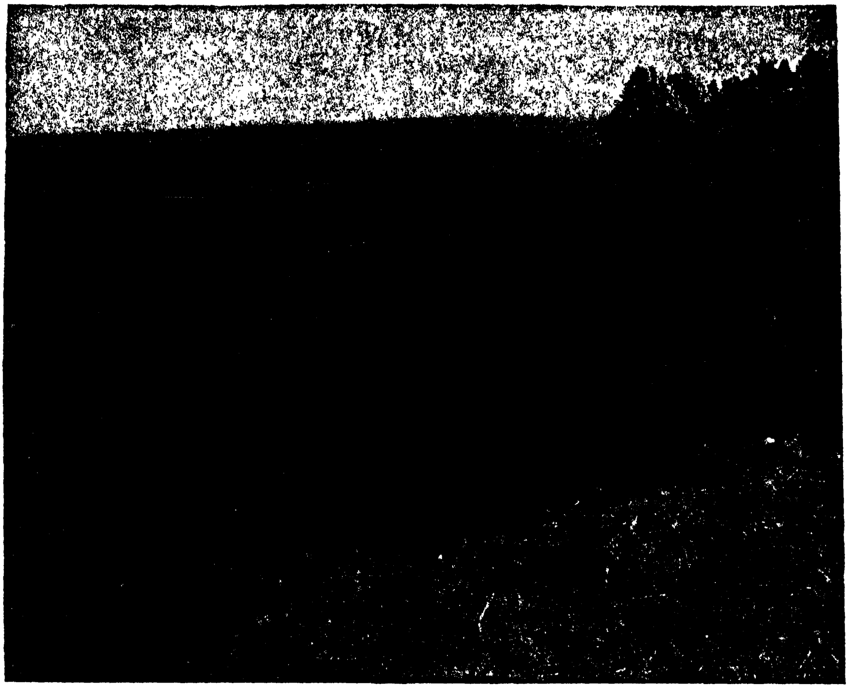

FIG. 16.—Former *Calluna* heath with *Juniperus communis* in hypodispersion (fire scar to right) in the Totengrund near Wilsede. (*Photo by Weigold.*)

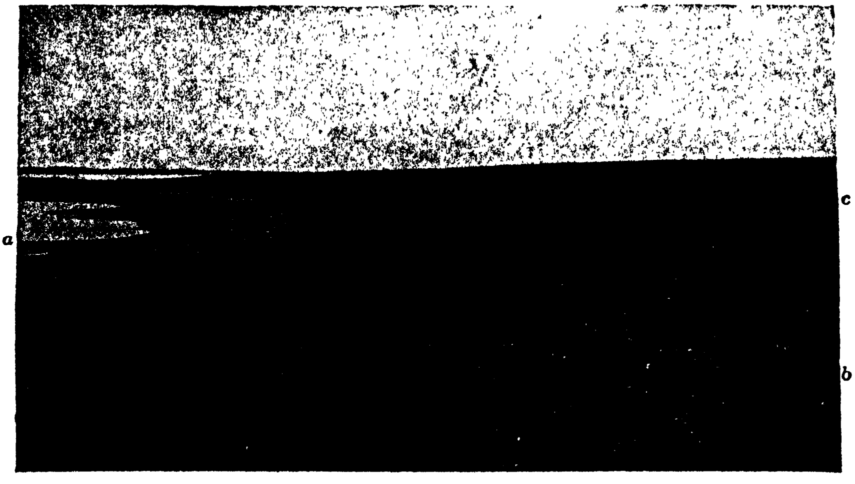

FIG. 17.—Homogeneous moss and lichen tundra at Svalbard, Spitzbergen; *a*, 7 m. belt of bright yellow *Lecanora polytropa; b*, a 14 m. belt, dark crustose lichen with *Rhizocarpon badioatrum, R. polycarpum, L. gibbosa, L. polytropa; c*, a dark brown moss and lichen belt, with widely spreading *Gyrophora cylindrica, G. erosa, G. arctica, G. hyperborea, Sphaeroporus globosus, Rhacomitrium hypnoides*, etc. (*Photo by Lid.*)

consideration, according to Kylin (1926). Hyperdispersion works the reverse; the greater it is the more heterogeneous appears the vegetation.

The homogeneity problem, brought forward by Nordhagen (1922), has been theoretically treated from the mathematical side (Kylin, 1926; Romell, 1926), without being fully cleared up.

In phytosociological practice, dominance and homogeneity are closely related. Areas in which one or a few species predominate, with even distribution, are considered homogeneous, since the more or less unevenly distributed but scarcer species are mostly hidden by the dominants. Regions with few species, with dense plant covering made up of crowded perennials (subarctic, arctic), present much more homogeneous communities than regions rich in species but with open vegetation and many therophytes (middle and south European mountains, subtropics) (Fig. 17).

This may explain the different concept and definition of the association held by many northern investigators. They regard fidelity as of less importance than homogeneity in the characterization of an association, the latter being more apparent in the north.

Frequency.—Frequency graphs, as determined by the Raunkiaer method, may be considered as an approximate expression of the

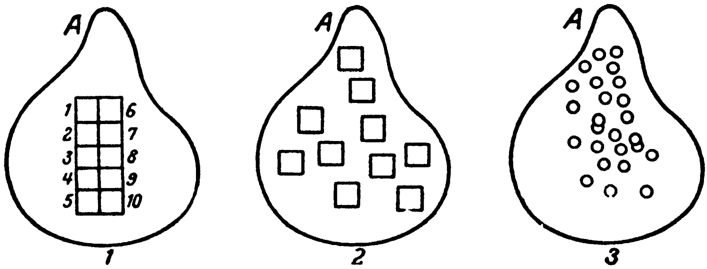

FIG. 18.—Sample plots for the determination of frequency, showing various arrangements, in a stand (*A*).

homogeneity of a stand. Raunkiaer (1913, 1918) based his studies of "frequency" upon small quadrats or circles of 0.1, 0.5, or 1 sq. m., taking 25, 50, or 100 at random in the stand investigated. The list of species of each small area was noted, without counting individuals.

Determinations of frequency (under the confusing name of constancy) recently have been made with fewer (10 to 20) and larger (1 to 4 sq. m.) quadrats (Fig. 18, *1*, *2*). The test areas as in the determination of density are arranged in a definite order (Clements, 1905; Lagerberg, 1915; Allorge, 1925) or are distributed at random in a uniform community (Raunkiaer 1918) (Fig. 18, *3*). The result may be expressed in a diagram, distributed in 5- or 10-frequency classes.

With increasing size of the test areas the highest-frequency classes enlarge, while the lowest decrease. Kylin (1926, p. 148) and Gleason (1929) have shown theoretically this displacement of classes. Figure 19 gives a practical example from the extremely homogeneous Rhynchosporetum albae.

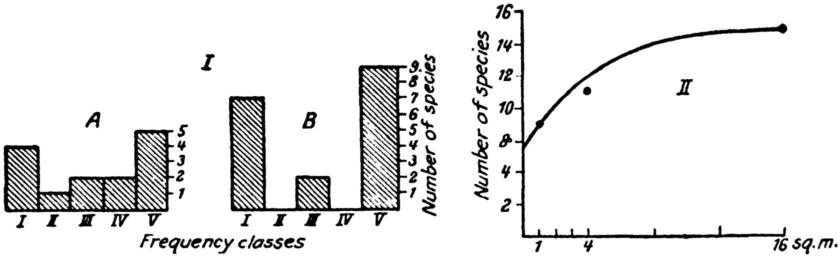

FIG. 19.—*I*. Frequency diagrams of a homogeneous *Rhynchospora alba* association at Zugerberg. *A*, from sample plots of 1 sq. m.; *B*, from sample plots of 4 sq. m. (10 samples); *II*. Species-number: area curve of the association.

Frequency diagrams are comparable, therefore, only when they are made from test areas of equal size.

With this provision, diagrams with relatively large numbers of species in the highest-frequency classes and fewer species in the lower classes indicate patches of vegetation which are floristically homogeneous. Those with smaller number of species in the highest classes and larger in the lowest indicate non-homogeneous vegetation. Figure 20*B* shows a very homogeneous community; Fig. 20*A*, one with medium homogeneity. That these graphs cannot be taken to indicate the maturity or the immaturity of a community is shown by the diagram of the Scirpeto-Phragmitetum (Fig. 20*B*). This is from a wide ditch dug about twenty years ago. Today it is covered for a long distance with a dense and extremely uniform vegetation.

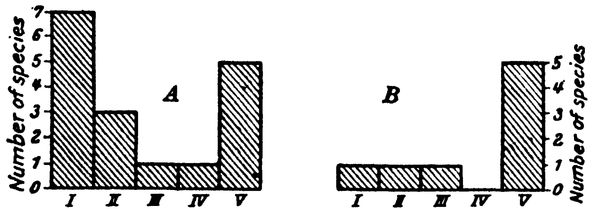

FIG. 20.—*A*, Frequency diagram from a *Carex rostrata-Sphagnum lindbergii* association in Norway; 20 samples of 1 sq. m. (*After Nordhagen.*) *B*, The same from a *Scirpus-Phragmites* association near Montpellier, France; 10 samples of 1 sq. m.

Communities which are apparently extremely uniform in physiognomy may actually show very little floristic homogeneity. The

Pinus montana forest of the Swiss National Park, with abundant *Erica* and wholly undisturbed by man, is an example of this (Fig. 21).

The frequency graphs often show two maxima: one in the highest-, the other in the lowest-frequency classes. This was proclaimed to be a regular phenomenon dependent upon the composition of natural vegetation, until Nordhagen (1922) showed that the apparent and puzzling drop from the highest to the next lower class really results from the unequal breadth of the classes, since the highest-frequency class is in fact not at all of equal value to the next lower.

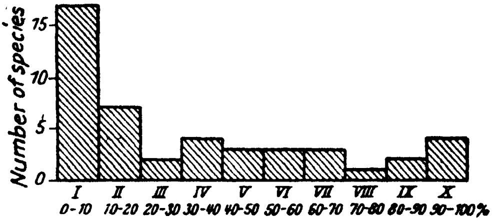

FIG. 21.—Frequency diagram of a floristically heterogeneous *Pinus montana* forest rich in *Erica carnea*. Ten quadrats of ½ sq. m. each.

The species of the highest-frequency classes are often termed "local constants," a misleading expression which should be avoided. The better and more correct form would be "very frequent" or "most frequent" species.

Layering.—The concept of layering goes back to Kerner (1863) and Ragnar Hult (1881). The latter in his descriptions of vegetation distinguished no less than seven layers and portrayed them graphically along with the corresponding life forms.

We now recognize four principal layers:

Tree layer.
Shrub layer.
Herb layer (*Feldschicht*).
Moss layer (ground layer).

These principal layers may be further subdivided. An upper and lower shrub layer may be distinguished in tall scrub; a lower, middle, and upper tree layer in the tropical forest. The graphic chart of layering according to Hult-Sernander (Fig. 22) gives along with the layering (horizontal strata) also the cover of each layer of vegetation.

The characteristic layering of plant communities is the product of a long-continued process of adaptation and selection, in which light is a dominant factor. The more numerous the upper layers are and the more completely these occupy the available space the greater must be the tolerance of the lower layers toward reduced light intensity.

On the other hand, the lower layers are less exposed to variations in heat, humidity, and wind movement. They are also dependent upon the indirect physicochemical influences of the plants composing the upper layers (root activities, type of decomposition, and chemical nature of the leaf mold).

Fusion of Layers.—Two or more layers of vegetation are often closely united and always appear together in certain societies, *e.g.*, the herb and moss layers in the Centunculo-Anthoceretum, the moss and shrub layers in certain types of high moor. An individual lower layer may either fuse with two or more higher layers or stand out distinctly by itself. In the first case we have united, in the second overlapping, layers. An example of overlapping layers is seen in the Rhodoreto-Vaccinietum of the Alps (in the *Pinus cembra-Picea excelsa* and *Larix decidua* forest), the *Rosmarinus-Lithospermum fruticosum* association of southern France (either with or without an upper layer of *Pinus halepensis*). A complete layer of *Calluna* or of *Thymus vulgaris* may appear in entirely different associations.

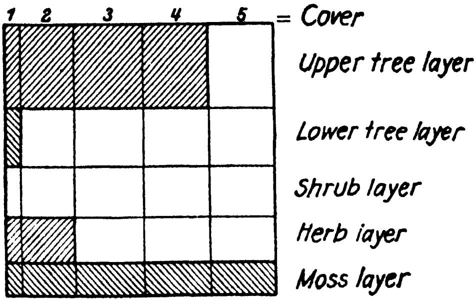

FIG. 22.—Layering in a spruce stand in the Black Forest. July, 1926.

Among closely united layers are found such as are dependent upon and conditioned by certain other definite layers. As such dependent layers may be cited the highly developed broad sclerophyll shrub layer in the *Quercus ilex* virgin forest of the Atlas mountains (Braun-Blanquet and Maire, 1924) and the lower layers in the *Alnus* swamps of Wangerin (1926, p. 189).

Subterranean Layers.—Layering is also found in the underground parts of plants, as Woodhead (1906) has pointed out. In North America Sherff (1912) has shown that in swamp communities the subterranean stems may lie at different depths in the soil and that their roots may be produced at different depths, causing a complementary rather than a competitive relation between the underground organs of the different species. The height of the water table was here the most potent factor in causing the layering. Weaver (1920, 1925) has demonstrated many cases of the influence of soil moisture, soil granulation, and distribution of nutrients upon root layering. Plants grown in the same soil but with different amounts of precipitation will show quite different root systems (Fig. 23).

The roots of some plants are very sensitive to light. Many are able automatically to regulate the growth of rhizomes according to illumination. Raunkiaer showed that the rhizome of *Polygonatum multiflorum,* on reaching the normal distance from the surface of the ground, grows horizontally forward but that if it is covered more deeply for protection, it grows obliquely upward.

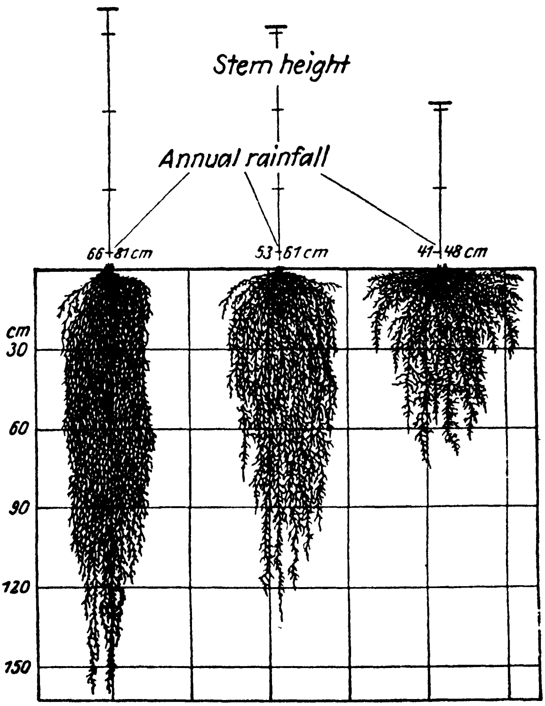

FIG. 23.—Root development in winter wheat under conditions of different annual rainfall. (*After Weaver.*)

The effect of aeration upon the course of roots is well known. In wet, poorly aerated soils the root systems are poorly developed and the roots tend to be spread out horizontally in the uppermost layer as in the pines and birches in high moors.

Soil acidity acts similarly when an alkaline calcareous soil is covered with a layer of acid humus. The roots of acidophilous plants which otherwise develop deeply are shortened and do not penetrate the basic soil (Fig. 98).

In his study of the conditions of life in the gravel-slide association Jenny-Lips (1930, p. 154) distinguishes an uppermost soil horizon without fine particles and without branching roots; below this a horizon with much fine soil in which the plants of the gravel slide develop their roots into a mat of very considerable density; and, still lower down, a horizon with very little fine earth into which the deep-anchoring roots penetrate (Fig. 24).

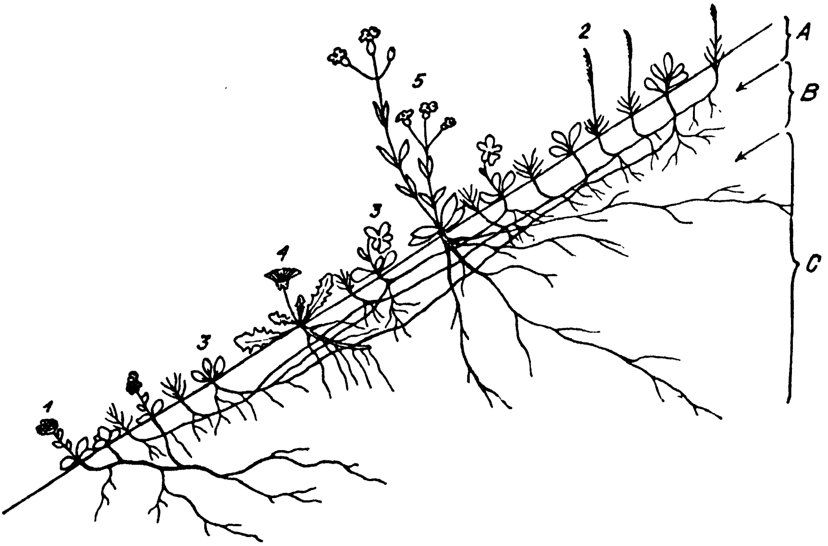

Fig. 24.—Root layering in a thick stand of the *Thlaspi* association on a gravel slide at 2,250 m., Swiss Alps; *1*, *Thlaspi rotundifolium*; *2*, *Trisetum distichophyllum*; *3*, *Viola cenisia*; *4*, *Leontodon montanus*; and *5*, *Silene alpina*; *A*, horizon of coarse gravel; *B*, horizon of absorptive roots; and *C*, horizon of anchoring roots. (*After Jenny-Lips.*)

Among others who have studied root layering are Kujala (1926), who has described the layering in Finnish forests, and Braun-Blanquet, who has investigated the phenomenon in the *garigue* of the Mediterranean region (Fig. 25). Such aerial and subterranean layering makes possible the coexistence of a number of ecologically different types and permits the maximum utilization of a given area.

Vitality (*Gedeihen*).—The fact that a plant occurs often and plentifully in a certain community does not necessarily warrant the conclusion that it prospers there. A species may be a constant member of a community and yet only be tolerated and be quite meaningless in the communal ecology. It completes its life cycle and produces seed only in certain other communities.

In the *Juncus acutiflorus* flat moor of the mountains of central France the tall (2 m.) composite *Ligularia sibirica* develops to its full capacity. Thanks to its efficiency in seed production and dispersal, seedlings of *Ligularia* are also distributed all over the immediately adjacent Trichophoretum. Very few, however, attain therein to a leafy stem, and none flowers, the young plants perishing very quickly. The vitality of *Ligularia* is evidently greatly reduced in the Trichophoretum.

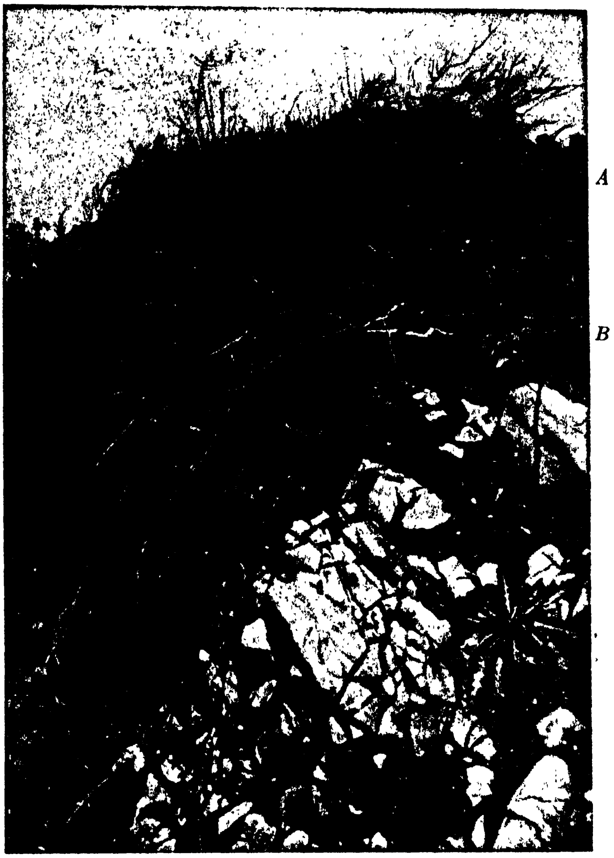

FIG. 25.—Root layering in the Mediterranean red-earth soil near Montpellier, France. *A*, Chestnut-brown horizon with roots of therophytes and geophytes, *Brachypodium ramosum* dominant; *B*, reddish brown horizon with roots of nanophanerophytes, *Quercus coccifera, Rhamnus alaternus*, and *Asparagus acutifolius; C*, horizon of rock fragments with roots of *Quercus ilex* in crevices. (*Photo by Braun-Blanquet and Keller.*)

Profound changes in vitality in the undergrowth follow admission of light or clearing of timber. Shrubs like *Vaccinium myrtillus, Calluna,* *Erica arborea,* and *Cistus salvifolius,* which are suppressed by the shade of trees, spring up, flower, and fruit luxuriantly as soon as the forest is cut. Many shade species, however, thrive badly when deprived of shade.

In deciding the sociological affinities of a species the vitality must be considered, and for an understanding of the ecology of the community it is necessary to know whether each constituent carries out its life cycle regularly and efficiently or just barely exists.

A seed plant is evidently at home only when it can produce flowers and fruit. Reduced vitality indicates, therefore, that the optimum of conditions for the species are either not attained or are overstepped. Many cryptogams which reproduce wholly asexually are exceptions. Yet even with cryptogamic communities vitality plays a definite rôle. Häyrén (1914) describes a *Lecanòra maura* community of the sea cliffs at Tvärminne in Finland, which is confined to the north or shaded side of a fissure, where *L. maura* occurs abundantly fruiting. On spots exposed to light the lichen grows but is sterile and depauperate. Many aquatic plants, low shrubs, and rhizome geophytes survive over large portions of their range without ever fruiting, as has often been reported by explorers in high mountains and in polar regions.

The trend of development of a community is often first indicated by changes in the vitality of the species, and conversely, feebly growing remnants indicate the earlier stages of development now outgrown by the community, *e.g.*, dying *Carex elata* tussocks in the Molinietum caricetosum hostianae.

Degrees of Vitality.—For expressing the vitality of the species in a community the following four grades and signs are used:

Well developed, regularly completing the life cycle (●).

Strong and increasing but usually not completing the life cycle (many mosses) (⊙).

Feeble but spreading, never completing the life cycle (◎).

Occasionally germinating but not increasing; many ephemeral adventive plants (○).

In studies of vegetation in which it is not necessary to consider vitality minutely it is still desirable to distinguish the species with reduced vitality and feeble growth. These may be indicated by a zero following the sociability grade as an exponential vitality sign (Soc. 2^0).

With parasitic fungi vitality expresses itself as power of infection. Hammarlund (*Hereditas* 6: 1925) has shown that the spores of various Erysiphaceae which germinate in the first 24 hr. have much greater power of infection than those germinating later. The vitality can be indirectly determined in these cases by the time elapsed before germination.

Periodicity.—The works of Diels (1918), Scharfetter (1922), and Alechin (1926) illuminate anew the general significance of rhythmic phenomena in the social life of plants. This includes much more than purely phenological phenomena.

Sociological periodicity depends upon the beginning, the duration, and the seasonal course of the struggle for existence. Superficially striking phenomena like flowering and fruiting (phenologically important characters) are less important than growth of shoots, duration of foliage, leaf fall, and root renewal (formation of absorptive roots). The important root relations, however, which greatly influence the seasonal development of higher plants have been little studied.

For an understanding of the simultaneous and successive life activities of plants, chance observations will not suffice; continuous and systematic records are necessary. In every study the stage of development of the species should be given.

For this special signs may be used, but in general the following abbreviations suffice:

fol. = in foliage.
s.fol. = leafless.
b. = buds.
fl. = flowering.
fr. = fruiting.
sdl. = seedlings.
ass. = assimilating (photosynthetic).

Aspect.—While the communities of the unfavorable climates of high mountains and the north show mostly only two clearly marked seasonal aspects—a hibernal and an aestival—in the temperate and subtropic regions there are several. Physiognomically they are shown by successive waves of flowering which give to each stage or aspect a wholly different appearance (Figs. 26, 27, 28, 29). The changes in the array and aggressiveness of the various species in the course of the year are sociologically more important. The greatest aggressiveness is not usually at the flowering time but at the height of shoot development.

Diagrams of Periodicity.—The best insight into the social rhythm of vegetation is given by graphic representations which cover the photosynthetic activities or the space demands of the species from time to time.

Salisbury (1925) distinguished four seasonal periods in the *Quercus robur* forest according to photosynthetic activities: a prevernal type, photosynthetic from February to June (*Ficaria, Anemone nemorosa,*

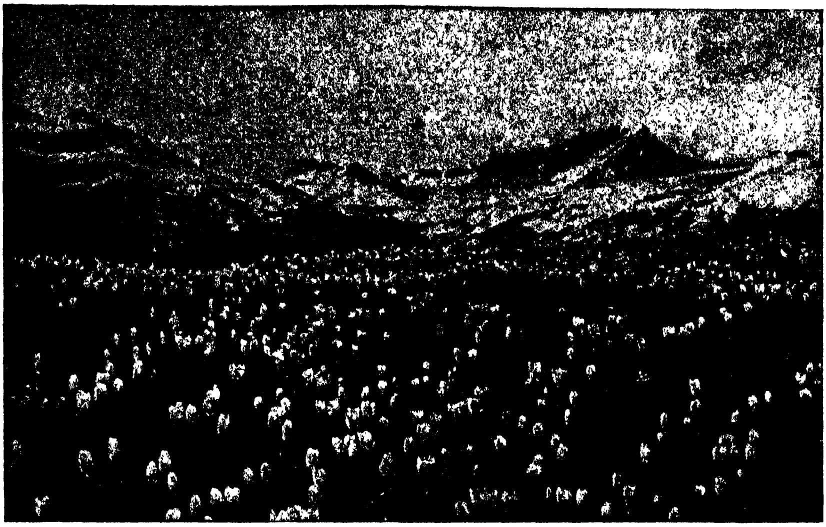

FIG. 26.—Vernal aspect (*Crocus albiflorus*) of the Trisetetum flavescentis of the Swiss Alps.

FIG. 27.—Aestival aspect (*Trollius europaeus*) of the Trisetetum flavescentis of the Swiss Alps.

FIG. 28.—Vernal aspect of a geophyte community with *Corydalis cava*, *Allium ursinum*, *Asperula odorata* in the central European beech forest. (*Photo by Uehlinger.*)

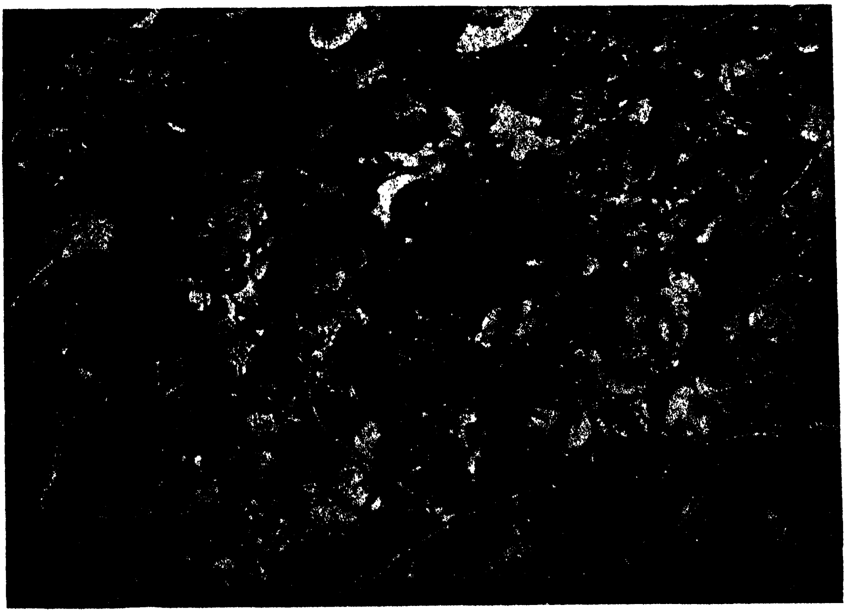

FIG. 29.—Hibernal aspect (evergreen) in the central European beech forest, *Asarum europaeum* (Soc. 3). (*Photo by Uehlinger.*)

Corydalis, etc.); a summer-green type, photosynthetic throughout the summer; a winter-green type, photosynthetic throughout the

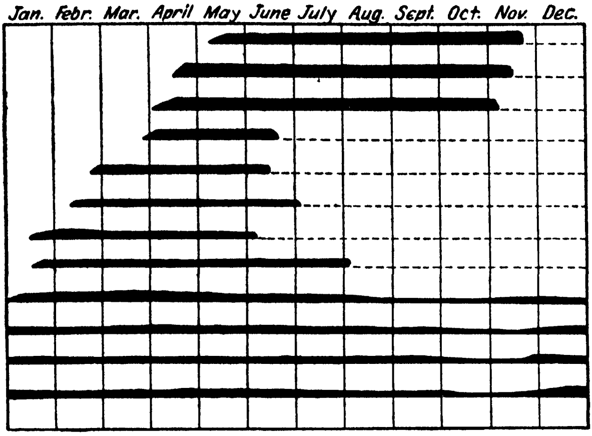

FIG. 30.—Assimilation period of typical species in the *Quercus robur* forest of England. (*After Salisbury.*)

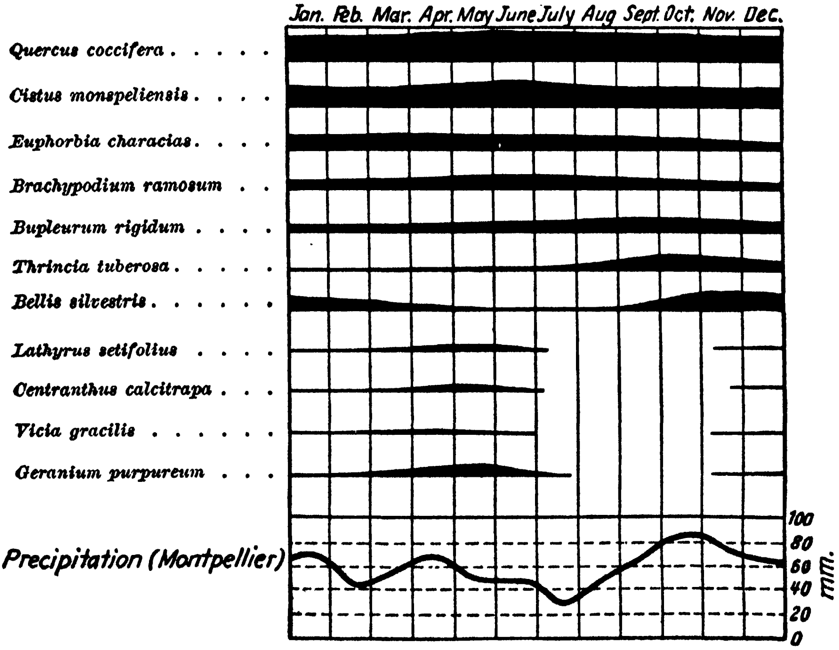

FIG. 31.—Annual variation in volume of some species of the Quercetum cocciferae of the Mediterranean garigué in southern France and the curve of precipitation.

year (*Galeobdolon*, *Ajuga reptans*, etc.); and an evergreen type (*Hedera*, *Vinca*, etc.) (Fig. 30). The prevernal type corresponds to the vernal aspect, and the winter green to the hibernal aspect, whereas the summer-green type determines the aestival aspect. The line of division between vernal and aestival aspects is given by the leafing out of the trees and shrubs. The vernal leafless "light phase" enjoys a light intensity in the undergrowth of 40 to 60 per cent. After leafing out the light intensity often falls in the aestival aspect to 1 per cent or less of the light requirement (*Lichtgenuss*).

The periodicity of the Mediterranean garigue is caused not by light relations but by the spring and autumn rains. To the four seasonal types mentioned above there is here added a fifth, the autumnal, with *Thrincia tuberosa, Bellis silvestris, Scilla autumnalis*, etc., corresponding to the reawakening of growth after the first autumn rains (Fig. 31).

Instead of the period of photosynthesis, the preceding diagram (Fig. 31) gives the seasonal variation in volume of each species. In this the summer drought comes out strongly with corresponding minimum of plant volume. On the whole, however, the *Quercus coccifera* garigue is "periodically saturated"; that is, it includes species which substitute for one another throughout all seasons.

CHAPTER IV

SYNTHETIC CHARACTERS OF THE COMMUNITY

Besides the analytical characteristics, which may be traced in every stand or every settlement, there are synthetic characteristics which result from the comparison of the records of as large a number of stands as possible taken from a maximum number of plant associations. The stand is the concrete representative of the association in nature. When a large number of complete records of well-developed stands within one association are tabulated side by side, the first synthetic character observed is the presence of the species—their more or less regular occurrence in the stands.

When this comparison is extended over the tabulations of all of the associations in a given region, conclusions are reached regarding the more or less rigid ties by which the species are bound to certain communities—their fidelity (*Gesellschaftstreue*). The supreme importance of the lists of species in the characterization of associations thus becomes especially clear.

Presence.—By presence is meant the more or less persistent occurrence of a species in all the stands of a certain plant community.

As far back as the time of Lorenz (1858) this concept was employed. However, it became established in geobotany only after Cajander (1904) had introduced the tabular presentation of individual records of plant lists of associations.

The first investigator to use this presence factor for the comparative study of plant communities was Brockmann-Jerosch (1907). He designated as "constants" those species which were present in at least half of the stands examined; as "accessory species" those which occurred in one-fourth to one-half of the communities; and as "accidental" those which were found in less than one-fourth of the stands. However, many sources of error prevented any striking success in the use of this method for the determination of presence.

Minimal Area.—A community of plants requires for its normal development a minimum area and also upon this area a minimum number of plant species. Minima of space and number of species are also requirements which must be assigned to an association. This concept has led to the technical use of the term "minimal area" to designate the smallest area which can contain an adequate representation of an association. All sample stands examined in the study of an association should be at least of the size of the minimal area and must have the characteristic combination of species. Minima of space and number of species differ for each and every association, and their fixation can be accomplished only by empirical methods.

Degrees of Presence.—The presence grades of the species of a community are conveniently expressed by a 5-degree scale:

5 or V = constantly present (in 80 to 100 per cent of the stands).
4 or IV = mostly present (in 60 to 80 per cent of the stands).
3 or III = often present (in 40 to 60 per cent of the stands).
2 or II = seldom present (in 20 to 40 per cent of the stands).
1 or I = rare (in 1 to 20 per cent of the stands).

In accounts of a rather general nature the words "constantly," "mostly," etc., may be used instead of the figures.

Presence may also be expressed as a fraction ($^{15}/_{18}$, $^{4}/_{9}$). The denominator gives the number of stands examined; the numerator, the number of occurrences. The species of the highest presence classes—those in at least four-fifths of the stands examined—may be designated as the "constants" of the association.

Determination of Presence.—The determination of presence is made upon normal mature stands (association individuals). It tells in how many of the stands examined the particular species occurs as a competitor. Ilvessalo and others have shown that the group of species showing the highest degree of presence varies greatly with the age of a timber stand. Initial stages, therefore, must not be mixed up with mature phases of an association. Further, the stands recorded should be distributed as evenly as possible over the region studied; but they must not be taken from stations with wide differences of altitude. Sub-associations and facies must be discussed separately.

The question of how many stands are necessary to conclude a study of presence cannot be answered by any general rule. Ten records often give a satisfactory picture; in those very rare cases of associations which are ecologically very strictly specialized throughout, fewer records will do. A few well-developed stands are better for the determination of presence than a large number of floristically heterogeneous examples.

Presence and Constancy.—There is no difference in principle between "presence" and "constancy." Practically, however, it is advisable to designate as studies of constancy those investigations of presence which are made with plots of sharply limited area (*e.g.*, 0.5, 1, 2, 10 sq. m.). Only such studies can be treated by mathematical-statistical methods. When so conducted they have a real value for deepening our understanding of the structure of plant communities.

At best, not all plant communities are suited to studies of constancy, since not all homogeneous areas are large enough, *e.g.*, aquatic societies, rock crevice, gravel, mosaic moor, terrace-turf communities. In such cases it is better to omit the determination of constancy and not sacrifice the unity and similarity of the stands.

Determination of Minimal Area; Species: Area Curves.—The increase in number of species with increasing area, first scientifically treated by Jaccard (1912, 1928), was later investigated in detail by Palmgren (1917). He showed that in the grazing regions of the Åland islands the number of species in one portion of the area stands in almost direct relation to the size of the sample plots. Palmgren's empirically derived values were shown by Romell (1925, 1930) to correspond with the curves theoretically calculated by the law of chance (Fig. 32). From this it is clearly seen that with increasing size of area the curve of the number of species at first rises very rapidly, then swings nearly to the horizontal, and continues with an almost imperceptible rise.

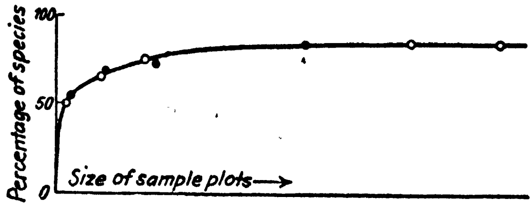

FIG. 32.—Species: area curve; ° = calculated values; • = empirical values. (*After Romell.*)

Similar empirical curves were later constructed by Brenner (1921), Ilvessalo (1922), and Braun-Blanquet (1926). Their form corresponds with Romell's curves, in spite of the fact that they were based on definitely bounded uniform plant communities.

Kylin (1926), starting with the law of probability, has established from theoretical considerations the curves discovered by purely empirical methods. He demonstrated that the communities studied by Brenner (1921), Du Rietz (1921), and Ilvessalo (1922) obey the law of probability with regard to number of species and area. The similarity of the curves theoretically deduced and the empirical species: area curves is really very striking.

Romell's distribution curve (Fig. 32) is a species-percentage: area curve. The ordinates represent the number of species expressed as percentage of the whole number. The course of this curve is conditioned by the size of the sample plots and by the density (distance between individuals) of each species.

The species-number: area curve is of more social significance. As Kylin (1926) showed, it is influenced by three factors: the number of species in the society, the size of the sample plots, and the density of the individual species. Instead of the percentage of the number of species, the absolute numbers of species are plotted as ordinates. Such a curve shows not only the relation of the number of species to the size of area but also the absolute number of species in the community (Fig. 33).

The curves given in the figure show that one of the two related associations of the Caricion curvulae alliance has twice as many species as the other and that the curve of the Festucetum halleri (which has more species) becomes horizontal later than the Curvuletum curve; and thirdly they demonstrate what is the average number of species on a given area of each association. Thus the species-number: area curve becomes a most valuable sociological statement.

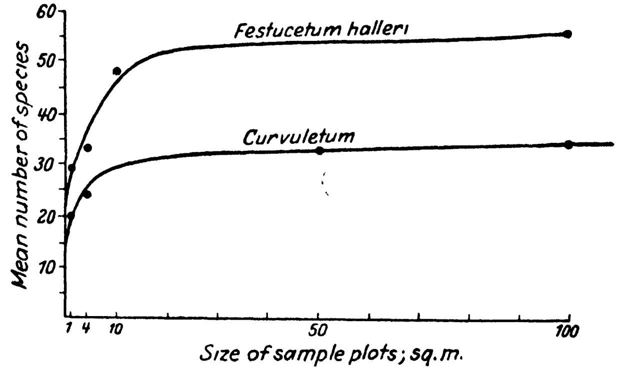

FIG. 33.—Curves showing the relation between the number of species and the size of the sample plots in associations of the Caricion curvulae. (*Braun-Blanquet and Jenny.*)

In the Curvuletum the horizontal course of the curve begins with areas of about 10 sq. m. and with about 30 species; but in the Festucetum halleri the curve flattens with areas of 20 sq. m. and with about 52 species. In other words, the minimal area of the Curvuletum is about 10 sq. m.; of Festucetum halleri, about 20 to 25 sq. m.

Determination of Constancy.—If the working out of the essential properties of communities were a purely mechanical process, it would be necessary, for the determination of constancy, only to tabulate plots of at least the minimal area and with a correspondingly high average number of species. All smaller plots and those with fewer species would be disposed of as fragmentary associations.

But sometimes the normal characteristic combination of species can be verified on smaller areas (see Table 4, Nos. 4, 9), and contrariwise it may under some circumstances remain incomplete on a plot considerably larger than the minimal area. Consequently in every record of an association taken for the purpose of tabulation it is necessary to be careful that the normal characteristic combination of species is present and that the requirements of the minimal area are approximately fulfilled.

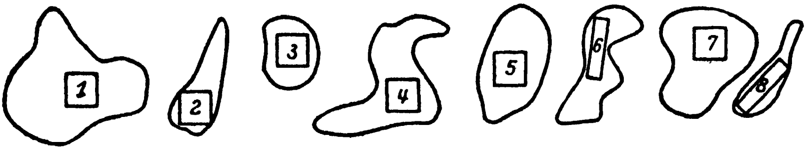

FIG. 34.—Sample plots of the same size taken from eight individual stands of the same association for the determination of constancy.

For the determination of constancy each stand may be examined only once by means of a sample bit of vegetation of a definite size (Fig. 34).

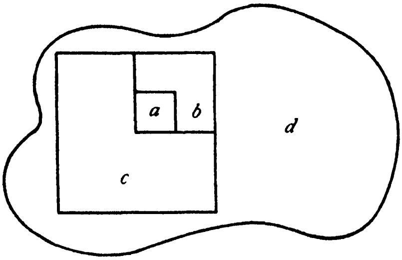

FIG. 35.—Plan for the determination of constancy and presence from the same stand beginning with the quadrat (a) which is 1 sq. m.

If the size of the sample areas chosen for determination of constancy is 10 sq. m., then the floristic composition of one 10-sq. m. plot in each stand will be examined minutely. The species lists are then tabulated together, and the species are distributed into 5 or 10 constancy classes according to their occurrence in the lists, as in the determination of frequency or presence. As with frequency, the constancy numbers depend on the size of the plots studied, the number of constant species increasing with the size of the plots.

Constancy determinations are readily united with presence determinations. In each normally developed stand a small definitely bounded trial plot is laid out (*a*), then a second and third larger (*b*, *c*), and then notes are taken on the species present in the stand (*d*) outside the trial plots (Fig. 35). A similar procedure may be followed in determining the species-number: area curve.

Constancy Diagrams.—The constancy curve and constancy diagram are for the association what the frequency curve and frequency diagram are for the stand (*Assoziationsindividuum*). The course of the curve is very different from that of frequency, in that the two lowest-class numbers show a distinct maximum. The highest-constancy classes have few species but would have more if the size of the test plots were enlarged. A sharply defined association, not very homogeneous but rich in species, like the Elynetum of Braun-Blanquet, gave the accompanying diagrams (Fig. 36). The areas used for these determinations of constancy were smaller than the minimal area of the association.

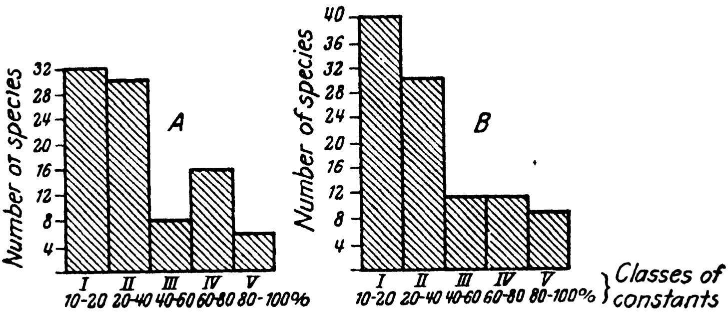

FIG. 36.—Constancy diagrams of the Elynetum. *A*, Ten samples of 4 sq. m. from 10 stands from central and eastern Grisons; *B*, the same with the addition of two 4-sq. m. areas from the southern Tirol.

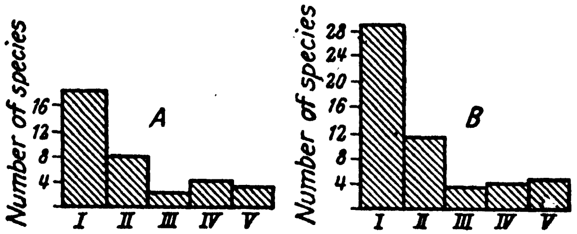

FIG. 37.—Constancy and presence diagrams of the Polytrichetum sexangularis of the Central Alps. *A*, Constancy from 10 tests in as many stands; *B*, Presence diagram of 15 well-developed stands of 2 to 10 sq. m.

But larger and more homogeneous areas of the Elynetum are not easily found.

With these may be compared the Polytrichetum sexangularis of the Alps, an association of very few species and of very great uniformity, whose minimal area does not exceed 1 sq. m. (Fig. 37). Of these diagrams *B* is based upon 15 naturally bounded, normally developed stands of 2 to 10 sq. m. Compared with the constancy diagram *A* based on plots of 1 sq. m. it shows a larger number of casual species in class I and also a greater number of species in class V.

General conclusions can hardly be drawn from the few trustworthy constancy diagrams now available. Most of the so-called "constancy diagrams" of the Swedish investigators are "frequency diagrams," and their data are from frequency and not constancy determinations.

It appears from the available studies that species of the higher-constancy classes can readily replace one another in different stands of the same association. The writer (Braun-Blanquet) cannot share the opinion that a composite framework of definite "constants," always present and unexchangeable, must be considered as an essential prerequisite of the association. He believes that in so far as it does not concern the species which condition the society, such "constants" may be replaced by non-constants, without lessening the unity of the association.

Constancy and Frequency.—Determinations of constancy can be made entirely apart from determinations of frequency. If constancy (in the sense of several Scandinavian authors) is combined with frequency, it is possible, according to Kylin (1926), to obtain, at least approximately, an idea of the homogeneity of the society, since frequency touches one side of the problem of homogeneity and constancy another (frequency-constancy = homogeneity in part). The "frequency-constancy" not only gives an appreciation of the homogeneity of a community but also permits the formation of a concept of the sociological importance of the species of each layer of the vegetation. For this the constancy figure must be added as an exponential of the frequency number. If *Salicornia fruticosa* is found in all 20 samples (1 sq. m.) from each of the 10 stands of the Salicornietum fruticosae examined, the result may be written 200^{10}. When it is found in only 16 out of the 20 samples in one of the stands but in all of the samples of the 9 other stands, the results may be written 196^{10}.

Fidelity (*Gesellschaftstreue*).—The concept of fidelity has to do with the sociological distribution of species. The degree of fidelity indicates the more or less rigid limitation of the plant to definite plant communities. Just as there are plants which are limited to very definite soils or to a sharply circumscribed local climatic complex, so there are those which are strictly confined to certain plant communities—species of exclusive fidelity. But those plants are more numerous which, while showing a decided preference for one or for several plant communities, do not show any strong social ties. There are also species, ubiquists, which flourish in quantity and are able to compete in very different plant communities. Of no species, however, can it be said that it flourishes or even occurs in every community of a region, no matter how broadly the communities are defined. A natural selection has taken place, and a limitation of species to certain plant communities is easily discernible, in which the place of each species is determined by its specific potentialities, its ecological individuality, its dependencies, its ability to compete with other plants, and even by its past history (migration). These factors give each species a wider or a narrower field for its sociological activities.

Degrees of Fidelity.—Five degrees of fidelity may be distinguished in the attachment of the species to the given community.

A. Characteristic Species

Fid. 5. Exclusive species (*treue*): species completely or almost completely confined to one community, *e.g.*, *Viola cenisia*, *Papaver alpinum* in the Thlaspeetum of the Alps, *Delia segetalis* in the Centunculo-Anthoceretum of Central Europe.

Fid. 4. Selective species (*feste*): species found most frequently in a certain community but also, though rarely, in other communities, *e.g* , *Phyteuma pedemontanum* in the Caricetum curvulae, *Crepis biennis* in the Arrhenatheretum of Central Europe.

Fid. 3. Preferential species (*holde*): species present in several communities more or less abundantly but predominantly or with better vitality in one certain community, *e.g.*, *Luzula luzulina* and *Pirola uniflora* in the Piceetum of the Alps and the Tatra.

B. Companions

Fid. 2. Indifferent species (*vage*): species without pronounced affinities for any community.

C. Accidentals

Fid. 1. Strange species (*fremde*): species that are rare and accidental intruders from another plant community or relicts of a preceding community, *e.g.*, *Peucedanum palustre* or *Carex elata*, relicts of the Caricetum elatae in the Molinietum; *Ammophila arenaria* as a relict in the shrub communities of coastal dunes.

Differential Species.—For sharper differentiation, especially of associations or sub-associations with few or no characteristic species, the so-called "differential species" are of value. These are species which on the basis of the above scheme cannot be designated as characteristic species of an association but normally appear only in one of two or more related societies (often genetically related). *Centaurea jacea, Knautia arvensis, Ononis repens* are differential species of the more mesic Mesobrometum as against the Xerobrometum. The differential species of the three sub-associations of the Molinietum coeruleae come out clearly in the association tables of W. Koch (1926).

Fidelity in Relation to Alliances and Orders.—Fidelity grades are primarily related to the association but have value also for any higher unit of vegetation: alliance, order, etc. Species which occur abundantly in several associations may be more or less confined to one certain alliance and so help to characterize it, *e.g.*, *Potamogeton lucens* in the Potamion eurosibiricum, *Salicornia macrostachya* and *S. radicans* in the Salicornion fruticosae, *Cardamine alpina* and *Arenaria biflora* in the Salicion herbaceae of the Alps. The same is true of the orders. The higher the systematic rank of the unit of vegetation the richer it is in characteristic species. Exceptionally large numbers of characteristic species in a community often indicate that we are dealing with two or more associations or with an alliance.

Determination of Fidelity.—Since fidelity can be correctly estimated only when a sufficient number of exact records are available, all statements of fidelity which are not supported by association lists are poorly founded and are to be taken with caution.

The first requirement for the determination of fidelity is a knowledge, as exact as possible, of the plant groups of the region. From such records it may be seen that certain groupings constantly occur under certain conditions. Some species (the exclusive) are confined to certain groupings, others (the selective or preferential) show their membership in certain groups by great vitality, especially vigorous growth, crowding of individuals, or high constancy. Groupings that correspond floristically are tabulated together. These tables, if characteristic species (fid. 3 to 5) or a large number of differential species are present, supply the indispensable foundation for further work on the associations. The association tables are to be established by records of as many stands as possible.

From a comparison of all the association tables of a region it then appears that certain species occur in only one table, others in several or in all of the tables, and further that one and the same species shows in the several tables (*i.e.*, in the several associations) very different degrees of constancy, frequency, sociability, and vitality.

The preparation and study of these tables are the work of years; but since they are fundamental to the determination of fidelity and the delimitation of the association, they cannot be omitted. In case the segregation of the exclusive and preferential species presents great difficulties, at least a preliminary group of characteristic species may be distinguished.

For the objective demonstration of degrees of fidelity by means of association tables, Szafer and Pawlowski (1927) have given a chart which is shown with slight modifications in Table 3.

TABLE 3.—SCHEME FOR THE DETERMINATION OF THE FIDELITY OF THE SPECIES OF A GIVEN ASSOCIATION

P = degree of presence; A = degree of abundance (total estimate, see p. 34)

Relationship of species with approximately the same vitality and sociability		Examples
In the given association	In other associations	
Fidelity 5:		
P 4 to 5; A 3 to 5	P 1; A to 1	*Juncus trifidus* in the Trifidi-Distichetum of the Tatra
	P 1 to 2; A to 1	*Schoenus nigricans* in the Schoenetum nigricantis of central Europe
P 4 to 5; A + to 2	P 1; A + to 2	*Ribes petraeum* in the Mughetum of the Tatra
P 1 to 3; A any degree	Lacking or very rare	*Chamorchis* in the Firmetum of the Tatra; *Listera cordata* in the Piceetum of the Alps
Fidelity 4:		
P 4 to 5; A 3 to 5	P 2 to 3; A + to 2	*Pinus mughus* in the Mughetum in the Tatra
	P 3 to 4; A + to 1 (as association relicts or pioneers)	*Ammophila arenaria* in the Ammophiletum
P 4 to 5; A + to 2	P 2 to 3; A + to 1(2)	*Saussurea alpina* in the Elynetum of the Alps
P 3 to 4; A + to 2	P 1 to 2(3); A + to 1(2)	*Koeleria gracilis* in the Xerobrometum of Germany
P 1 to 3; A + to 2	P trifling; A very trifling	
Fidelity 3:		
P anything; A 3 to 5	P + 3; A + to 2	*Trisetum flavescens* in the Trisetetum flavescentis in the Alps
P anything; A anything	P and A trifling or rather trifling or A trifling, vitality reduced	*Empetrum nigrum* in Empetreto-Vaccinietum in the Alps
Fidelity 2:		
P, A and vitality in two or more associations approximately equal	P, A and vitality in two or more associations approximately equal	
Fidelity 1:		
P 1; A + up to 1 Vitality reduced Species occurring only on the outskirts or on disturbed parts of the stand	P 1; A + up to 1 Vitality reduced Species occurring only on the outskirts or on disturbed parts of the stand	*Prunus avium* seedlings in the Piceetum or in the Fagetum *Rumex alpinus* in the Trisetetum flavescentis; *Sibbaldia procumbens* in the Arabidetum coeruleae

In determining fidelity, two general rules should be observed.

1. Sociological mixtures are first to be eliminated. The occurrence of characteristic species of the Xerobrometum in the open pine woods along with *Bromus* cannot diminish the degree of fidelity of these species in the Xerobrometum; neither can their occasional occurrence

in other disturbed societies or in artificial habitats which have no social characteristics.

2. Only the tangible sociological observed facts are of value. Occasional human intervention (clearing, burning, or flooding) causes sudden changes of vegetation, often giving a sociologically unstable but temporary transition phase, with the occurrence of relicts of a former vegetation (forest or swamp relicts) or of isolated pioneers of the succeeding association. Consequently the developmental stage of the vegetation must be considered.

Regional and General Fidelity.—The vegetation of a region with uniform climate and uniform geological history shows usually great uniformity in the species and in their grouping. But since general climatic conditions are never alike over extensive areas and the historical relations of the flora differ from region to region, it is plain that both the grouping (Du Rietz, 1923, gives numerous examples) and the fidelity of species will show regional changes. We have therefore to distinguish between regional and general fidelity, according to whether a species is characteristic of an association throughout the entire range of the association or only in a part of its range. *Silene otites* is an exclusive species of the Xerobrometum in all the alpine foothills and in a part of southern Germany. But in the dry spots of the inner alpine valleys it thrives also in the Festucetum vallesiacae and in other associations closely related ecologically to the Xerobrometum. *Silene otites* is therefore a regional characteristic species of the Xerobrometum. Fidelity always involves the question of how a species is related to a certain community. Of secondary importance is the question of the social relations which this species has in all parts of its range. Thus, one and the same species may be exclusive in different regions to two or more distinct and different communities. *Crepis biennis* in the region of the Arrhenatheretum is a characteristic species of this association, but in another region it is characteristic of the Trisetetum flavescentis. These two tall grass associations replace one another in climatically different regions.

Obviously determinations of fidelity must not be taken on too small an area. But in the present stage of research these limitations need hardly be mentioned.

Causes of Fidelity.—The narrow social confinement of highly characteristic species is the result of various causes.

1. Many paleoendemics of geologically ancient regions are sociologically narrowly localized, *e.g.*, Tertiary species of Mediterranean associations. Long-continued rigorous selection seems to have confined these species to narrowly circumscribed habitat relations, so that many

(especially geographically isolated types) have lost their capacity for variation and dissemination—*Berardia subacaulis*, *Saussurea depressa*, *Xatartia scabra*, *Borderea pyrenaica*,—characteristic species of certain gravel-slide associations of the southern Alps and the Pyrenees are very good examples.

2. Besides these characteristic relict species there are others whose fidelity is due to a narrowly specialized adaptation to definite physicochemical relations of the habitat, such as associations of rock crevices, dunes, and epiphytes; *e.g.*, the association Violetum calaminariae on zinc soils investigated by Schwickerath (1931) contains several characteristic species narrowly limited to this special substratum.

3. Certain combinations of genes of polymorphic groups are more vigorous and of greater efficiency in certain communities than in others and increase more rapidly than related types. This gene combination is thus enabled gradually to crowd out the others. Thus there results a break in the series of polymorphic forms, and the new gene combination which prospers so vigorously in a certain community (association, alliance) may attain the rank of an elementary species. This segregation is helped by geographic isolation of certain gene combinations (*e.g.*, *Chrysanthemum vulgare* var. *delarbrei* of the Festucetum spadiceae of Auvergne and many "races" of mountain species of *Androsace carnea*, *Saxifraga moschata*, etc.) whereas it would encounter great difficulties where the presence of a polymorphic population constantly made possible an exchange of genes. A. Kozlowska (1925) concludes from her studies of variability in *Festuca ovina* that the association is an important factor in the segregation of elementary species.

Apogamy likewise favors the differentiation of sociologically more or less specialized forms such as the characteristic species of the Festucetum halleri from the Pilosellina group and those of the Seslerieto-Semperviretum from the Villosa and Vulgata groups of *Hieracium*.

4. Many species are less selective in a region (*e.g.*, Central or northern Europe) with optimum conditions of life, and flourish in several plant communities, but in other regions (*e.g.*, southern Europe) they become exclusively characteristic species of certain associations, because there they find their life requirements fulfilled in only one definite community, *e.g.*, *Neottia* in the Fagetum, *Centaurea jacea* var. *typica* in the *Arrhenatherum-Narcissus tazetta* association.

5. Characteristic species may be considered such ecologically specialized forms as stand in direct dependence upon certain organisms or groups of organisms or upon the life conditions brought about by these. Here belong many mycotrophic species, saprophytes, nitrophiles, and many acidophilous and humicolous plants. Parasites are

often confined to a certain host or habitat and, much less frequently, to one community exclusively. There are cases reported, however, where fungus parasites are more strictly confined to a certain plant community than their host plants.

6. Competition is an important factor in developing fidelity. In the severe struggle with better adapted species, the more imperfectly adapted are confined to certain definite communities, although nothing but competition prevents them from occupying other habitats, and they actually do grow in other habitats when competition is removed, as in garden culture. One recalls various characteristic species of cultivated communities in vineyards, grain fields and gardens. Natural vegetation furnishes similar examples, *e.g.*, the Mesobrometum of central Switzerland with its characteristic annual species, such as *Arenaria leptoclados, Cerastium brachypetalum, Saxifraga tridactylites, Vicia tetrasperma* and *Myosotis collina.* In the moist oceanic climate of the alpine foothills the Mesobrometum, because of its open stand (the perennial chamaephytes and hemicryptophytes often cover not more than four-fifths of the ground), is the only grassland in which these annuals can find space to grow. Similar conditions exist in the *Cyperus flavescens* region of Central Europe, particularly in the Eleocharetum where extreme habitat conditions obtain on account of the short vegetative period after the annual sinking of the water table. This causes a strict selection of a few species exclusive to the habitat (W. Koch, 1926).

Sociological Indicator Value of the Characteristic Species.—The characteristic species furnish a connecting link between statistical-structural studies and the ecological study of communities. Because of their finer ecological adjustment the group of characteristic species and to a lesser degree the differential species have very high value as ecologic indicators.

1. The characteristic species are primarily decisive for the floristic individuality of a community.
2. They are collectively the best indicators of the ecological condition of the community.
3. They permit an estimate of the stage of development attained by a community.
4. They permit the drawing of conclusions as to the present and former distribution of certain communities.
5. They are of special value in determining the natural affinities of plant communities, thus making possible a classification of communities on a floristic basis.

Indicators of the Specific Ecology of Communities.—Since the characteristic species are more sensitive to the determining ecologic factors than the indifferent species, they react to much finer differences and are therefore more precise indicators of the optimum conditions for the community. An example of this would be the distribution of the characteristic species and of the species of highest degrees of constancy of the Caricetum curvulae and the Elynetum in relation to such a dominant factor of the habitat as the soil reaction (Figs. 38*a*, *b*).

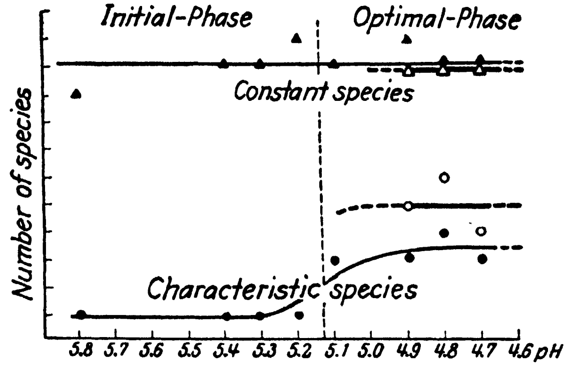

FIG. 38*a*.—Idealized curves of the constant and the characteristic species in the Curvuletum: Heavy line, normal facies; light line, *Campanula scheuchzeri-Alchemilla glaberrima* facies. Each circle and each triangle represent a stand examined. (*Braun-Blanquet and Jenny.*)

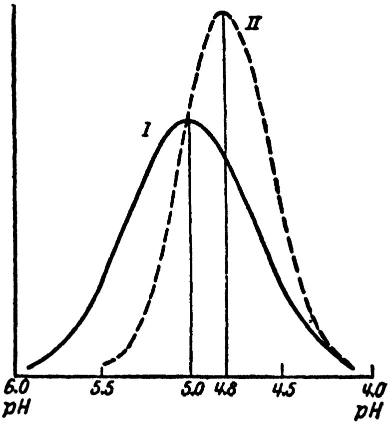

FIG. 38*b*.—Curves for the pH variations for *Carex curvula* (*I*), and for the Curvuletum (*II*). (Tests from 100 individuals or stands.) Ordinates, frequency; abscissae, pH values. (*Braun-Blanquet and Jenny.*)

From the shape of the curve it is seen that the greatest accumulation of the characteristic species occurs on soils of pH 5.1 to 4.6. This optimum of the association corresponds to the optimum of the dominant species *Carex curvula*, as determined by 150 pH tests (Fig.

38*b*, I). (The sole characteristic species which figures at all in the curve at pH 5.8 to 5.5 is the preferential *C. curvula.*) The number of constant species is evidently not influenced by change in acidity; its graph is a straight line.

Similar curves showing the massing of characteristics in the optimum region are given by the Elynetum (see Fig. 168).

Artificial interference with the ecology of the community quickly drives out the characteristic species. If the Xerobrometum is manured, the orchids, as well as *Koeleria gracilis, Anemone pulsatilla, Potentilla arenaria, Trifolium scabrum*, and other characteristic species, disappear at once, whereas the dominant grasses *Bromus erectus, Festuca ovina* and many other constants may continue for a long time in spite of heavy manuring.

The characteristic species of the flat-moor associations react similarly to a lowering of the water table; so also do the characteristic species of forest communities to the admission of light.

The concept of fidelity has been used consciously or unconsciously by many ecologists who do not employ the term. Thus Ilvessalo speaks of the exclusive species of Finnish forest types, and Clements parallels the concept in his plant indicators.

If numerous characteristic species of an association reappear together in another association of a far distant region, this proves the ecologic relationship of the two communities.

The moss-carpeted *Picea sitchensis* forest of Alaska, with *Hylocomium loreum, Aspidium spinulosum, Listera cordata*, and *Pirola uniflora*, as described by Cooper (1923), has undoubtedly similar life conditions and exists under external relations similar to those of the climax spruce forest of the Alps, where the same characteristic species occur in the Piceetum.

Syngenetical Indicators.—The narrow range of the characteristic species and their resulting social specialization make it possible to use their grouping in judging the stage of development of a plant society. Our investigations in the eastern Swiss Alps (Braun-Blanquet and Jenny, 1926) have shown that a maximum of characteristic species goes with the optimum development of an association (*cf.* also Fig. 39).

In the progressive reforestation of the national domain in the high Cévennes, the characteristic species of the Fagetum come in gradually, exactly in proportion as the association approaches its original condition. Only in the undisturbed high forest do we find their full number and their highest development.

From the comprehensive demonstrations of Linkola in Finland it appears that *Lycopodium complanatum, L. annotinum, Pirola chlorantha,* *P. uniflora*, *Listera cordata*, *Linnaea borealis*, and other species practically always appear only in the older (50- to 100-year) timber stands. The first two show marked preference for the *Pinus silvestris* forest; the others, for the spruce woods. Similar examples could be multiplied.

On the other hand, if a timber type is found outside its natural range, its group of characteristic species will not appear, even after hundreds of years of undisturbed growth. The presence or absence of the group may serve, therefore, as in the alpine foothills, to distinguish natural from planted spruce woods.

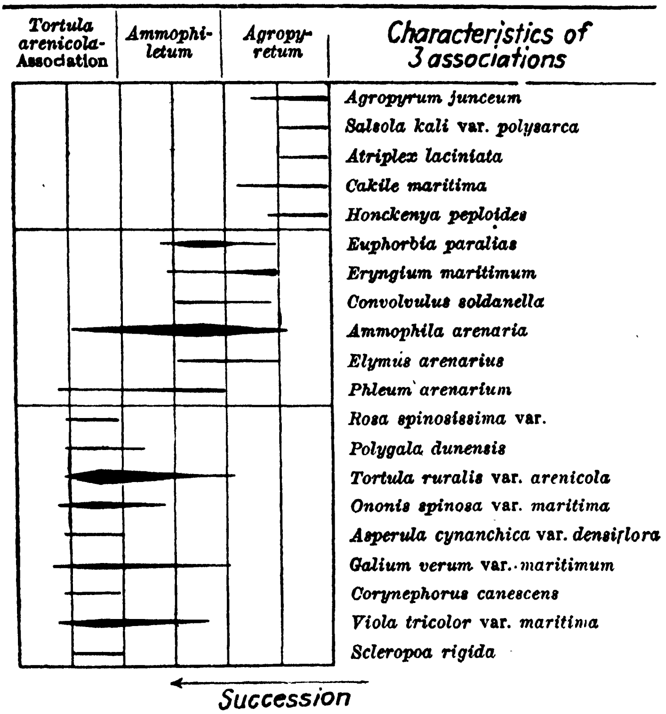

FIG. 39.—Development of the characteristic species in three genetically related associations of the Flemish littoral. (*After Hocquette.*)

Distribution of Communities and of Characteristic Species.—Ponderous manuals and masses of plant lists tell us with increasing exactness about the occurrence and distribution of the species of our flora. These sources can also be made useful synchorologically by means of the fidelity of species.

Oftentimes an obscure floristic paper may enable us to predict the presence of a certain association. If several characteristic species occur together in one locality, the presence of the association in question may be predicted with a high degree of probability, as far as this is possible from historico-geographic evidence.

In tracing out the rare but floristically rich association of *Helianthemum hirtum*, *Onobrychis caput-galli*, and *Barbula gracilis* and also in bounding the area of the Xerobrometum in southern Germany and northern Switzerland, the records of localities of the characteristic species served as unfailing guides (Braun-Blanquet, 1925, p. 138). To find a well-developed Piceetum in the alpine valleys, it is necessary only to seek out a place from which *Listera cordata*, *Pirola uniflora*, and *Lycopodium annotinum*, the characteristic species of the association, have been recorded.

On the other hand, surprising discoveries often result from careful study of fidelity, such as the presence of *Sibbaldia procumbens* in the Tatra (Pawlowski) or of *Polygonatum officinale* in the oak scrub of the Gelting peninsula (W. Christiansen).

The use of characteristic species for classification of communities will be discussed in another connection.

Characteristic Combinations of Species.—The characteristic species together with those of the highest degrees of constancy, *i.e.*, species present in at least 60 per cent of the stands compose the complete combination of species characteristic of the community. As a rule, a single example of an association will not include all of the characteristic species nor all of the species of high constancy. From the association tables may be deduced which of these species, on the average, will occur in a well-developed example. Thus average characteristic and more or less constant species taken together compose the normal characteristic combination of species. The larger the ratio of the number of constant species to the total number of species the more uniform is the association; the larger the ratio of characteristic species the more sharply the association is characterized floristically or ecologically. Those associations are best established which fulfill both conditions.

Procedure Recommended for Making Records of Vegetation and Constructing Association Tables.—The following example is taken from a vegetation record of a pure beech wood between Krüzenbühl and Hohenkrähen, Hegau, South Germany—date: June 8, 1927. This high forest lies on a non-calcareous morainal terrace (high terrace gravel), sloping eastward at 580 m., and is utilized by selective cutting. On this account there are two facies of undergrowth. The facies dominated by *Carex pilosa* in the more open places has a light ratio (*Lichtgenuss*) of ¼ to ⅓. The *Asperula odorata* facies in the denser places has a light ratio of only 1⁄12. In the *Asperula* facies tree tops eight-tenths closed, cover 4. On 500 sq. m. there is an average of eight beeches, sixty to eighty years, 15 to 20 m. tall, slender, branches beginning at 8 to 10 m. Epiphytic societies fully developed, not examined. In *Asperula* facies a 100-sq. m. homogeneous sample is marked off and investigated:

1. Relief: very slight, 2 deg., sloping eastward.
2. Soil: leaf cover 2 to 5 cm., then 20 to 30 cm., of mild humus with earthworms (Lumbricidae). Soil profile exposed and sketched in notebook. From each principal root layer 200 to 400 g. of soil is collected in numbered bag. The profile serves as a record of root layering.
3. Height of the different layers and cover of each layer in the sample are determined and recorded.
4. Species lists and numerical values in the 100-sq. m. area are arranged as follows (shrub layer absent):

HERBACEOUS LAYER

A soc.[1]	
3 · 4	*Asperula odorata* (fr.).
2 · 2	*Veronica chamaedrys.*
1 · 1	*Anemone nemorosa* (parasitized by *Puccinia fusca*).
1 · 1	*Ajuga reptans* (fl.).
+ · 1	*Milium effusum.*
+ · 2	*Festuca heterophylla* (fl.).
+ · 1	*Poa nemoralis.*
+ · 2	*Carex silvatica.*
+ · 2	*C. digitata* (fr.).
+ · 1	*C. pilosa.*
+ · 2	*Luzula pilosa.*
+ · 2	*L. nemoralis* (fl.).

A soc.	
+ · 1	*Majanthemum bifolium* (fl.).
+ · 1	*Neottia nidus avis.*
+ · 1	*Viola silvestris.*
+ · 1	*Hedera helix.*
+ · 1	*Epilobium montanum* (fr.)
+ · 1	*Phyteuma spicatum.*
+ · 1	*Galeobdolon luteum.*
+ · 1	*Veronica officinalis* (fl.).
+ · 1	*Solidago virga aurea.*
+ · 1	*Marasmius* spec.
+ · 1	*Boletus* spec.

SPECIES WITH LOW VITALITY[2]

+ *Epilobium angustifolium*^{0}.
+ *Stachys silvatica*^{0}.
+ *Scrophularia nodosa*^{0}.
+ *Taraxacum officinale*^{0}.

SEEDLINGS

2 *Fagus silvatica.*
several *Picea excelsa.*
1 *Quercus pedunculata.*
1 *Prunus avium.*

MOSS LAYER (SCANTY)

+ · 1	*Fissidens taxifolius.*
+ · 1	*Eurhynchium schleicheri.*
+ · 1	*Brachythecium velutinum.*
+ · 1	*Tortula subulata.*

The soil is about two-thirds covered with vegetation. Outside the 100-sq. m. area occur also in the *Asperula* facies covering about 800 to 1,000 sq. m.:

Tree layer: *Fraxinus excelsior* (one specimen).

Shrubs: *Rosa arvensis* (+ · 2). *Crataegus monogyna*^{0} (+ · 1), etc.

Herbs: *Poa chaixii, Polygonatum multiflorum,* etc. (all + · 1), etc.

Mosses: *Catharinea undulata, Brachythecium salebrosum, Mnium stellare, Polytrichum formosum.*

Development: The stand represents the climatic climax, much modified by man. Regeneration is by natural reproduction of beech in the more open places (*Carex pilosa* facies), caused by cutting (or natural death) of old trees. In large openings there is danger of reduction to an herb stage by dense crowding of *C. pilosa,* which hinders forest reproduction.

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[1] *A* = abundance and constancy (see p. 34); soc. = sociability; fr. = in fruit; fl. = in flower.

[2] See explanation page 46.

TABLE 4.—ASSOCIATION TABLE FOR THE ELYNETUM OF THE CENTRAL ALPS

Number of stand examined	East Grisons													South Tirol		Constancy class
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Ecological characteristics:																
Size of stand, square meters	—	4 (10)	—	1 (4)	6	4 (20)	4 (20)	4 (100)	1 (c.20)	4 (40)	4 (50)	4 (50)	50 to 100	4	1 (c.4)	
Altitude, meters	2,400	2,400	2,330	2,520	2,600	2,500	2,570	2,460	2,550	2,600	2,590	2,600	2,750	2,440	2,560	
Exposure	W.	S.	E.	—	—	W.	SE.	Level	NW.	SW.	SW.	SW.	E.	SE.	W.	
Slope, degrees	c. 5	0	0 to 5	0	0 to 5	5	5	0	5	5 to 10	0	5 to 10	5 to 10	5 to 10	0	
Wind exposure	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	Exp.	
Duration of snow cover, months	0 to	0	0 to	Short	0 to	0 to	0 to	1 to 2	0	0 to	0 to	0 to	Short	0 to	Short	
Rock of substratum	Rhetic	Raibl	Dolom.	Dolom.	Rhetic	Serp.	Limestone	Dolom.	Rhetic	Rhetic	Rhetic	Rhetic	Talus	Dolom.	Dolom.	
Thickness of fine soil	—	—	5 to 10	—	—	10 to 20	—	—	—	10 to 12	5 to 10	c. 15	—	—	5 to 10	
Water content of soil, per cent	—	7.7	13[1]	—	—	7.6	5.0	4.5	6.4	7.8	8.7	7.6	—	—	—	
Humus in root horizon, per cent	—	27	52	51	—	35	27	22	33	34	50	31	—	—	—	
pH of root horizon	—	6.7	6.2	6.2	6.1	6.0	6.0	5.8	5.8	5.7	5.6	5.5	—	—	—	
Floristic composition. Characteristic and dominant species:																
↑[2] *Elyna myosuroides*	4·3	4·3	3·3	4·3	4·3	4·3	3·3	4·3	4·3	4·3	4·3	4·3	4·3	4·3	4·3	V
Dianthus glacialis	—	—	—	—	—	(+)[4]	—	—	—	—	—	—	1·2	—	—	I
Draba siliquosa	—	—	—	—	+	+	+	(+)	—	+	+	+	+	1·1	(+)	IV
Carex capillaris var. *minima*	+	1·2	1·2	—	+	+	—	1·2	1·1	+	+	+	+	+	+	V
C. atrata	—	—	+	+	+	1·1	(+)	1·1	+	+	+	+	+	—	—	IV
Cerastium alpinum var. *lanatum*	—	—	—	—	(+)	(+)	(+)	+	—	—	(+)	—	—	—	—	II
Arenaria ciliata ssp. *tenella*	1·2	+·2	+·2	+	+	+	—	+	+	(+)	+	+	—	1·2	+	V
Saussurea alpina	+	—	1·1	+	1·1	—	+	1-2·1	1·1	1 to 2·1	1·1	1·1	+	—	—	IV
Erigeron uniflorus	+	(+)	+	+	+	(+)	—	+	(+)	+	+	+	+	+	+	V
Gentiana tenella	—	—	+	—	—	1·1	+	+	+	—	(+)	(+)	—	—	—	III
Viscaria alpina	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	I
Characteristic species of the Alliance: [3]																
↑ *Festuca pumila*	2·2	1·2	+·2	+·2	1·2	1·2	2·2	2·2	1·2	1·2	2·2	2·2	1·2	+·2	(+)	V
↑ bas.[5] *Sesleria coerulea* var. *calcarea*	1·2	1·2	2·2 to 3	+	1·2	+	(+·2)	+·2	+·2	+·2	(+·2)	1·2	—	1·2	2·2	V
↑ *Carex rupestris*	+	+	1·1 to 2	+	1·1	+	+	—	1·1	+	+	+	1·1	1·1	(+)	V
bas. *Minuartia verna* var.	1·1	+	+·2	+	+	+	—	—	+	—	(+)	+	+	+	—	V
bas. *Gentiana verna* var.	+	+	+	—	+	—	(+)	(+)	+	(+)	—	+	—	+	+	IV

bas. *Pedicularis verticillata*	+	+	1 · 1	–	+rr	–	+	–	–	–	(+)	–	–	–	(+)	III
bas. *Leontopodium alpinum*	–	+	+	–	+	+	–	–	–	+	–	–	–	+	–	II
bas. *Carex firma*	+	+	–	–	–	(+rr)	–	–	–	–	–	–	–	–	–	II
bas. *Sedum atratum*	+	–	–	(+)	–	–	–	–	–	–	–	(+)	–	–	–	I
bas. *Helianthemum alpestre*	+	–	+	–	–	(+)	–	–	–	–	–	–	–	–	–	I
Characteristic species of the Order:[7]																
Potentilla crantzii	1 · 1	–	1 · 1	–	+	+	1 · 2	1 · 1	+	+	1 · 1	+	1 · 1	1 · 1	1 · 1	V
bas. *Oxytropis campestris*	–	1 · 2	1 · 2	–	+	–	+	(+)	–	(+)	+	(+)	1 · 2	+	+	IV
bas. *Hedysarum obscurum*	–	–	+	–	+	–	–	–	+	(+)	(+)	(+)	–	–	1 · 1	III
Aster alpinus	–	+	+	–	+	+	(+)	–	–	+	–	(+)	–	1 · 1	–	III
Indifferent and neutrophilous companion species:																
Polygonum viviparum	+	+	1 · 1	–	+	1 · 1	+	+	+	1 · 1	–	+	+	1 · 1	1 · 1	V
Silene acaulis	+ · 2	+ · 2	+ · 2	+ · 2	+	+	–	(+)	(+)	(+)	+ · 2	+ · 2	1 · 2	+	–	V
Antennaria carpatica	1 · 1	–	+	1 · 1	+	–	(+)	(+)	+	1 · 2	(+)	(+)	+	1 · 1	+	V
Carex ericetorum	1-2 · 1	+	+	+	+	+	(+)	+	(+)	+	+	–	+	–	–	IV
Ligusticum simplex	–	–	1 · 1	(+)	+	1 · 1	+	(+)	+	1 · 1	+	+	–	+	+	IV
Campanula scheuchzeri	+	–	1 · 1	(+)	+	(+)	–	1 · 1	+	+	1 · 1	+	–	+	+	IV
Agrostis alpina	–	1 · 2	2 · 2	+ · 2	+	+	–	+ · 2	–	+	+	1 · 2	–	+	–	IV
Gentiana brachyphylla	+	–	1 · 1	–	+	+	–	(+)	+	(+)	+	+	–	–	+	IV
Poa alpina	+	–	–	–	+	+	1 · 2	(+)	+	+	+	+	–	–	–	III
Gentiana nivalis	+	–	+	–	–	+	(+)	+	(+)	+	+	(+)	–	–	–	III
Anemone vernalis	–	–	+	+	+	(+)	–	–	–	–	(+)	+	+	+	–	III
bas. *Draba aizoides*	+	(+)	–	(+)	+	–	–	–	–	–	(+)	+	–	+	+	III
Lloydia serotina	–	–	–	–	+	1 · 1	1 · 1	+	–	–	+	+	+	–	–	III
Alchemilla colorata	+	–	+	–	+	–	–	–	(+)	+	1 · 2	+	–	–	–	III
Selaginella selaginoides	–	+	+	(+)	(+)	–	–	–	+	–	(+)	–	–	–	+	III
Galium anisophyllum	+	(+)	+	–	–	–	–	–	(+)	–	–	+	(+)	–	–	II
Minuartia sedoides	–	–	–	–	–	(+)	(+)	+	–	–	–	–	–	+	+	II
Gentiana campestris	–	–	–	–	+	–	–	+	–	–	(+)	(+)	–	–	–	II
Botrychium lunaria	+	–	+	–	(+)	–	–	–	–	–	+	–	–	–	–	II
Carex sempervirens	–	–	–	–	+	–	(+)	–	–	–	–	–	–	+ · 2	1 · 2	II
Salix serpyllifolia	+	(+)	–	–	–	–	–	–	(+)	–	–	–	–	–	+	II
↑ bas. *Dryas octopetala*	+ · 2	–	1 · 2	–	(+)	–	–	–	(+)	–	–	–	–	–	–	II
bas. *Veronica aphylla*	–	–	+	–	(+)	–	–	–	+	–	–	–	–	–	+	II
Acidophilous species (from the Caricion curvulae):																
Avena versicolor	–	(+)	–	+	–	1 · 1	+	–	(+)	(+)	1 · 1	(+)	+	+	(+)	IV
Luzula spicata	+	–	+	–	–	(+)	+	–	(+)	+	+	(+)	1 · 1	–	–	III
Euphrasia minima var. *minor*	–	–	+	–	–	(+)	(+)	+	(+)	+	+	(+)	–	+	–	III

TABLE 4.—ASSOCIATION TABLE FOR THE ELYNETUM OF THE CENTRAL ALPS.—(*Continued*)

	Number of stand examined	East Grisons													South Tirol		Constancy class
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
	Androsace obtusifolia	–	–	–	(+)	+	–	–	–	(+)	(+)	–	+	+	–	(+)	III
	Veronica bellidioides	–	–	–	+	–	–	+	–	(+)	+	1 · 1	+	–	–	–	III
	Phyteuma hemisphaericum	–	–	–	–	+	–	–	+	+	+	1 · 1	+	–	+	–	III
↓	*Sesleria disticha*	–	–	–	–	–	–	(+)	+ · 2	(+)	1 · 2	(+)	+	1 · 2	–	–	III
↓	*Carex curvula*	–	–	–	–	–	–	–	(+)	–	(+)	(+)	(+)	1 · 2	–	–	II
	Hieracium glanduliferum	–	–	–	–	–	+	–	–	–	–	(+rr)	–	+	+	–	II
↓	*Festuca halleri*	–	–	–	–	–	–	1 · 2	–	–	–	1 · 2	+	+	–	–	II
	Potentilla aurea	–	–	–	–	–	(+)	–	–	(+)	–	–	–	–	–	–	I
↓	*Agrostis rupestris*	–	–	–	–	–	–	–	(+)	–	–	(+)	–	–	–	–	I
	Leontodon pyrenaicus	–	–	–	–	–	–	–	(+)	–	–	(+)	–	–	–	–	I
Moss layer:																	
	Cetraria islandica var. *crispa*	1 · 1	1 · 1	1 · 1	+	+	1 · 1	1 · 1	1 · 2	1 · 1	+	+	+	1 · 1	1 · 1	+	V
	Cladonia pyxidata	+	+	+	+	+	+	–	+	+	+	+	+	+ · 2	1 · 2	+	V
	Thamnolia vermicularis	–	+	1 · 1	–	+	+	+	+ · 2	1 · 1	+	+	+	+	+ · 2	–	V
	Cetraria nivalis	–	+	1 · 1	–	+	+	+	+	1 · 1	+	+	+	+	–	–	IV
	C. cucullata	1 · 1	–	1 · 1	–	–	1 · 2	+	1 · 2	–	(+)	+	(+)	2 · 2	1 · 1	+	IV
	C. juniperina	–	+	–	–	+	(+)	+	–	–	+	(+)	(+)	1 · 1	+	–	III
	Peltigera rufescens	–	(+)	–	+	+	+	+	–	–	–	+	(+)	–	–	–	III
	Cladonia silvatica	–	+	–	2 · 2	+	–	+	–	–	–	–	–	2 · 1	–	–	II
	Rhytidium rugosum	–	+	+	–	+	+	+	(+)	+	+	–	–	+	1 · 2	–	IV
	Tortella tortuosa	1 · 2	+	+	+	+	–	–	–	(+)	(+)	(+)	+	–	–	–	III
	Polytrichum juniperinum	–	(+)	–	+	+	–	+	–	–	+	(+)	+	+	–	–	III

[1] Heavy figures indicate averages from many determinations.

[2] ↑ = constructive for Elynetum; ↓ = destructive for Elynetum.

[3] Including species from other associations of the same alliance, Seslerion coeruleae.

[4] Figures in parentheses are for species outside the stand.

[5] bas. = basophilous species.

[6] rr = Only one to two specimens.

[7] Of the Seslerietalia coeruleae.

Epiphytic Communities.—The structure of epiphytic communities has been critically studied by Ochsner (1928). On one tree are often found several associations under different external conditions, so that the following relations should always receive attention:

1. Species of the host plant, exposure (in the open or not), human intervention.
2. Height of tree, width of crown, height to first branch, diameter of trunk or circumference 1 m. above soil, form of stump (base).
3. Course of water from the crown (centrifugal or centripetal); in mountains, average depth of snow.
4. Character of bark: thickness, physical peculiarities (smooth, rough, furrowed, etc.), water capacity.
5. Collection of humus on the host plant.
6. Height and exposure of the epiphytic society.

According to Ochsner, trees show four well-defined parts, which correspond to four different habitats (Fig. 40):

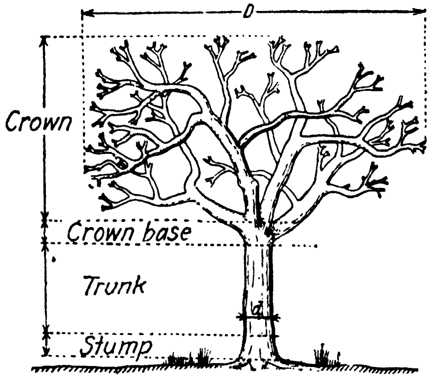

FIG. 40.—Habitats of epiphytic communities on trees. (*After Ochsner.*)

a. Crown, in the crotches of which humus often collects.

b. Crown base, protected from direct sunlight in exposed trees and therefore also more moist than the middle of the trunk.

c. Trunk, the middle part, which in open stands is exposed to wind and sun (Fig. 41).

d. Stump, where the vegetation catches the water that runs down, and retains it longest.

In the investigation of the structure of the association it is sufficient to record the cover and perhaps the vitality of the species.

Association Tables.—The absolutely necessary foundation of every critical study of communities is the "association table." At the head of the table is placed the most precise possible statement of the ecological characteristics of each sample (stand). Such a statement reduces the requirements for ecological description in the text and establishes the ecological resemblances of the communities. These, unfortunately are too often based more on an inner feeling than upon exact investigation. An assurance is also gained that the ecological investigations really refer to a definite floristically circumscribed community. In the preparation of the tables many a relationship becomes clear; and only on the basis of adequate tabular material can conclusions be drawn concerning the relationships of the social units. For ecological characterization we consider also the record of the boundary of the single stand.[1]

FIG. 41.—A climax epiphytic community on the trunk of *Quercus mirbeckii* at Djebel Bir, Tunis; consisting of mosses, *Polypodium vulgare*, *Umbilicus pendulinus*. *Stellaria apetala*, and *Cardamine hirsuta*. (*Photo by Hueck.*)

In all cases where an examination of a small sample plot is included with the floristic record of the stand, this should be mentioned specially; in the table the species found only in the larger area are placed in parentheses. The size of both areas should be given. From the same column one may read both the record of the definite small plot (which need not be square) and the entire record of the homogeneous stand. The graphic representation of the foregoing specimen table of the Elynetum (Table 4) is given in Fig. 168.

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[1] In the text of a report there should also be noted the course of the boundary (distinct, indistinct, rectilinear, wavy) and the arrangement of the individual stands (whether zonal, mosaic, in broad plains, etc.).

Analysis of Floating Communities and of the Phytoedaphon.—With plankton, as with higher plants, communities may be characterized by density, dominance, sociability, vitality, layering, periodicity, constancy, and fidelity. The definitions given for communities of higher plants may be carried over to the plankton communities (*cf.* Allorge, 1922; Denis, 1925, pp. 68–73; Steiner, 1925; Huber-Pestalozzi, 1925).

Phytoplankton.—Density and dominance of plankton can be only approximately given by net catches and may be expressed in words or figures (1 = very rare; 5 = very abundant, dominant). More exact results are obtained by collecting samples in flasks, so that the plankton is not concentrated by filtration. Immediately after taking, 50 to 100 cc. of the fluid is fixed with formalin. Before examining, the sample is carefully stirred up, and 1 cc. at a time is counted in a Kolkwitz plankton chamber. The number of organisms and species present is reckoned per liter of water. Obviously this method is useful only where the density of individuals is rather high.

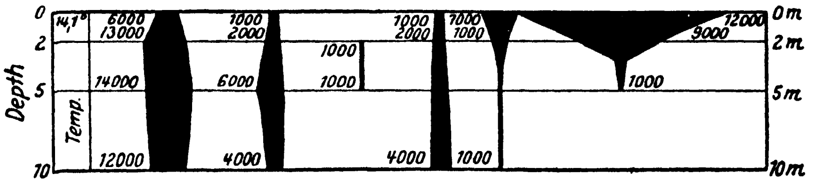

FIG. 42.—Plankton stratification in Lake Zurich near Rapperswil, Oct. 17, 1924. Number of individuals or of colonies per liter of lake water.

With plankton organisms the aggregation of individuals into groups and colonies is not unusual and must be considered (*Dinobryon* bunches, *Oscillatoria* threads, *Tabellaria* colonies, floating gelatinous masses). Messikommer has made use of a scale of 6 deg. to express the amount of sociability of plankton organisms.

Denis (1925, p. 72) considers it also very important to note the vitality and stage of development of the species (vegetative condition, zoospores, aplanospores, etc.). According to him, vitality and abundance of algae are most intimately connected. Layering also plays a special rôle in plankton. To show this, a block diagram is found useful (Fig. 42).

Since the recognition of the importance of plankton for aquatic life in the sea and larger inland waters, the study of its periodicity has been vigorously pursued. It is expressed in the same manner as layering. Graphs may express the annual and seasonal variations (Fig. 43). The question remains open as to how far these annual variations are true aspect phenomena and how far they represent the replacement of one community by another.

The differences in dominance from one year to another are primarily traceable in these communities to differences in precipitation. During the extraordinarily dry year 1921 in Europe (288-mm. rainfall) there occurred a great outburst of Protococcales and a reduction of Desmidiaceae. In the following year (804-mm. rainfall) the relations were reversed and the desmids greatly predominated.

For the development of plankton communities the temperature of the water, its salt content, its acidity, and its nutritive content are of decisive importance. Upon this last factor Thienemann (1926) distinguishes three great types of continental waters: dystrophic, with Sphagnum and Desmidiaceae, water rich in humus with acid reaction; eutrophic, poor in humus, often rich in calcium, with a broad zone of rooted plants, including *Phragmites*, *Potamogeton*, Cyanophyceae, and many other forms; and oligotrophic, distinguished quantitatively from the eutrophic, possessing only a narrow zone of rooted forms because of the rapidly deepening waters (*cf*. Ström, 1928).

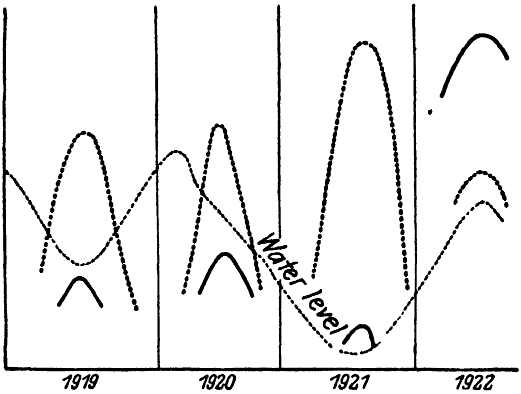

FIG. 43.—Annual fluctuations in total plankton in a pond near Fontainebleau. Solid line, Desmidiaceae; dotted line, Protococcales. (*After Denis*.)

Phytoedaphon.—The quantitative investigation of the edaphon and aeroplankton is still in its infancy, and one must be content to get by means of the culture methods of the bacteriologists an approximate idea of the great wealth of species of the air and soil floras. The number of organisms per gram of soil as reported by many investigators must be taken with much reserve. By culture under determined artificial conditions certain organisms will naturally be favored and will develop rapidly. At the same time other species which perhaps were originally very abundantly present may fall behind or be wholly suppressed by the luxuriant growth of competitors.

The fungus vegetation of the soil also changes in the course of the year and exhibits a species maximum at the beginning of the warm period and a minimum in the winter. Moreover, the soil fungi, mostly saprophytes, seem not to differ appreciably in the different grass associations of the coastal area of eastern England. Elliot (1930), who studied these conditions, found the same soil fungi in the Glycerietum maritimae and in the Armerietum; and even the soil of the Salicornietum showed the same soil flora with the exception of two species (*Chaetomium spirale* and *Macrosporium commune*). The floristic composition of the soil fungal vegetation was examined by means of single spore cultures.

A vibration method has been used by Whittles (1923) for counting soil bacteria. In the vibrator vessel the organisms are freed from the colloids which normally surround them. Thereafter the colonies grow rapidly and in four days reach their maximum, which is much more than would be expected from previous methods.

On the seasonal variations in bacterial content of the soil and the relation of bacterial development to that of their destroyers, the Protozoa, Cutler, Crump, and Sandon (1922) have given interesting data.

PART III

SYNECOLOGY OR COMMUNITY ECONOMICS

CHAPTER V

CLIMATIC FACTORS

Studies of the structure of vegetation are likely to fail in their object if not accompanied by a search for the underlying causes of the social union and the mutual dependence of the component plants. This research into the household economics of the community is the function of synecology.

The serious study of the problems of synecology is now at its very beginning, because the chief interests of most ecologists have centered in autecology, the life relations of the individual plant. Autecology can be studied in gardens, plant houses, and laboratories, but the problems of synecology must be investigated in the open, under natural conditions.

The impossibility of separating the various factors that are operative in nature greatly hampers these studies. Those investigators who regard synecology as the foundation of phytosociologic classification and, indeed, of the whole structure of plant sociology, must not forget how insecure that foundation still is. Wholly new problems and fundamental changes of viewpoint have come forward recently with surprising suddenness, especially in the field of synecology.

Synecology is inseparably bound to the concept of the plant community. The fathers of geobotany, Heer, Lecoq, Sendtner, and Kerner, sought to understand the basic causes of the social relation of certain plants. In Sendtner's classic "Vegetationsverhältnisse Südbayerns nach den Grundsätzen der Pflanzengeographie" (1854) not less than 136 pages are devoted to the influence of climate and soil on vegetation. Kerner's "Pflanzenleben der Donauländer' (1863) was epoch making. In glowing terms it brought even to the layman an understanding of the relation of the principal plant communities of Austria-Hungary to the environment.

The most important landmark in the development of synecology since Heer was Warming's textbook of ecologic plant geography published in 1895 in Danish, 1896 in German, 1909 in English. It is an inexhaustible mine of trenchant observation and fertile suggestion. Here for the first time the social life of plants was presented from the standpoint of the influence of species upon one another. Attention was also directed to the competition between species and communities.

The last two decades have brought a great increase in the number of synecological studies, especially of those concerned with agriculture and forestry. Ecologic stations have been established, and it looks as if plant physiologists wished to emerge from the confinement of their autecological studies and enter upon the study of the household economics of communities. Such a deepening of interest in synecology is undoubtedly one of the most urgent demands of modern plant sociology.

In the first chapter it was pointed out that for an adequate understanding of plant communities three causal complexes must be considered.

1. Historical factors, summarized under paleosyngenetics, paleosynecology, and paleosynchorology. These historical factors have been responsible for the plant populations of the earth's surface and thus have made possible existing combinations of species, genera, and families.
2. Competition, as outlined in Chap. I.
3. Operative measurable factors of the habitat.

These are the forces that really determine communities, govern competition, and from the infinite number of possible combinations of species bring about the selection of a relatively limited number.

The operative factors of the habitat which are essential for the ecologic description and characterization of associations are best considered under four heads:

1. Climatic or atmospheric factors.
2. Edaphic or soil factors.
3. Orographic or topographic factors.
4. Biotic factors or the effects of the living environment.

Each group of factors may be considered separately, with its effects upon the plant covering of the earth. We must not, however, overlook the fact that in nature we always meet not a single factor but a whole complex of them. The single factors have manifold interrelations, and the influence of each factor depends upon the whole congeries of factors. These interrelations of factors have received little attention, little synecological consideration, although they offer a rich field for investigation. The establishment, however, of any orderliness based on definitely known conditions, the elaboration of any positive substitution of one factor for another represents an advance for science and leads to a better understanding of the prodigious complexity of the social life of plants.

When a plant community, an association, or a subdivision of it is recognized and floristically circumscribed, the investigation of the habitat and habitat factors must be undertaken. Obviously such investigations can have a general application only when carried out in several or many representatives of the association (individual stands) in different localities. Isolated measurements have little value, and that only for comparison. For the measurement of climatic factors which change rapidly from time to time (light, heat, humidity, etc.) continuous observations in one habitat are necessary. Self-registering apparatus as used by American investigators is very desirable.

1. TEMPERATURE[1]

Sunlight, the most important source of energy for organic life, either is absorbed by the plant directly as heat, or functions as light by being transformed into potential chemical energy. The heat and light of the sun are due to different groups of rays. Light rays belong mostly to the blue-violet part of the spectrum, while the most potent heat rays lie in the yellow and red parts (Fig. 44).

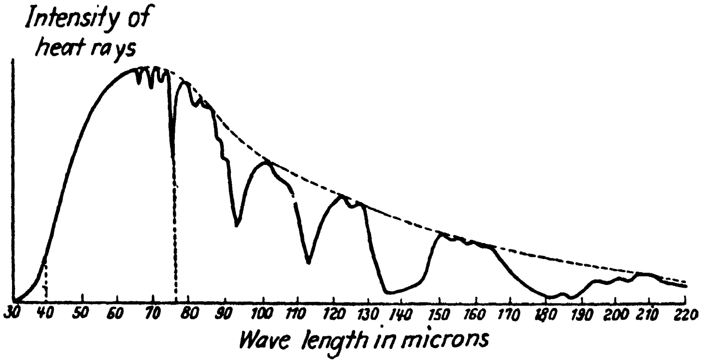

FIG. 44.—Distribution of energy (heat) in the normal spectrum of sunlight. (*After Langley.*)

According to Langley (*cf.* Hann 1908), however, the maxima of heat and light in the spectrum fall rather close together. In passing through the atmosphere the short-waved blue rays are more dispersed than the long-waved red rays. Whole groups of waves, moreover, at the red end of the spectrum are completely absorbed by the atmosphere and serve to heat the air. This is important for the temperature economy of plants, since the radiation of heat by the plant body is thus reduced.

Absorption and Radiation of Heat.—The heat of the sun on a clear day at noon amounts to about one gram calorie[2] per square centimeter at sea level or about two gram calories at high altitudes. In its passage through the atmosphere more than 50 per cent of the energy from the

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[1] The centigrade scale is used throughout this volume in all temperature measurements.

[2] The amount of heat required to raise one gram of water from 0° to 1°C.

sun is absorbed. The ecologically effective solar heat consists of the total income of heat minus that lost by radiation. The curves in Fig. 45 show the total solar energy, with average clearness of sky, in high mountains and in the Swiss lowlands.

Direct solar radiation is measured by the use of the black-bulb thermometer in a vacuum tube. Unfortunately this instrument has various inaccuracies. The most serious is due to radiation from neighboring objects, which cannot be measured. At best the black thermometer gives only a very inadequate idea of the amount of heat actually imparted to the vegetation, for the latter is influenced both by the intensity of solar radiation and by the capacity for absorption of the illuminated parts of the plant.

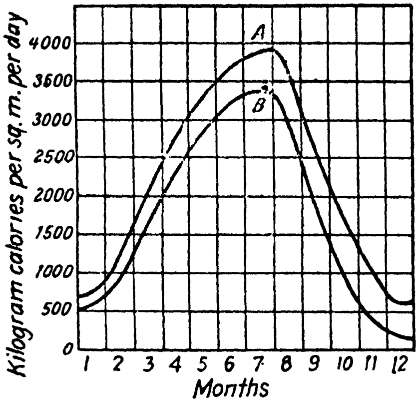

FIG. 45.—Solar energy with average clearness of sky in the high mountains (*A*) and in the northern valleys (*B*) of Switzerland. (*After Maurer.*)

The outgo as well as the income of radiant energy differs according to both time and place. Radiation (outgo) in middle latitudes, under clear skies, at night, reaches 0.12 to 0.15 gram calorie per square centimeter and is influenced by the depth of the atmosphere and its humidity. Radiation is most marked just above the surface of the earth. Hellmann (*Sitzb. Berliner Akad. Wiss.* 38: 1918) at Potsdam found a mean annual difference of 1.80°C. between the temperatures 5 cm. and 2 m. above the ground. At Vienna the official thermometer 1.5 m. above the ground stood higher than the one just above the turf by 3.5°C. in April, 4.0°C. in May, and 2.5°C. in summer (Hann, 1911).

The mean minima at the surface of the ground and 1.5 m. above on sod ground at Montpellier (France) were −8° and −5.4°C. in January, 1914. This explains how, in arid climates, water may freeze when the temperature at the height of a man's head is several degrees above zero centigrade.

The climatological measurement of nocturnal radiation is made by means of a minimum thermometer placed on bare ground and almost covered with earth. Or it may be placed horizontally just above a covering of short grass. The difference between the minimum temperature on the ground and 1.5 m. above gives a measure of the intensity of radiation. Such measurements have only rarely been made. They would throw light on many peculiarities of vegetation in regions with cold winters and little snow. The minima of the surface of the ground furnish an important selective factor for the sensitive seedlings of trees and shrubs.

Temperature Graphs.—In order to determine the amount of heat which plant communities actually receive, it is necessary to have self-registering apparatus in the habitat.[1] The problem is complicated by the fact that, strictly speaking, each layer of vegetation has its own peculiar temperature requirement. The upper layers influence the lower, making the climate more equable.

G. Kraus (1911) carried out minute (though not self-registering) determinations of the air temperature of the habitat in the Wellenkalk region of Würzburg. From his data we have confirmation of the well-known fact that air temperature even in a very small area is subject to great local variation and often to very sudden changes. Bühler (1918) has given us temperature graphs throughout the year for several layers of vegetation in an economically important forest community.

Maxima and Minima.—The influence of extreme temperatures is more readily demonstrable than the relation of communities to the general range of temperature or to definite means. Excessive heat coagulates the protoplasm. Extreme cold kills the plant by precipitation of the proteins. By the formation of ice within the plant, water is withdrawn from the cells, and as a result an irreversibie coagulation of the colloidal substances of the protoplasm takes place. Such results from frost are much more frequent than mechanical injury from ice crystals rupturing the tissues. The sociological effect is a reduction in the ability of the species for competition. Long-continued damage from frost or heat or frequent repetition of lesser injury may put one species at a disadvantage and thus favor a less sensitive competitor.

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[1] For aquatic communities ordinary measurements have given useful suggestions. Next to calcium content, water temperature is one of the most important factors in the composition of aquatic communities. In the *Bryum schleicheri-Philonotis seriata* flora of the springs of Feldberg in the Black Forest *B. schleicheri* dominates where the water temperature is 4 to 5°C. in early summer, but *P. seriata* where it is 7 to 8°C. Otherwise the habitats are alike, and the companion flora identical.

Examples are seen in the north and in high mountains. In the cold and relatively snowless winter (in Europe) of 1924–1925, many low shrubs, like *Empetrum*, *Arctostaphylos uva ursi*, and *Vaccinium uliginosum*, suffered severe frost injury on naked, unprotected places in the eastern Alps. In 1925 their growth was decidedly reduced. The alternating but less sensitive areas of *Loiseleuria procumbens* and tufts of *Festuca halleri*, however, suffered hardly at all. They grew luxuriantly the next summer and extended their territory at the expense of the frost-bitten low shrubs.

The duration of low temperatures seems often as important as the degree of frost. Shreve (1914) has shown that the giant cactus, *Cereus giganteus*, will survive 19 hr. exposure to a temperature of −8.3°C. but is killed if this temperature persists for 29 hr. or longer.

Injury from extremes of temperature is enhanced by other unfavorable factors. For example, the low winter temperatures of high mountains and the far north have increased biological effect on account of strong drying winds. The high summer temperatures of subtropical deserts are combined with intense light, radiation from the bare ground, and extreme drought. In such cases it is wholly futile to attempt to evaluate the effect of the temperature factor alone. Injury to protoplasm by heat coagulation very rarely occurs in nature, except in the case of fire. Heat and drought usually work together, and the latter often deals the death blow.

In central and southern Europe the winter minima seem often to reach the threshold of sociological importance. But this needs more precise determination. Communities of gregarious evergreen shrubs and trees, such as *Cistus* spp., *Buxus sempervirens*, *Ilex aquifolium*, *Rubia peregrina*, and *Quercus ilex*, would be favorable objects for study (Fig. 46). Besides the absolute minima, the duration and distribution of minimum temperatures are important. Late frost is so harmful because it catches the plant in full activity, at a time when the sugar of the tissues is mostly converted into starch. Foresters and agriculturists are therefore especially interested in the limits of the frost period and the number of frosty days.

Frost Pockets.—Especially unfavorable temperature conditions may result from lack of air circulation and accumulation of cold, stagnant air in valleys and troughlike depressions. The frost pockets (*Frostlöcher*) of the southwestern Swiss Jura are well known and shunned. Similar conditions cause the *Sèches*—shallow troughs which, although in the midst of the forest zone at 1,000 to 1,300 m., are entirely treeless and at best covered with unshapely dwarf spruces, which yield to neither ax nor saw. The spruce branches are beset with hundreds of thousands of short twigs, so crowded together that one can hardly push an alpenstock into the tangle. The temperature of these *Sèches* is much below that of surrounding areas. In June, and again in August, there are many frosty days with minima from −1° to −6°C. Pillichody (1921) published temperatures for three years taken in the frost pocket of La Joux near Les Ponts (1,100 m.). The mean minimum of the week Feb. 20 to 27, 1901, was −29°C. in the frost pocket; in the high forest just south, only −14°C. Even in the second half of May a mean minimum of −5.1°C. was found; and from June 19 to 25, one of −2°. In the same week of June the mean minimum in the bordering high forest was 4.6°C.

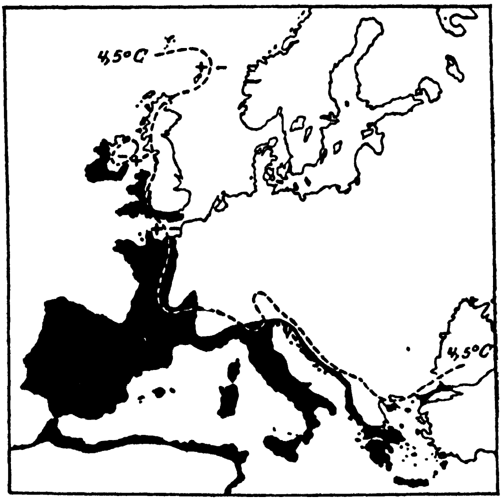

FIG. 46.—The January isotherm of 4.5°C. and the distribution of *Rubia peregrina*. (*After Salisbury.*)

Temperature Inversions.—Another phenomenon due to stagnation of cold air in valleys is the temperature inversions on mountains in midwinter. Very striking is the difference between the truly Siberian winter temperatures of the forested valleys of the Oberengadine and the surrounding naked passes and mountain ridges. In the winter of 1905 Saint Moritzbad (1,780 m.) had minima of −36° and −38°C. More than 500 m. higher, at Bernina (2,310 m.), the extreme minimum was −24°C. Hence it follows that the upper limit of the forests of *Picea, Larix,* and *Pinus cembra* in the Alps is certainly not due to low winter minima. Besides, in northern Siberia larch forest (*Larix sibirica*) withstands temperatures of −70°C.

Temperature inversions in the Santa Catalina mountains of Arizona have been shown by Shreve (1912) to be due to cold-air drainage.

Streams of cold air, 15 to 25 m. deep, flow down the radial mountain canyons. By virtue of these streams the minimum temperature conditions of canyons and other topographic depressions, below elevations of 2,000 m., are equivalent to those of ridges and slopes which are 600 m. higher up.

Protection from Cold.—The ability to endure low temperatures depends upon the specific constitution of the protoplasm and also upon the physiological condition of the plant. Hence the well-known fact that one and the same plant has very different degrees of resistance to frost at different times. Since Lidforss' classic researches on wintergreen plants (1907) an important function has been ascribed to sugar as a protection to the colloids of protoplasm.

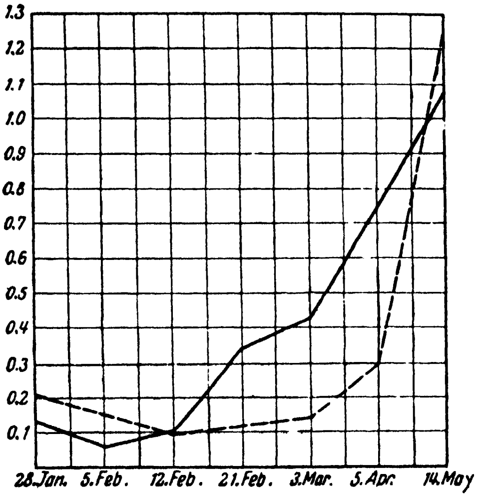

FIG. 47.—Ratio of starch to sugar in winter and spring. Solid line, *Arbutus menziesii;* broken line, *Stellaria media.* (*After Rigg.*)

The presence of a non-electrolyte like glucose reduces the danger of protein precipitation. Leaves of plants in the cold season, though under the snow, show little or no starch. The carbohydrates are all in the form of sugar, and in hardy leaves very considerable amounts of sugar may have accumulated. This has the property of preventing the coagulation of the albuminous parts of the protoplasm at low temperatures. Sugar is therefore to be regarded as a protective substance. The further the transformation of sugar into starch advances the more sensitive to cold will be the protoplasm. As shown in Fig. 47, sugar predominates over starch in the leaves of *Arbutus menziesii* and *Stellaria media* from January to May, but in

May starch gains the ascendancy. This change in form of the carbohydrates greatly influences the hardiness of the leaves.

As long ago as 1727 Hales, discussing the injury to plants by cold, said, "Oil is an excellent preservative against the injuries of cold"; and more recently Harvey (1930) has discussed the chemical reasons for such protection. Not only do such northern trees as species of *Pinus*, *Betula*, and *Prunus* form oil from carbohydrates during the autumn and winter, but in such genera as *Linum*, *Helianthus*, and *Cannabis* the same species show higher oil content in lower as compared with higher temperatures. The action of the oil seems to be concerned with the maintaining of the fluid condition of the protoplast at low temperatures.

Temperature Changes.—Changes of temperature are the more dangerous to plants the more suddenly they occur. Adjustment to gradual changes of temperature is possible within limits (*cf.* Harvey, 1918). In nature there is generally a sharp distinction between hardy communities which withstand large changes of temperature and those which are restricted to a narrow range. To the first class belong the Loiseleurietum cetrariosum of ridges exposed to wind, the Caricetum firmae, and the Elynetum. These withstand −30° to −40°C. in winter without injury, while on clear summer days the surface soil is heated to 50°C. or more. The thickets of *Rhododendron* and *Vaccinium* of the Rhodoreto-Vaccinion are communities confined to narrower amplitudes of temperature.

Schade (1917) reported the extremes of temperature to which a patch of *Pohlia nutans* was subjected during five years, in the Teufelsschlüchten of Elb sandstone mountains, on a northeast slope. This plant, fully exposed to the sun, endured without harm an annual range of temperature of 66.5°C. (maximum 56.8°, minimum −9.8°C.). The temperature of a liverwort sod (*Leptoscyphus taylori*, *Calypogeia neesiana*, *C. trichomanoides*, *C. media*, *Odontoschisma denudatum*, etc.) on a shaded rock face was much more equable. The annual range was only 23° (maximum 17°, minimum −6°). Two local climates of quite opposite nature here stand side by side.

It is naturally much easier and more satisfying to work out such contrasts than to determine with painstaking care the optimum temperature relations of a definite plant community.

Influence of Vegetation upon Temperature of Air.—Vegetation tends to moderate the temperature. This equalizing effect increases with number and height of the layers. Under communities of two or more layers the extremes of temperature are nearer together: the maxima are lower, the minima higher than in the open. Hence the common observation that individuals and communities of less hardy plants occur under the protection of trees and shrubs and are the more restricted to this protection the nearer they come to the limits of their range. Thus in the Rocky Mountains of Colorado many comparatively delicate plants, such as *Polemonium pulcherrimum*, *Pedicularis grayi*, *Adoxa moschatellina*, and *Pirola secunda*, reach their altitudinal limits under the protection of a layer of alpine spruce and pine at 3,500 m.

This need of protection is very pronounced in the case of *Ilex aquifolium* and *Daphne laureola* in their outposts in the alpine foothills, whereas *Ilex* stands completely in the open in oceanic western Europe and becomes a magnificent tree. In southern Europe the mouse thorn, *Ruscus aculeatus*, and *Viburnum tinus* react similarly. If they are exposed by lumbering operations, they freeze out in regions with winter minima of −7 to −8°C.

Temperature in the Forest.—An abundance of data on temperature in forests and in the open is given in Mütterich's annual reports of observations of the forest meteorological stations. Mean temperatures from records of 18 years at 17 different places in Germany give 2.2°C. less range of temperature in the forest than in the open. The mean maximum was 1.6° below, the mean minimum 0.6° above the simultaneous readings in the open. In spruce forest the daily range was 2.6°; in pine woods, 1.9°C. less than in the open.

The mean annual temperature, according to the observations of Bühler (1918), is lower in forest than in the open: in spruce wood 0.9° to 1.3° lower; in beech wood, 0.1° to 0.7°C. Temperature of the lower layers of air is influenced by soil temperature: it is cooler under the trees in summer and during the day, warmer in winter and during the night, than in the open. Stebler and Volkart (1905, p. 76) found similar conditions under separate fruit trees. In February and March they found night temperature near the ground 1.0° to 2.0°C. higher under fruit trees than in the open. For this reason and also on account of the absorption of radiant energy by trees, every tree and, still more, every stand of trees forms in winter a local center of warmth. This explains also why the snow melts sooner in orchards and the grass greens earlier under the trees than elsewhere.[1]

Sociologically the habitat under protection of fruit trees forms a sharply bounded inclusion within the central European Arrenatheretum elatioris grassland. The floristic peculiarity of this protected plant community (*Gagea lutea-Corydalis cava* association) is

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[1] The rapid melting of the snow is favored by the drip from the branches, which makes the snow denser and therefore a better conductor of heat.

especially marked by bulb and rhizome geophytes, such as *Arum maculatum, Allium ursinum, Leucojum vernum, Scilla bifolia, Tulipa silvestris, Gagea lutea, Muscari botryoides, Ranunculus ficaria, Anemone nemorosa, Adoxa moschatellina.* These tender species distinctly show the locally warm conditions under fruit trees in the great Alpine valleys (Rhine valley, Rhone valley, etc.).

The daily range of temperature in the deciduous forest and the neighboring dry grassland at Bellinchen, on the Oder, is shown by the curves in Fig. 48.

Temperature and Periodicity.—Attempts to obtain summations of heat from weather bureau data and to relate them to definite life processes of plants—leafing out, flowering, fruiting—have long been made. Boussingault (1837) found the sum of the mean temperatures above zero for the duration of the life process of plants under consideration. A. P. de Condolle selected for each species of plant a specific zero point for the beginning of his reckoning. Merriam (1898) made summations of temperature from daily means above 6°C. Aside from the fact that these summations should be made from temperatures of the habitat and not from weather bureau records, the very inadequate results of these methods cannot throw much light on the question.

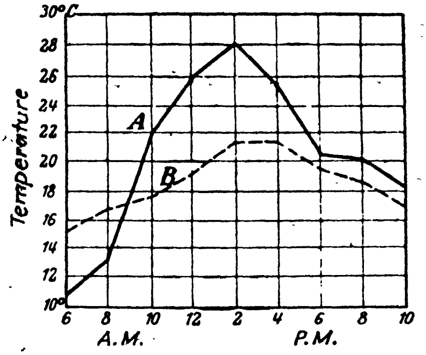

FIG. 48.—Daily temperature range in a deciduous forest (*B*) and in a closely adjacent dry grassland (*A*) in Bellinchen, July 17, 1925. (*After Hueck.*)

On the other hand, the so-called phenological charts with curves connecting places where plants are in the same stage of development at the same time express the climate of a region very well and are useful in forestry and agriculture.[1] There is no doubt that the periodic phenomena of vegetation rest fundamentally upon the relation of the

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[1] The phenological charts of Novak and Simek (1926) for Moravia and Silesia are excellent examples.

species to the daily and seasonal march of temperature (*cf.* McCrea, 1924).

McCrea has made minute investigations of the relation of flowering to temperature in northern England and has expressed the results by graphs (Fig. 49).

In most plant communities two or more distinct flowering "aspects" may be recognized.

In the California chaparral the species are grouped according to time of flowering into five distinct aspects. The first group blooms in January and February with a mean minimum of 5° and a mean maximum of 10°C. The second follows in April and May (mean minimum 10°, mean maximum 15°); the third in June (mean minimum 15°, mean maximum 20°); the fourth in July (mean minimum 20°, mean maximum 25°); and the fifth in September with a mean minimum of 25° and a mean maximum of 30°C. The individual waves of bloom released by increasing heat appear at regular intervals, according to Setchell (1925), separated by a difference of about 5°. Graphic expressions of succession of bloom in various associations of western Switzerland are given by H. Gams (1918). The sociological side of the study of aspects has been discussed on an earlier page (47).

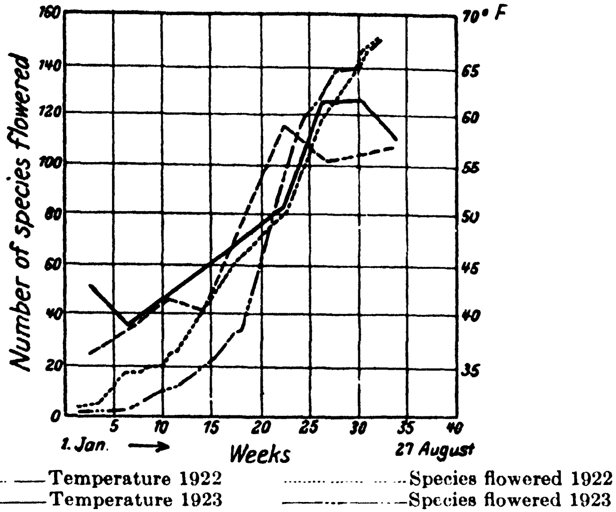

FIG. 49.—Number of species of plants which had flowered and the temperature curve for the north of England for the first 40 weeks of the years 1922 and 1923. (*After McCrea.*)

Isotherms and Boundaries of Vegetation.—The exact relation between the boundaries of vegetational areas and temperature has often been sought. Especial emphasis has been placed upon the position of certain isotherms. These attempts have usually overlooked the fact that boundaries of vegetation can be uniform and comparable only when based upon the occurrence of a definite plant species or upon a well-defined plant community. For example, the much discussed tree line, or limit of forest, is not, biologically speaking, based on uniform and equivalent data, since each of the tree species which helps to form the boundary has its own ecologic reactions.

Proposals for characterizing climates according to temperatures and correlating them with conspicuous species or boundaries of vegetation have been offered by Merriam (1894), Vahl (1911), Samuelsson (1915), Brockmann-Jerosch (1919), Enquist (1924), and Livingston and Shreve (1921).

Merriam (1894) states that the northern range of organisms is determined by the sum of the positive temperatures for the entire season of growth but that the southern limit is due to the mean temperature of a short period at the hottest time of year. This concept has been modified by Livingston and Shreve (1921) by recognizing that the efficiency of a degree of temperature for plant growth varies much in different parts of the temperature scale.

Enquist (1924) considered of first importance the extremes of temperature and their duration. These determine the boundaries of vegetational areas. He distinguished between the heat requirement which bounds an area on the colder side and the cold requirement which bounds it on the warmer side. In the first case a certain maximal temperature and a certain minimal temperature must be exceeded during a definite number of days. In the second case a definite number of days with a certain maximal temperature and a definite number with a certain minimal temperature must not be exceeded. The cold limit of the beech is attained where less than 217 days reach maxima above 7°C.; that of the holly, *Ilex aquifolium*, where less than 345 days have maxima above 0°.

Temperature Zones.—Next to mean annual temperature the most important temperature factor for determining the general character of vegetation is the annual range of temperature. Mean annual temperature, dependent upon the distance of an area from the equator, determines the beltlike arrangement of the great vegetational zones of both hemispheres and on the slopes of mountains. This fundamental arrangement, however, suffers many variations and displacements, because of variations in temperature due to the position of the great continental land masses. The mean temperatures gradually decrease from the equator to the poles, but the range of temperature increases. The range also increases very widely and rapidly from the seacoast to the interior of the continents (Table 5). In the interior the decrease of temperature toward the poles is more rapid than on the coasts. Large bodies of water have an equalizing effect, since the surface water is somewhat cooler than the air at low latitudes and considerably warmer at higher latitudes.

TABLE 5.—DIFFERENCE BETWEEN THE MEAN TEMPERATURES OF THE COLDEST AND WARMEST MONTHS OF THE YEAR
(After Hann)

	Degrees Centigrade
Valentia, Ireland	7.8
Münster, Westphalia	16.0
Warsaw, Poland	23.0
Orenburg, Russia	36.9
Irkutsk, Siberia (490 m.)	39.2
Nerchinsk, eastern Siberia (600 m.)	51.8

From the above it clearly follows that the temperature zones must be divided in two directions. The simple classification of de Candolle is:

Megathermic, the zone of warm climate.
Xerophilous, dry regions.
Mesothermic, warm temperate climates (mean annual temperature 15° to 20°C.).
Microthermic, cold temperate climates (mean annual temperature 0° to 14°C.).
Hekistothermic, cold climates.

This arrangement does not do justice to the actual conditions. Even with subsequent changes, the scheme gives only a very general and superficial basis for the arrangement of zones of vegetation according to temperature. Following De Martonne, but also taking into consideration oceanic and continental influences, it seems necessary to recognize the following latitudinal zones: equatorial (without dry season), tropical (with a dry season), subtropical, warm temperate, cold temperate, subarctic, and arctic. These are subdivided into oceanic, suboceanic, median, subcontinental, and continental regions (*Gebiete*). From the standpoint of temperature, the daily and annual range of temperature determines the oceanic or the continental character of the climate.

On this basis, the climate of north central Siberia is subarctic-continental, the eastern Mediterranean region is subtropic-subcontinental, and Great Britain is mostly cold temperate-oceanic. In characterizing these climates, humidity and cloudiness must be included (*cf.* p. 106). McDougall (1925) has attempted to express temperature and humidity of climate graphically (Fig. 50), and

Livingston and Shreve (1921) have plotted the moisture-temperature divisions of the United States from scanty data but with considerable success.

Ocean Currents and Wind.—The temperature of a land mass is greatly influenced by ocean currents and winds. Currents like the Gulf Stream, which flow poleward, bring water from warm seas and transmit their heat to the overlying air. Ireland is indebted to the Gulf Stream for her colonies of Mediterranean plants such as *Arbutus unedo* and *Rubia peregrina* and for her Tertiary relicts of mosses and liverworts. This distribution is paralleled by the presence of *A. menziesii* and *Quercus garryana*, members of the broad sclerophyll forests of California, on Vancouver Island, due to the warm currents of the Pacific. The Gulf Stream also makes possible the advance of tender Atlantic species and communities as far north as western Norway and the Faroe Islands (Fig. 51). Its "Atlantic waters," very rich in plankton, at Iceland still have a temperature of 11° to 13°C.

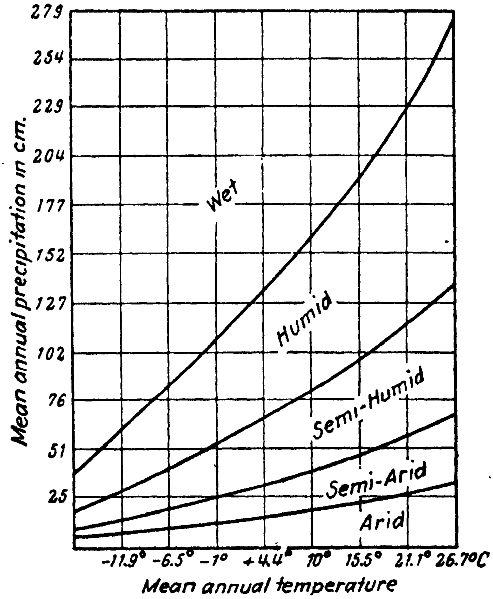

Fig. 50.—Climatic humidity based on precipitation influenced by temperature. (*After McDougall.*)

Cold ocean currents reduce the temperature of adjacent coastal regions. The southwestern and northwestern coasts of Africa are thus cooled, with corresponding effects upon vegetation. The east Greenland current, poor in plankton, lowers the temperature of the sea water by 1° to 5°C.

The effect of wind upon temperature and vegetation is sometimes favorable, sometimes unfavorable. In western Siberia the icy north wind reduces the temperature several degrees, but the warm southwest

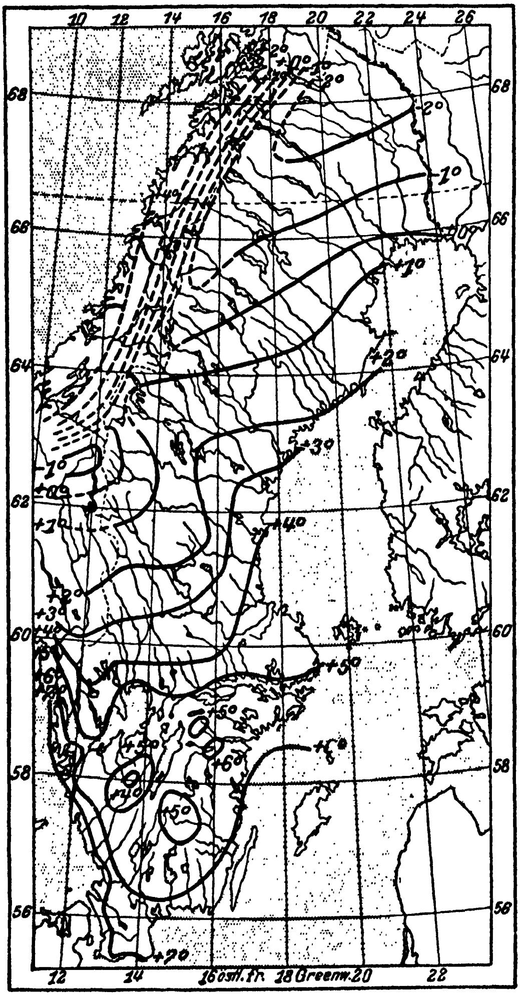

FIG. 51.—Effect of the Gulf Stream upon the mean annual temperature of Scandinavia. (*After Hamberg.*)

wind raises it. Descending winds (*Fallwinde*) may be markedly cooling (mistral, bora) or warming (foehn, chinook). The warm foehn gives a southern aspect to the vegetation of many a mountain valley on the north slope of the Alps (Christ 1879; Hager 1916; Schmid, 1923). This wind gives to the valleys of Linth, Reuss, and

and *Cassia marylandica* in flowerless condition for eight years under conditions of short-day illumination. Controls flowered each year under the influence of the full length of the summer day at Washington, D. C. The sedums, in which flowering had been suppressed for eight years of short-day illumination, flowered in an apparently normal manner when they were exposed to long-day illumination.

These investigators conclude that:

> A wild plant in its natural invasions from an original center of occurrence must find itself subjected to the factor of length of day during the growing season as well as to other climatic and soil conditions. If its distribution depends upon successful seed production, its limits of distribution must depend largely upon those conditions of summer-day length favorable to successful flowering and the production of fertile seed. Whether it can maintain itself in a region unfavorable to flowering would depend upon whether natural methods of vegetative propagation are at its disposal and whether sufficient nutrition reserves can be maintained to support healthy growth in the plants from year to year.

FIG. 56.—*Rudbeckia nitida* showing responses to different lengths of day. The plant ceases flowering with a light day somewhere between 14.5 and 14 hr. long. The control with a light day nearly 15 hr. long flowered perfectly; days of 14, 13.5, and 13 hr. allowed the development of leafy rosettes only. (*Photo by Allard, courtesy of U. S. Department of Agriculture.*)

Measurement of Light Intensity.—Methods of measuring light are discussed in detail by Wiesner (1907), Rübel (1922, 1928), Braid

(1923), Lundegårdh (1930), Morton (1927), and Klugh (1927). Physically unimpeachable methods of measuring light are so complicated that they are not available to the plant sociologist. Approximate and comparative measurements can be had by the photographic-paper method of Wiesner, which is still generally used. It depends on the darkening of a sensitive silver chloride paper. Vouk and Eder-Hecht have elaborated the method of Wiesner. The Graukeil photometer of Eder-Hecht, as now used, serves for determining both the momentary light intensity and the summation of light for definite periods of time. It can be had at a reasonable price, with instructions for use and accessory equipment from the Photographische Industriegesellschaft Herlango, Vienna. Lundegårdh has constructed a self-registering apparatus for measuring light.

Intensity of light is measured by exposing a sensitive paper to the light for a definite time and comparing the resulting coloration with a standard. Bunsen and Roscoe give as unity the intensity that gives the standard color in one second.

The absolute illumination of a habitat is expressed as a fraction whose denominator is the number of seconds required to produce the standard color ($\frac{1}{5}$ = 5 sec. exposure).

The relative light requirement (*Lichtgenuss* of Wiesner) is the relation of the light intensity of the habitat to full sunshine measured at the same time. This is also expressed as a fraction. Relative light requirement of $\frac{1}{3}$ signifies that the light of the habitat is one-third that of full sunlight.

On account of the great and often sudden changes in intensity of light, absolute measurements in a definite habitat or in a definite plant community (average summation of light) are useful only when continuously registered. This may be accomplished, to a certain extent, by the use of a pair of Livingston's atmometers: one with a white bulb, the other with a black, mounted side by side. All factors influencing the rate of evaporation from the two instruments are the same except that radiant energy is absorbed by the black bulb only.[1] The resulting rise in temperature increases the evaporation of water from the black atmometer. The difference in the water loss of the two atmometers thus gives a measure of the amount of radiant energy during the period of exposure.

The measurement of relative light intensity in two adjacent habitats gives useful results when accomplished by means of a simple photographic apparatus like "Wynne's infallible exposuremeter." The relative light requirement may be approximated by single simul-

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[1] A very small amount of radiant energy is absorbed by the white bulb.

taneous observations in two adjacent habitats such as within and without a forest (Fig. 57). By observing the time required for the paper to reach the normal shade under the trees and in full sunlight the results may be expressed as a fraction or as a percentage.

The decrease of light under different layers of a forest of *Betula* in North Germany is given by Hueck: in the open, 100 per cent; under the tree canopy at 150 cm. above the soil, 34 per cent; under the *Pteris aquilina* layer at 39 cm., 4 per cent; under the *Vaccinium myrtillus* layer at 5 cm., 0.7 per cent; and under the *Vaccinium* only a few small mosses were growing (*cf.* Zon and Graves, 1911).

In an effort to measure with relative accuracy the different parts of the visible spectrum, Klugh (1925) has devised an instrument in which panchromatic photographic plates are exposed beneath a set of neutral percentage filters. After development, the results from the exposures at lower intensities are read against those from exposure at the highest intensity, and the readings expressed directly in percentages. Klugh (1927) has also presented an excellent critical review of methods in ecological photometry.

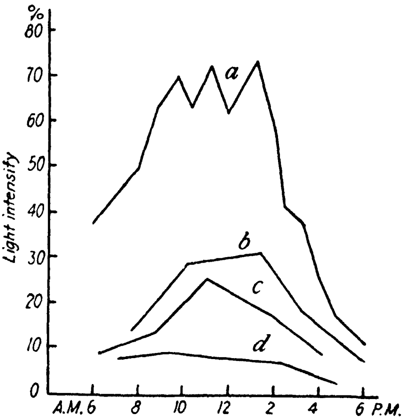

FIG. 57.—Simultaneous light curves made on May 23 in the open (*a*); in the forest under *Alnus* (*b*); under *Quercus* (*c*); under *Fagus* (*d*). (*After Vallin.*)

Light Climates.—It is well known that shade plants of the south, or of the lowlands, may grow wholly in the open farther north or on mountains. Their light requirements change with latitude and altitude. Light measurements such as Wiesner (1907) made for *Betula alba, B. nana, Acer platanoides,* and other species in Central or northern Europe and in the arctic show that the minimum light requirement increases rapidly from south to north. It was 1/55 for *A. platanoides* in Vienna, 1/37 in Hamar (Norway), 1/28 in Drontheim, 1/5 in Tromso. From this

Wiesner concluded that the light requirement of a plant is greater the nearer it approaches its polar boundary, but it must not be forgotten that Wiesner's method measured heat rays along with light.

The light climate of the far north is characterized by a great uniformity in the intensity of the light and by its increased duration. The intensity of direct sunlight is low, because of the low altitude of the sun. The importance of diffuse light, however, increases greatly from the tropics to the poles. The ultra-violet radiations unfavorable to plants are greater toward the poles than in Central Europe or in the United States. In consequence, the boreal and arctic plants possess adaptations against too intense and too prolonged insolation. These consist of reduced chlorophyll content, red and yellow pigments in cell wall and in cell sap, and waxy coverings which reflect the light (Lippmaa, 1929).

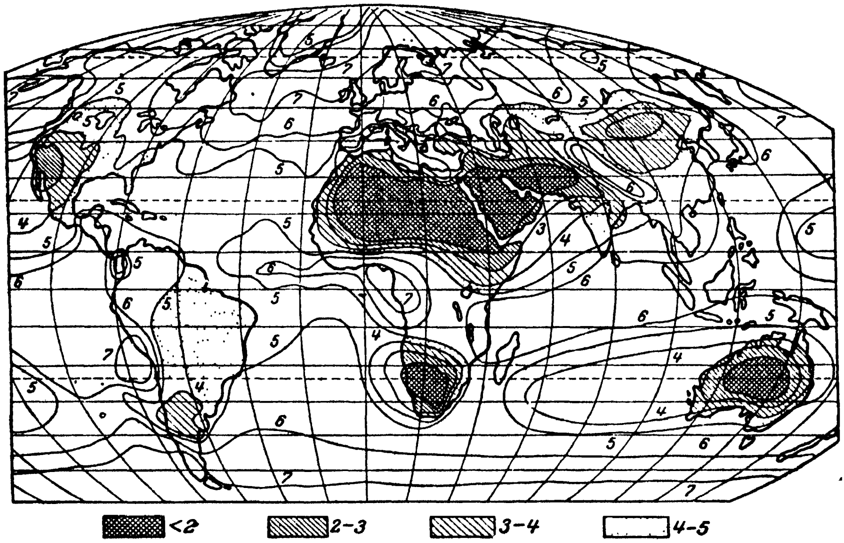

FIG. 58.—Mean annual cloudiness. Degrees of cloudiness 1-10. (*After Szymkiewicz.*)

The greatest intensity of direct sunlight as compared with diffuse light is found in the equatorial zone. Hence in this region the effect of light upon vegetation is most pronounced. In the deserts and steppes of the subtropics the total light is not so strong as would be supposed (Rübel, 1910). This is doubtless due to the dust content of the air, which is seldom cleansed by rain. But in these regions the summation of light reaches significant values because of the very slight cloudiness. The mean cloudiness at 60° N. lat. is 61 per cent; at 30° N., 42 per cent, at the equator 58 per cent; at 30° S., 46 per cent; at 60° S., 75 per cent. The extreme cloudlessness of arid regions is still better shown in Fig. 58.

The extremes of light intensity in cloudless arid regions are not very great. The plants of deserts and steppes are not injured either by too much or by too little light. Shade vegetation plays here a negligible part.

On account of the great transparency of the air on mountains, total light increases with altitude while diffuse light decreases. The greatest light intensity ever observed—2,083 Bunsen units—was measured by Wiesner (1907) at Old Faithful in Yellowstone National Park (over 2,000 m.) under a cloudless sky (altitude of sun 50° 47′).

Snow by reflection considerably increases the light supply to exposed vegetation. From frozen snow as much as 89 per cent of the incident light may be reflected (Rübel, 1912, 1928). On account of the cloudiness of mountain regions, plants receive more diffuse than direct light, in spite of the fact that direct light increases and diffuse light decreases with altitude.

Significance of the Light Factor for Plant Sociology.—The individual plant performs its life processes within a certain range of light intensities. Similarly, plant communities have their definite light requirements, depending on locality (latitude, altitude, exposure, slope, covering), on their position in relation to other communities or layers, on length of growing season, and on duration of the snowless period.

Just as there are heliophytes (light plants) and sciophytes (shade plants) corresponding to extremes of light, so also light- and shade-loving communities are recognizable. All one-layered communities and the uppermost portions of many-layered communities in regions with low or medium cloudiness are termed heliophilous. Their optimum light requirements are full sunlight. Submerged aquatic vegetation, many communities of steep northern slopes, of rock crevices, and of caverns; the late-appearing communities of arctic and alpine snow-land; many epiphytic communities; and in general the lower layers of stratified communities, whose light requirement decreases from upper to lower, are designated as sciophilous. Even leafless upper layers may intercept large amounts of light. On Mar. 27, at noon, Wiesner measured 0.166 Bunsen unit in the shade of the leafless trees of a mixed deciduous forest, near Vienna, whereas the total light in the open measured 0.712 unit. The rôle of light in the forest was critically studied by Cieslar (1904) and by Park (1931). Malta (1921) has emphasized the importance of light in the control of associations of bryophytes.

Studying the vegetation of Lapland, Lippmaa (1929) noted the influence of light on the formation of red pigments in different groups of plants. He constructed a phytochromatic spectrum and demonstrated that certain color types have their maximum in certain definite plant communities. The maximum of red pigmentation, corresponding to the greatest insolation, was in the dwarf-shrub associations, which also contain the minimum of species that show distinctly green pigmentation. He insists that there is also a marked agreement between the phytochromatic spectrum and the anatomy of the species of each group studied.

The annual light curve under a cover of evergreens runs rather evenly. In the several-layered deciduous forest communities the ground layer experiences a well-lighted and favorable springtime (vernal-flora aspect), followed by a period of low light intensity caused by the maximum of the foliage and having a maximum development of summer shade plants (Fig. 59). In beech woods and other deciduous forest communities with deep shade the annual rhythm of vegetation is most intimately connected with the course of the light curve.

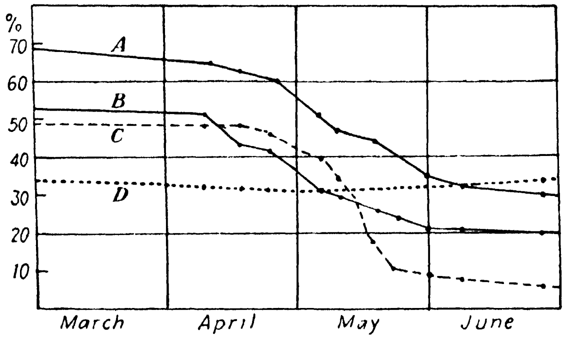

FIG. 59.—Decrease in the light intensity in the lower layers with the advance of the season and the unfolding of leaves (*A*) in birch forest with *Vaccinium* undergrowth; (*B*) in *Alnus glutinosa* forest; (*C*) in *Fagus silvatica* forest; and (*D*) in *Pinus silvestris* forest.

The relative minimum of light, that is, the light requirement of the most feebly illuminated assimilating leaves, is nearly constant at the same latitude but decreases toward the poles. The minimum for the larch is $\frac{1}{5}$, for the beech $\frac{1}{60}$ to $\frac{1}{80}$ of the total light in the open. According to Hesselman (1917), the light requirement of trees on poor soil is greater than that on good soil.

The relative light minimum may become a deciding factor in the competition between two plant communities with different light requirements. The literature of forestry and of plant sociology furnishes many examples. As a rule, the tree layer that has the lowest relative light requirement wins. In many parts of central Europe *Fagus silvatica* forms the victorious tree layer; in mountains, *Picea excelsa;* in southern Europe, *Quercus ilex*—all species with small light minimum. In north central United States (Minnesota) the *Abies balsamea-Picea canadensis* forest, giving the densest shade, triumphs over all other plant communities as the climatic climax. Somewhat farther south *F. grandifolia, Acer saccharum,* and *Tsuga canadensis* together form the beech-maple-hemlock climax forest. The relative light intensity, a quantity related to the relative light minimum, was graphically represented by Lee (1924) for several forest types in Minnesota (Fig. 60).

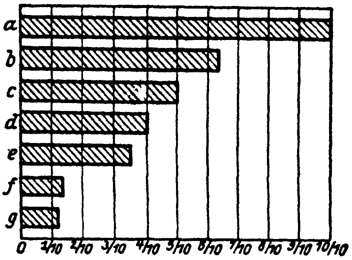

Fig. 60.—Relative light intensity in different forest types in Minnesota: *a*, mature *Pinus banksiana* forest; *b*, mature *P. resinosa* forest; *c*, mature *P. strobus* forest; *d*, young *P. resinosa* forest; *e*, young *P. banksiana* forest; *f*, pure deciduous forest; and *g*, mature *Abies-Picea* forest. (*After Lee.*)

The arrangement of forests according to light intensity corresponds in general to their order in the succession.

Brown (1919) studied the significance of the light factor in the origin of plant communities in the Philippines. MacLean (1919) made significant studies of the light relations in the virgin forests of southern Brazil, finding that the light distribution was very uneven. The available light under the many-layered canopy averaged about 1/140, but sunny spots at times received as much as 1/8. Usually the shrub layer cast the densest shadow, since its close leaf mosaic intercepts more light than the filmy upper canopy in which the fine leaflets of the Mimosaceae predominated.

In central European forests, plants may bloom in 1/90 of total light, and fruit in 1/160 (Kästner). Sterile plants and seedlings seem to thrive in caves with much less light. Mosses extend their range to 1/2,000 (*Leskeella*); Algae such as *Gloeocapsa* and *Protococcus*, to about 1/2,500. *Adiantum capillus veneris* was found by Morton (1927) in the Quarnero caves at 1/1,700. In that case it seems that higher temperature can to some extent compensate for lack of light.

Submerged vegetation of lakes and seacoasts shows a pronounced zonation due to light (*cf.* p. 246). Pearsall (1917–1918) has traced the light zonation of the communities of higher plants in the English lake district (Fig. 61). In this region the *Nitella flexilis* association endured the least illumunation. In Lake Constance, Zimmerman (1927) found the following distribution of algae primarily dependent upon light: the *Spirogyra adnata* association to a depth of 10 m.; the *Cladophora profunda-Chamaesiphon incrustans* association between 10 and 20 m.; and the *Hildenbrandtia rivularis-Bodanella lauterborni* association from

20 m. to a depth of 35 m. The individual associations were very sharply delimited.

Linsbauer (1905), Klugh (1925), and Oberdorfer (1928) have constructed special apparatus for measuring light under water. Linsbauer found in clear mountain lakes at a depth of 1 m. 19 per cent of the total light above water; at 5 m., only 1.4 per cent.

Plant communities of snow-land require very small amounts of light, but on exposed snowless ridges and in equally bare rock clefts the Potentillion caulescentis, Androsacion multiflorae, etc., have a very high light requirement. According to the investigations of Rübel (1912) at the Bernina Hospice (2,300 m.), the old shrunken snow cover lets very little light pass through. Loose, powdery, fresh-fallen snow, however, allows at least 1/2,000 of the total light to penetrate to a depth of 50 to 80 cm. Communities like the Salicetum herbaceae or the Polytrichetum sexangularis, which are not exposed until July, have therefore a very small annual light requirement. When in spite of these facts green foliage is found under a meter of permanent snowbank (*cf.* Braun-Blanquet, 1913), the question arises whether this may not be due to a prolonged storage of chlorophyll.

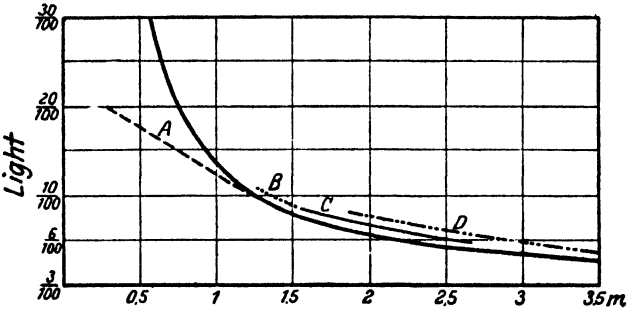

FIG. 61.—Light intensity at various depths of water and the distribution of association in the Esthwaite, England. *A*, Litorelletum; *B*, *Myriophyllum alterniflorum* association; *C*, Isoetetum; *D*, *Nitella flexilis* association. (*After Pearsall.*)

3. ATMOSPHERIC CARBON DIOXIDE

Under natural conditions plants obtain carbon dioxide from both the soil and the atmosphere. As carbon is one of the chief constituents of all organic substances, its absorption from the air plays a notable rôle in the gas exchanges between plants and the atmosphere. The assimilation of carbon dioxide by the forest is very considerable and is subject to decided variations. The ordinary amount of atmospheric carbon dioxide averages 0.03 per cent, but under the cover of trees the lower layers of the air may reach a concentration of 0.08 per cent. This high percentage of carbon dioxide compensates, to a certain extent, for the low light intensity of the forest floor.

Gut (1929) found in general a diminution of the carbon dioxide content of the forest atmosphere during the early hours of the day, a slight increase in the afternoon, which generally continues into the evening, and a restoration to the normal by the "respiration" of the soil during the night. In the deciduous forest there is sometimes a decided but transient increase in the carbon dioxide content toward evening, which might be explained by the accumulation of the products of metabolism in the leaves to the extent that it hinders the rate of further carbon assimilation. In the forest the lowest content of atmospheric carbon dioxide, as well as its greatest variations, occurred in the spring; in the autumn its highest content was reached.

It is impossible at present to estimate the ecological importance of carbon dioxide and its variations. It seems certain that the normal atmospheric content of carbon dioxide represents a minimum rather than an optimum amount for plants. The determinations of its variations are still too fragmentary to have great ecological value. It must suffice to call the attention of phytosociologists to the possible importance of this factor.

The determinations of Lundegårdh in the Swedish oak forests, confirmed by Gut, show that the carbon dioxide content of the air is subject to greater fluctuations in the beech than in the pine forests. It therefore appears that in the deciduous forest the gas exchanges are more active but there is a slower rate of growth.

The sources of atmospheric carbon dioxide are combustion; the respiration of man, animals, and plants; volcanic emissions; and the gases arising from the sea and from the soil.

Determination of Carbon Dioxide Content of the Air.—Of the numerous methods for the determination of the carbon dioxide content of the atmosphere the only one that appears to be practicable for phytosociologists is the volumetric method of Gut. Even this is complicated and difficult. For details the reader is referred to the description by Gut (1929, pp. 18–29).

4. WATER

Water is the plenary agency that sets in motion the nutrients of the soil and makes them available to plants. More than any other factor of the habitat, water affects the inner and outer morphology of those plant organs that together determine the physiognomy of vegetation. In the large, water causes the divisions within the vegetational zones of the earth due to temperature. On a smaller scale, it regulates the structure and arrangement of plant communities. Even the slightest differences in water supply are clearly shown in the accompanying vegetation.

Moisture, as a climatic habitat factor, is determined by the amount, duration, and seasonal distribution of the precipitation as rain or snow and by the humidity of the air.

Soil moisture will be considered in connection with edaphic factors.

A. PRECIPITATION

The water economy of the plant aims at an equality between income and outgo of water, between absorption and transpiration. The water requirement is generally met by rain and dew, precipitating the water vapor of the air in liquid form. Hoarfrost and hail, though only occasional, are harmful to vegetation. It is quite otherwise with snow. The effect of snow upon the forms of vegetation in the cold and cool-temperate regions has been rightly appreciated only within the last few decades.

Rainfall.—Next to the distribution of heat the annual distribution of rain is the most important factor for the general character and periodicity of vegetation. The longer and more intense the dry season the more obvious is the tendency of vegetation to complete its chief development during the rainy season. In Europe the difference between the sharply periodic wet and dry climate of the Mediterranean region and the rainy climate of the Atlantic region with its evenly distributed precipitation is conspicuously expressed in the vegetation. In the Atlantic region luxuriant evergreen meadows, Ericaceae heaths, and broom thickets (*Ulex, Sarothamnus, Genista*) are continuously photosynthetic. In the Mediterranean region, with its spring and autumn vegetative periods separated by dry summer and winter, we have the dull colors of the broad sclerophylls and therophytes (Fig. 62). Eastward and southward the rain periods of the autumn and spring seasons converge into an autumn-winter rain period (southern Italy, northern Africa).

As we approach the great desert plateaus of Africa and Asia, the summer drought becomes more intense and the winter rains more sparse. Here the beginning and the end of the yearly cycle of vegetation are bound up with the duration of the winter rains. In the desert, at the limits of life, a few halophilous chamaephytes and emphemeral therophytes wait for years in a drought rigor only to shoot forth in an hour into new life with the vivifying rain.

Contrasts in Precipitation.—The sharpest known boundaries of vegetation are formed by high mountain chains lying across the course of the rain-bearing winds. The windy side catches the precipitation; on the other side there is a minimum of rainfall. The Limagne in the shadow of the Mont Dore of Auvergne, the low plains of the upper Rhine east of the Vosges, the eastern slopes of the Scandinavian mountain plateau are relatively dry spots in "rain shadows." The peculiar xeric vegetation of the deep inner valleys of the Alps represents a minimum of rainfall between two pronounced maxima.

Anyone who has traveled across the Alps between Berne and Domo d'Ossola, or between Bolzano and Bregenz, will certainly remember the sudden change of vegetation on entering and on leaving the great longitudinal valleys of the Central Alps. In the humid outer ranges, on both sides, beech wood and mixed deciduous forests with abundant epiphytic lichens and mosses grow luxuriantly in the resulting moisture from the two maxima of rainfall. Within the valleys (Valais, Vinschgau, Unterengadine) are pine forests, juniper bushes, and sunburned dry grassland, overarched by the azure rainless skies of the Central Alps.

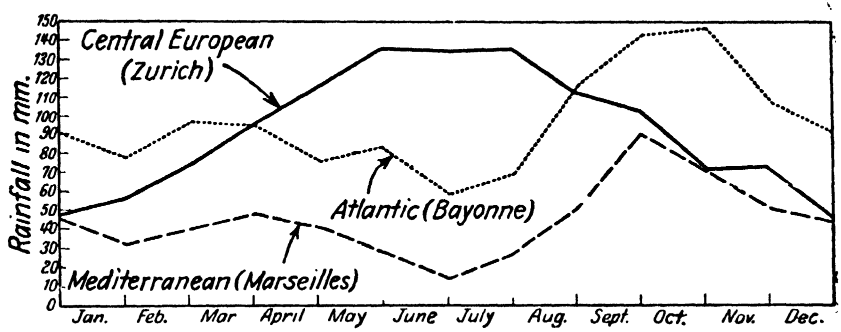

FIG. 62.—Periodicity of the Mediterranean, Atlantic, and Central European rain climates.

Quite astounding is the sudden transition from the belt of cedars and oaks on the rainy western slopes of the middle Atlas (with 70 to 80 cm. of precipitation) into the blazing, scorching desert steppe of the upper Moulouya (annual rainfall about 20 cm.). Within a few hours the traveler may traverse two worlds. Still more violent contrasts in climatic moisture are met in the Himalayas. But altitude also figures there, and the distances are on a gigantic scale.

Perhaps nowhere in the world is the influence of mountain ranges on rainfall more strikingly shown than in western North America. The Cascade Mountains intersect the states of Washington and Oregon from north to south, dividing them into a western slope with a rainfall varying from 200 to 300 cm. yearly and an eastern basin with an annual precipitation of only 25 to 40 cm.

Rainfall in Small Areas in Relation to Plant Communities.—Places with equal rainfall are connected on a map by lines called isohyets. The study of the distribution of specially significant species and plant communities has shown that their boundaries within a small, climatically uniform region agree to a remarkable degree with certain isohyets. Thus, the most peculiar xeric colonies and associations of the Alps are strictly confined to the centers of extreme drought with 55 to 70 cm. annual precipitation. These include such Sarmatic species as *Carex stenophylla*, *C. supina*, *Kochia prostrata*, *Astragalus austriacus*, *A. vesicarius*, *A. exscapus*, *Seseli varium*, *Dracocephalum austriacum*, and *Achillea tomentosa*, and the dry-turf communities of *Festuca vallesiaca*, *Poa concinna*, *Stipa capillata*, *C. supina* found mostly as sharply defined associations. The regions of minimum rainfall of the interior of the Alps can be located by the presence of these communities.

A few Sarmatic species of the oak woods and the Xerobrometum of northern Switzerland and southern Germany have similar indicator value. The Xerobrometum erecti with its characteristic companion species is strictly confined to the region with 70 to 90 cm. annual precipitation. In habitats that are edaphically especially favorable, on dry southern slopes of the porous Jurassic limestone, this association occasionally oversteps the isohyet of 90 cm.

From 90 to 130 cm. rainfall, in the northern alpine foothills, the place of the Xerobrometum is everywhere taken by the more mesic Mesobrometum, as shown by Scherrer (1921) and by Koch (1926).

Measuring Rainfall.—The characterization of climate according to rainfall is the business of the weather service. Daily precipitation is measured and from this are obtained the monthly and annual means and the number of rainy days and their distribution throughout the year. The last two points are of especial importance for biology. In uninhabited places, especially in high mountains, the total annual precipitation alone is taken by means of rain collectors. The ample collecting vessel, with windshield, is supplied with 6 kg. of calcium chloride to prevent freezing. A thin layer of oil poured over the contents prevents evaporation. Thus one annual measuring and emptying suffices. This "totalizer," by acting as dust collector, also gives important data on soil formation (*cf.* p. 176). The establishment of rain collectors at high altitudes in the Pyrenees and the Alps has brought out the important fact that the total precipitation in mountains increases up to very great heights.

For the measurement of the amount of rainfall actually reaching different plant communities and layers, rain gages must be set up in the most varied places within definite plant communities. In stratified communities, whose upper layers catch a part of the falling rain, measurements must be made in the ground layer close to the earth, and in the herb, shrub, and tree layers if present, in order to determine the water-retaining effect of each layer. The water running down the trunks of trees, so important for epiphytic vegetation, can be measured by specially devised collecting vessels.

Duration of Rain.—Data concerning the kind and duration of rainfall are much more difficult to obtain than records of total precipitation, although such data are important for an understanding of vegetation. Equal amounts of rainfall produce very different ecological effects, according to whether they fall in a few hours in violent downpours or as a fine continuous drizzle.

The mountain wall on the north of the Mediterranean basin receives a large rainfall (Valleraugue 350 m., 165 cm.; Locarno 210 m., 194 cm.; Tolmezzo 242 cm.; Crkvice in the bay of Cattaro 464 cm. per year). It falls for the most part in heavy showers, which sometimes overflow the rain gages so that the amount can only be estimated. For example, Lasalle in the southern Cévennes on Sept. 26, 1907, received 40 cm., the highest maximum for one day for Central and southwestern Europe. But in spite of this temporary excess of precipitation, the vegetation of the southern Cévennes has many xeric features: extensive *Cistus* scrub, and the sclerophyllous *Quercus ilex* macchia covers the flanks of the mountains up to 800 m. above sea level. The western slope of the Cévennes, on the contrary, with less annual precipitation, is covered with mesic deciduous forests and rich green meadows. The summer drought is hardly noticed, for the number of rainy days is twice as many as in the Mediterranean valleys, and fine and continuous rains prevail.

Effects of Heavy Showers.—Heavy gusts of rain are harmful because they drown out the fine soils and puddle the ground. Plant colonization of denuded and slightly sloping ground is made difficult or impossible. Seeds that are blown in, if not immediately washed away by violent showers, germinate poorly on the residual soil, devoid of loam and humus. And since the seedlings are subject to drowning out as well as to intense heat and drought, very few can survive such conditions in a warm temperate climate.

Thinly vegetated erosion slopes are especially common and striking in semiarid regions. In the western United States large areas of such bare slopes give rise to an edaphic desert known locally as "Bad Lands"

(Fig. 63). The Bad Lands of South Dakota have a rainfall of some 40 to 50 cm. About the Mediterranean and in the Western Alps naked, scoured, marly slopes play a far too prominent rôle in the landscape (Fig. 64). Even in a forest climate newly exposed subsoil presents insuperable difficulties for the establishment of woody plants on account of its physicochemical character. The blue-gray marls of the Aptien of the southwestern Alps and northern Africa and the Miocene, Eocene, and Permian marls of Languedoc are notorious in this respect. The study of these rain-erosion phenomena and the efforts to halt their destructive effects lead to a recognition and classification of the plant species of dynamic genetic importance. These plants offer a decided resistance to erosion and in addition act as first pioneers leading to a revegetation of the areas (Fig. 65).

Fig. 63.—An erosional edaphic desert; the "Bad Lands" of South Dakota. (*Photo by Hayward.*)

Dew.—Dew provides a water supply for cryptogams, especially in regions of scanty rainfall.

Plantefol (1927) experimented on the absorption of dew by cushions of *Hylocomium triquetrum*. He found that in August and September, after rainless nights, the water content of the moss cushions had increased to 100 per cent of the dry weight, whereas on the previous day it was 20 to 30 per cent. At subalpine levels at Lus-la-Croix-Haute, the water content rose to 233 per cent of the dry weight after a heavy dew and by evening of the same day fell to 87 per cent. These figures show the value of a ground layer of mosses for reducing evaporation from the soil.

Volkens (1887) believed that dew made possible the short-lived vernal vegetation of the Lybian desert. One advantage of dew over rain is its regularity (*cf.* Hiltner, 1930).

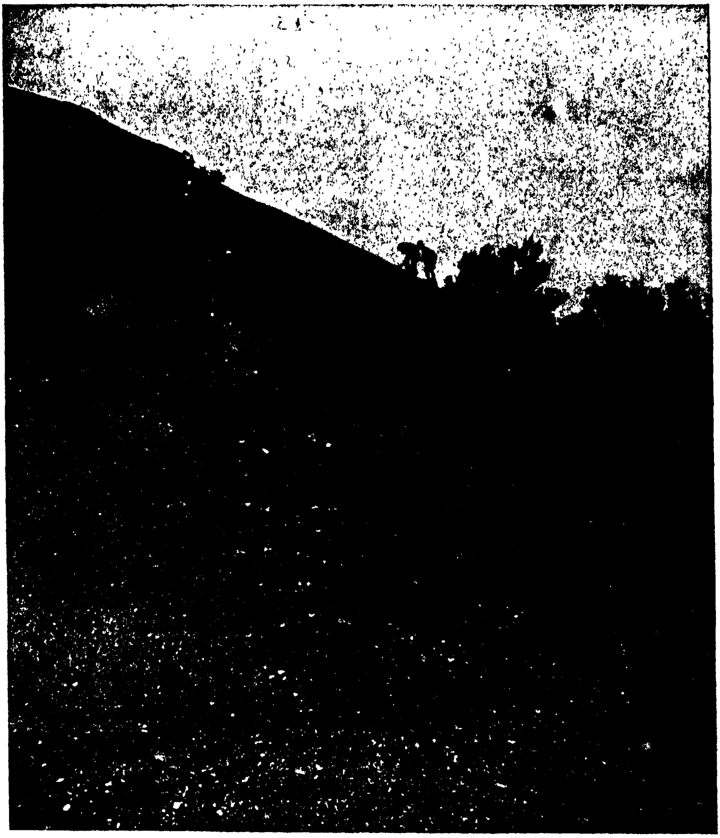

Fig. 64.—Washing away of the vegetation by rain (Aptien-marl of the Oued Cheinour, Province Constantine). A few cleander bushes remain as relicts. (*Photo by Daguin.*)

Snow.—Snow is injurious in warm temperate climates because it beats down plants, especially the broad-leaved evergreens, but it is valued for its water-storing capacity. The significance of snow increases toward the poles and toward the summits of mountains. In the arctic and arctic-alpine zones, snow becomes the leading factor in halting the march of vegetation.

Schröter (1926) has discussed the autecological effects of snow and given a careful survey of the literature. Extensive accounts have also been given by Fries (1913), Braun-Blanquet (1913), and Nordhagen (1928). Schröter groups the effects of snow according to its benefits and its harm to vegetation.

He recognizes as beneficial the protection from drought, from cold, and from early sprouting; the retention of heat in the soil favoring the spring flora; the increase of the sun's heat by reflection; the promotion of fertility by collecting and retaining dust; the regulation of the water supply by gradually melting; and the providing of smooth surfaces for the distribution of seeds by the wind.

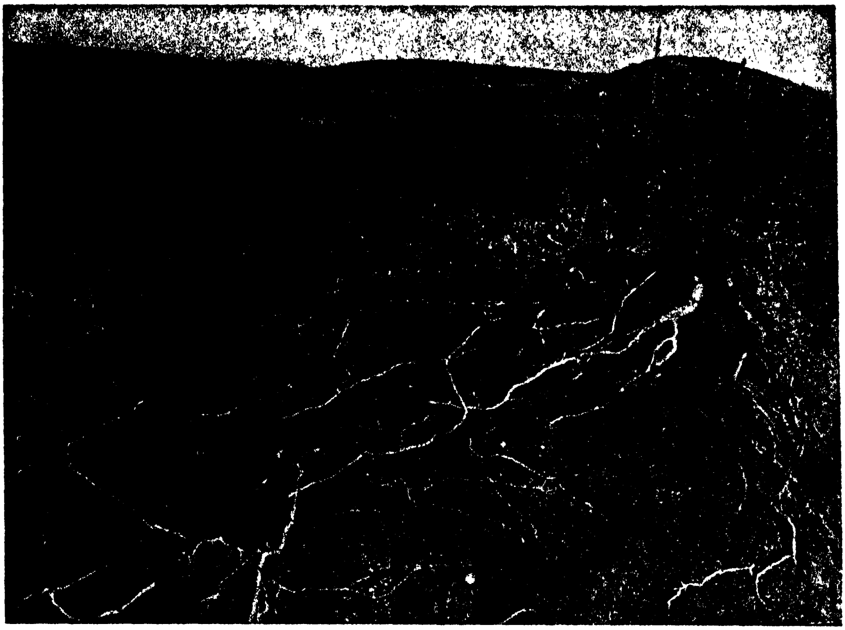

FIG. 65.—Disintegration of the *Rosmarinus-Lithospermum fruticosum* association. Heavy rains have exposed the root system of *Rosmarinus*, *Genista scorpius*, and *Lavandula latifolia*. (*Photo by Braun-Blanquet and Keller.*)

Injurious effects are the abrasive action of particles driven by the wind; the formation of a cold danger zone on the surface of the snow; the shortening of the vegetative period due to the snow cover; mechanical injury due to weight and sliding; and the favoring of soil washing and soil sliding.

To these harmful effects should be added the deformation of woody plants by snow pressure and breakage as well as physiological injury, reducing vitality, especially of the taller woody plants.

Lakari (1920) found that snow injury of spruces in Finnish forests led to reduction of annual growth and decreased crops of cones and seeds.

Further harm is due to the favoring of certain parasites by the snow cover. The parasitic fungus *Herpotrichia nigra* (Sphaeriaceae) envelops the twigs of *Pinus montana* and *Juniperus nana* in snowy hollows with a dark brown, slimy mycelium killing whole plantations, while the same species hard by, but covered for a shorter period with snow, suffer little or no injury.

In the regions of snow injury in Finland a number of fungus parasites are often very destructive (especially species of *Fomes*, *Fomitopsis*, and *Trametes pini*). Lakari (1920) studied snow injury in forests minutely and reviewed the literature.

Snow-favored and Snow-injured Species.—In snowy regions two extreme groups of plants may be distinguished: those species favored by snow (chionophilous species), which occur only where they are covered late in the season by snow; and those injured by the snow cover and seemingly avoiding snow (chionophobous species), which are not found where the snow lies long upon the ground. A few species are more or less indifferent to the duration of snow cover but occur both on permanently snowless areas and in places with prolonged snow cover, *e.g.*, *Poa alpina*, *Agrostis rupestris*, and *Carex nigra* in the Alps. Chionophily and chionophoby depend primarily upon the greater or lesser resistance of the species to cold and drought. But chionophilous plants must be able to continue their life processes in almost total darkness under the snow and bloom and fruit within a few weeks after the melting of the cover.

The injurious effect of artificial removal of snow cover from vegetation accustomed to being covered for several months was studied by Grisch (1907) in a *Trisetum flavescens* meadow at 1,240 m. The uncovered area showed not only a rapid change in the proportionality of the species but also a great reduction in the amount of vegetation produced. The number of seedlings in May was 17 per square foot on the snowless area, against 104 on the snow-covered area.

Since the seeds of many alpine plants germinate in late autumn and winter, and many species overwinter with green shoots, without any autonomous winter rest, or are very easily stimulated to growth (*cf.* Braun-Blanquet, 1913, pp. 45–52; Rübel, 1926), it is especially in high mountains that the importance of snow cover is most obvious as protection from cold and drought.

Woeikoff (1889, p. 14) in Petrograd on Mar. 10, 1888, took the following temperatures, showing how cold decreases with depth of snow. Air temperature −17°C.; snow surface −15°; 5 cm. deep in snow −11.3°; 12 cm. −9.2°; 23 cm. −8.4°; 42 cm. −3°; 52 cm. −1.6°.

Under 1 to 2 m. of snow in the Alps the ground is rarely frozen. Hence many species of plants continue to grow under the snow, and some actually bloom. *Soldanella alpina* and *S. pusilla* were found blooming under 0.5 m. of snow; so also were *Crocus vernus, Scilla bifolia,* and *Saxifraga oppositifolia* (Braun-Blanquet, 1913) and in eastern Europe *Scilla sibirica* (Keller, 1927). On Jan. 22, 1904, in the Malixer Alp near Chur (1,700 to 1,800 m.) under 50 to 120 cm. of snow (soil moist, not frozen, 0°C.; air temperature 12°C.) the following species had green turgescent foliage: *Luzula multiflora, Potentilla aurea, Sieversia montana, Trifolium thalii, Pirola minor, Vaccinium myrtillus, Soldanella alpina, Gentiana kochiana, Ajuga pyramidalis, Galium pumilum, Homogyne alpina, Hieracium alpinum.*

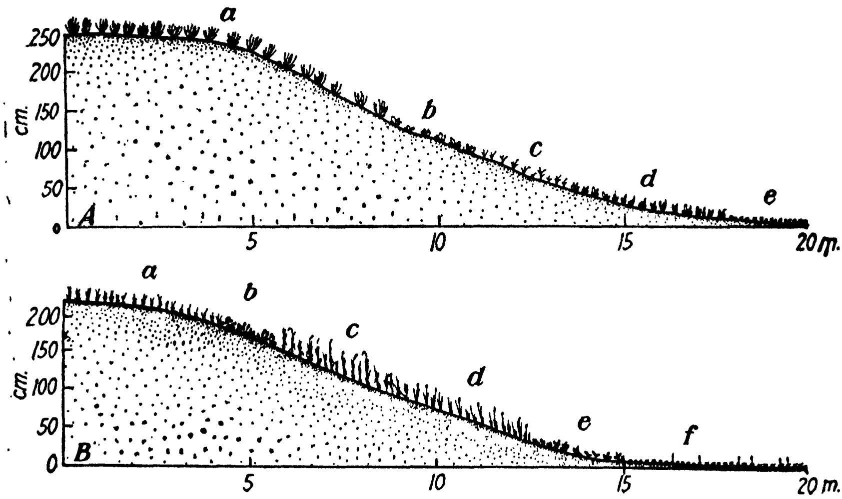

FIG. 66.—Parallelism in the zonal arrangement of certain acidophilous associations according to the duration of snow cover. *A*, In the eastern Alps at 2,340 m.; *a*, associations of *Carex curvula; b, Salix herbacea* with some *Carex; c, Gnaphalium supinum; d, Salix herbacea;* and *e, Polytrichum sexangulare.* (*After Braun-Blanquet.*) *B*, In Sylene, Norway; *a*, associations of *Juncus trifidus; b, Vaccinium myrtillus; c, Deschampsia flexuosa; d, Carex rigida; e, Salix herbacea;* and *f, Polytrichum sexangulare.* (*After Nordhagen.*)

Snow Cover and Plant Communities.—The vegetation of the high mountains and the far north may be simply classified according to its relation to duration of snow (Fig. 66). This has been done in Scandinavia by Vestergren (1902) and by Fries (1913). In the high mountains of central Europe also there are pronounced snow-avoiding communities on exposed ridges, *e.g.*, Loiseleurietum cetrariosum, Trifidi-Distichetum, Elynetum, Caricetum firmae, etc., and communities on snow ground, favored by the protective covering of snow. The snow-avoiding communities are also always wind hardy. Between these fundamental ecological groups there are associations more or less favored by snow, such as the Curvuletum and the Festucetum halleri. In the calcareous Alps the following associations occur on closely adjacent surfaces: Elynetum on exposed slopes often swept bare of snow during the winter; Seslerieto-Semperviretum a little lower down on slopes covered during the winter, but from which the snow disappears early; *Festuca violacea-Trifolium thalii* association in depressions where the snow lies late but where the water supply is good; and Arabidetum coeruleae on areas where the snow lies very late.

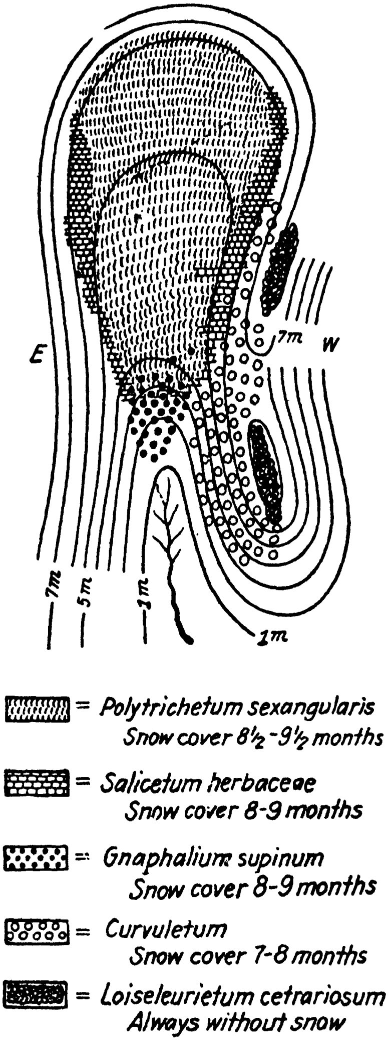

FIG. 67.—Topographic arrangement of some associations with various duration of snow cover in the Farur Alps, 2,350 m. (*Braun-Blanquet and Jenny.*)

Snow-land Communities.—Snow-land communities are adjusted to a very short growing season. They tolerate 8 to 11 months spent in hibernation. Indeed, there are facies of the *Polytrichum sexangulare* association which in snowy years are never exposed (Figs. 67, 68).

In the high mountains of northern Scandinavia, according to Fries, the *Phippsia algida* and the *Anthelia nivalis* associations are denizens of extreme snow-land. The *Ranunculus glacialis* and *R. nivalis* meadows as well as the *Salix herbacea* association with its abundant liverworts and mosses endure a very long continued snow cover. The snow-land communities of the Alps and the Tatra mountains fall into three floristically different alliances:

The Arabidion coeruleae; on calcareous snow-land, a pronouncedly basophilous community.

The Androsacion alpinae; on non-calcareous residual gravel (pH 6.4 to 4.7), an acidophilous community of moderately damp coarse gravel.

The Salicion herbaceae; on non-calcareous fine gravel, glacial clay, and permanently saturated humus soils approaching podsol (pH. 6.5 to 4.6), also acidophilous.

The Salicion herbaceae attains a considerable extension in the upper belt of the alpine levels. It was described by Oswald Heer (1836) under the suggestive name of *Schneetälchen* and has ever since been the prototype of alpine snow-lands.

This alliance is divided into several associations and many facies, which have different adjustments to the length of the snowless growing period (Figs. 67, 68). The Salicetum herbaceae requires an average exposure of 2½ to 4 months. The Polytrichetum sexangularis, a community of mosses and liverworts, thrives with 1½ to 3 months free from snow but may exceptionally endure more than a year of snow-cover. In the beginning stages of this association on raw soils *Anthelia juratzkana, Gymnomitrium varians, Dicranum falcatum,* and *Pohlia commutata* are the pioneers. In their cushions *Polytrichum sexangulare* likes to colonize and may finally become dominant.

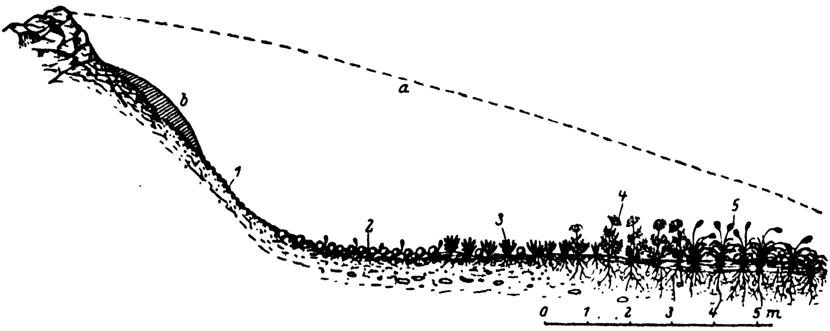

FIG. 68.—Arrangement of associations according to duration of snow cover, Minor Pass, Bernina, Switzerland, 2,450 m., Northwest exposure. *a,* Winter snow blanket; *b,* snow, July 21, 1927; 1, *Polytrichum sexangulare* association; 2, Normal facies; 3, *Gnaphalium supinum* facies; and 4, *Ligusticum mutellina* facies of the *Salix herbacea* association; 5, *Carex curvula* association.

The pioneers of the snow-pocket associations at the extreme limits of life are adapted in many ways to the short growing period and present therefore a biotic group that is sharply characterized ecologically. The most important adaptations are:

1. Extensive preparation and development of leaf and flower buds under the snow. All the mosses and most of the flowering plants, such as *Arenaria biflora, Cerastium cerastioides, Cardamine alpina, Soldanella* sp., and *Gnaphalium supinum,* overwinter with green shoots beneath the deep snow layer.

2. Vegetative increase by creeping shoots as in *Luzula spadicea*, *Salix herbacea*, *Arenaria biflora*, *Cerastium cerastioides*, *Alchemilla pentaphyllea*, *Veronica alpina*.
3. Dense sod or tussock-forming growth, with capacity for spreading peripherally. No annuals.
4. Utmost reduction of the individuals. The snow-pocket plants are the pygmies of the alpine flora. Accessory leafy shoots are suppressed and the reproductive activity extended to the limit. On a tiny stalk is perched the terminal inflorescence. *Cardamine alpina*, *Ranunculus pygmaeus*, *Soldanella pusilla*, *S. minima*, and *Gnaphalium supinum* are each among the smallest members of their respective genera.
5. Extremely rapid development after the snow melts, and early ripening of seed. Within a few weeks the life cycle is completed from bud to fruit.

FIG. 69.—Snow pockets with *Salix herbacea* in the Tatra (1,960 m.) showing *Salix herbacea*, *Ligusticum mutellina*, *Soldanella carpatica*. (*Photo by Zlatnik.*)

The Salicion herbaceae (Fig. 69) is marked by a series of pronounced characteristic species, whose optimum of life conditions falls within the realm of the community, *i.e.*, *Cardamine alpina*, *Arenaria biflora*, *Alchemilla pentaphyllea*, *Soldanella pusilla*, ancient endemics of the central European alpine system.

Even in the forest areas of the subarctic zone and of the subalpine levels of the Alps and lower mountains, the effect of snow upon the forms of plants is everywhere demonstrable. Heavy snow masses which are not too late in melting favor the development of stands of shrubby willows and alpine alders of the Rhodoreto-Vaccinion and the fields of tall herbs, *Adenostyles*, *Cicerbita alpina*, *Cirsium spinosissimum*, etc. (Fig. 70). All the snowy mountains of the temperate zone have such fields of tall herbs.

Undergrowth and ground layers of forests receive very different amounts of snow under different kinds of trees, since the crowns of the trees catch and hold the snow in different degrees. According to Bühler (1918), the spruce holds back 55 to 80 per cent of a snow in its crown; the beech, only 10 to 15 per cent; a fifteen-year-old low forest of *Carpinus*, *Corylus*, etc., only 3 per cent. Hence in low forest and among shrubs we may expect the greatest influence of the snow upon the ground layer.

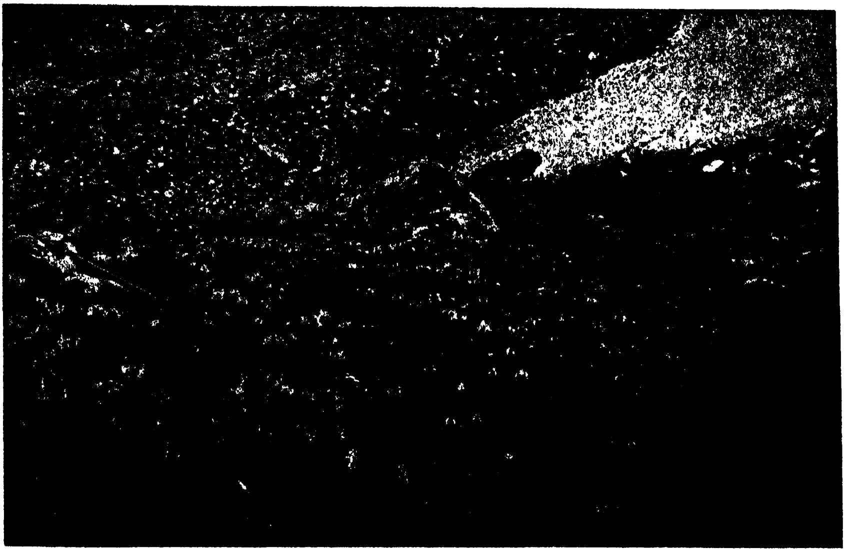

FIG. 70.—*Cirsium spinosissimum* tall herb meadow in July, after melting of snow (Val Sampuoir, 2,200 m.). (*Photo by Heller.*)

In the *Pinus montana* low forest of the calcareous mountains between Inn and Etsch, several facies can be distinguished, dependent on snow cover:

1. The Pinetum montanae cladoniosum with an undergrowth of fruticose lichens (maximal snow cover 7 months) on northern slopes and in the depressions known as snow pockets. *Cladonia alpestris*, *C. rangiferina*, *C. silvatica*, *Cetraria islandica*, with *Vaccinium uliginosum* mostly cover the ground.
2. The Pinetum montanae hylocomiosum, with 2 to 4 weeks' shorter snow-cover. The dominant plants are mostly *Hylocomium splendens*, *H. triquetrum*, *Hypnum schreberi*, with *Vaccinium myrtillus*.

3. The Pinetum montanae rhodorosum. Snow cover for 5½ to 6 months mostly on steep warm slopes. *Rhododendron hirsutum* is dominant. The mosses *Hylocomium triquetrum* and *Hypnum schreberi* in dryer places, *H. splendens* in moister places, and the shrubby *Erica carnea* are abundant.

4. The Pinetum montanae ericosum. Snow cover similar but on more level ground. *Erica carnea* and *Vaccinium vitis idaea* are dominant.

Obviously, in this distribution the duration of snow cover is not the only factor, but it is one of the most influential.

B. HUMIDITY

The humidity of the air regulates the loss of water by transpiration; the dryer the air the greater the water loss. All conditions of the habitat which reduce humidity, such as high temperature of the air, intense radiation, strong winds, are accompanied by an increase in the loss of water.

Gordjagin (1930) has shown that the loss of water from the leaves of conifers and evergreen oaks continues even during the coldest weather and that toward the end of the winter the losses by transpiration of *Quercus pedunculata* are compensated by the water drawn from the oldest parts of the tree.

Hygromorphy, Xeromorphy.—Humidity of the air directly influences the form and structure of plant organs. Eberhardt's (1903) experiments showed that moist air favors growth, delays flowers and fruit, and suppresses hairs.

Experimental plants grown in moist air were characterized by simplification of the palisade system and increase of the intercellular spaces of the spongy parenchyma, reduction of vascular tissue, delayed lignification, enlargement of epidermal cells, great enlargement of cortical and pith cells, formation of intercellular spaces where they are normally lacking, delayed development of cork, and a reduction of the number of stomata.

In contrast with this, dry air retards growth (nanism) and favors in high degree the development of hairy coverings. It induces a great development of the root system and hastens formation of flowers and fruit. The following anatomical changes are among the effects of dry air: reduction in diameter of epidermis cells and in width of cortex and pith; hastening of the formation of sclerenchyma, cork, and wood; thickening of leaves, especially by increased number of rows of palisade cells; and an increase in number of stomata. Dry air induces xeromorphy. Transpiration is, however, such a complex process that the relations between humidity and the income and outgo of water are difficult to grasp.

The first step toward an ecological understanding of water economy leads to a grouping of plants according to water balance into the following graded series:

1. Hydatophytes or water plants.
2. Hygrophytes, moisture-loving species with favorable water economy.
3. Mesophytes, species with medium water relations.
4. Xerophytes, drought plants, with small water requirement.

Most of the representatives of a group with a definite water relation show many similarities in the form and structure of the organs of transpiration, as well as in the finer structure of the internal tissues. These structural arrangements seem to indicate the vital activity of the species in adjusting itself to the environment. They are therefore considered as adaptations to the conditions of the habitat. Hygrophytes have morphological devices that permit the free loss of water. Xerophytes on the contrary have many structural characteristics which serve to reduce transpiration and more particularly cuticular transpiration, such as reduction of surface in relation to volume, reduction of the intercellular spaces, thick outer epidermal walls with much cutin and heavy cuticle, abundance of wax in the epidermis, and coatings of wax, depression of stomata, covering of leaves with dead hairs, frequently a water-storage system, and an extensive conductive and absorptive system (Fitting, 1926, p. 18).

This teleological exposition, although fundamentally right, has received much criticism and correction from modern experimental physiology.

The prevalent misunderstanding has been undoubtedly intensified by the indefinite and ambiguous definitions of the concepts hygrophyte and xerophyte. Whereas some writers mean plants with hygromorphic or xeromorphic adaptations, others designate thereby species which occupy wet or dry habitats. At present it is unanimously agreed that every species must be examined by itself before judgment can be passed upon its water relation. The visible morphological arrangements for resistance to drought are far less important in their effects than the purely physiological conditions. Consequently, plants of pronounced xeromorphic structure, like the Ericaceae of our moors and many Cyperaceae, grow persistently in moist or wet habitats.

Ecologists of the Schimper school would explain all these phenomena by the indefinite hypothesis of "physiological dryness." Meanwhile the careful investigations of Montfort (1918) and others have shown that there is no such thing as physiological dryness, in the Schimper sense, due to the difficulty of absorbing water from moors rich in humus acids. No characteristic xeromorphy is demonstrable in deciduous Ericaceae of peat moors or in many other plants of high moors. Indeed, comparative studies have shown that many Sphagnum moor plants exhibit decided hygromorphy.

Loss of water by plants is increased by guttation. Water stomata (hydathodes) excrete liquid water in drops. Since, according to Schimper, guttation is especially common in warm, moist, tropical forests,[1] it is easy to conclude that this is a partial substitute for the reduced transpiration. According to MacLean (1919) and Fitting (1926), it is very doubtful whether special protection against feeble evaporation is needed at all. Dietrich (1925) made a painstaking study of the transpiration of sun and shade plants in relation to habitat. His results indicate that in this case also the accepted doctrine that increased surface of shade leaves is generally of service for increasing evaporation needs further proof. Agreeing with Stocker (1923), Maximov (1929), and Keller (1925), Dietrich showed that transpiration per unit of area is less in shade plants than in sun plants. The benefit of large transpiring surface of shade leaves is wholly canceled in many species by the decreased rate of surface transpiration.

The necessity of promoting the passage of water into a saturated atmosphere is still very uncertain, but everyone has observed the deadly effect of atmospheric drought upon vegetation. At first the plants wither; if water deficit continues, death ensues. In arid regions morphological arrangements for reducing loss of water (*cf.* p. 125) are especially common. Many of these protective mechanisms are now genotypically fixed through heredity. Others, like leaf structure, size of leaves, hairiness, root development, may be more or less modified by the environment. Within limits set by heredity, the habitat has an influence upon form, determining the degree of xeromorphy.

This is accomplished especially by increasing the efficiency and capacity of the mechanisms for increasing absorption and conduction and for reducing the transpiration. However, it is difficult to obtain an unequivocal numerical expression of this effect. The amount of water given off per unit of surface of transpiring organs gives no information whatever about the drought resistance of the plant. According to Maximov (1929) and Szymkiewicz (1925), xerophytes often transpire more than mesohygrophytes. Besides, transpiration varies not only from species to species but also from individual to individual in different habitat conditions and, indeed, from shoot to shoot and from

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[1] However, MacLean (1919) was unable to demonstrate any guttation among the hygrophytes of the Brazilian rain forest, and Shreve (1914*a*) found in the rain-forest vegetation very few hydathodes.

leaf to leaf on the same plant. In woody plants, short shoots transpire more than long shoots, and one-year-old shoots more than two year old (Ivanov, 1924). Hence calculations of the total amount of transpiration are extremely difficult. Attempts to deduce a measure of xerophytism from the transpiring power of plants (*cf.* Bakke, 1914; Pool, 1923) have yielded no very satisfactory results.

From observations of Walter (1925) it appears that a unit surface of foliage is not significant as a measure for comparison of amounts of transpiration. For, if the transpiration per unit of surface is measured for larger and smaller leaves, the smaller leaves show a greater amount.

Root Suction and Osmotic Concentration.—Fitting (1911) first called attention to the absence of xeromorphic adaptation in certain north African steppe and desert plants such as *Peganum harmala.* These mesomorphic species withstand the longer summer drought without forming protective devices of morphoanatomical nature. The absence of drought-resisting mechanisms in these plants is made up for by a high suction power. Poma (1922) showed that when the osmotic concentration of the culture solution increases, the suction tension of the roots, that is, the intracellular osmotic pressure, constantly increases.

TABLE 7.—INCREASE IN THE SUCTION TENSION (IN ATMOSPHERES) OF ROOTS OF SPECIES OF THE JUNCETUM MARITIMI, FOLLOWING THE INCREASED OSMOTIC CONCENTRATION OF THE CULTURE MEDIUM
(After Poma)

Osmotic concentration of the culture solution	0	6	11	22
Triglochin maritimum	10	20	24	30
Glyceria maritima	10	23	27	34
Juncus maritimus	7	20	23	

The daily curve of suction tension runs parallel to the curve of saturation deficit of the air. It rises with increasing deficit (decreasing humidity) up to midday, then falls until the following morning. The fluctuations of humidity correspond to fluctuations in the suction power in the plant. Table 8 gives measurements of these fluctuations.

The highest suction tension was therefore found in rainless periods on days of great variation in humidity. Ursprung discovered the interesting fact that when water absorption by roots is hindered by frozen soil, an increase in osmotic pressure follows just as in desert plants. The suction force of expressed sap of the perianth of *Helleborus* rose to 50 atmospheres in winter as against 10 atmospheres in May.

TABLE 8.—RELATION OF SUCTION TENSION IN *Bellis perennis* TO ATMOSPHERIC HUMIDITY
(After Ursprung)

Date	Daily variation		Rainfall on day of observation and on two previous days, millimeters
	Atmospheric humidity, per cent	Suction tension in *Bellis*, atmospheres	
Nov. 13	6	0.6	0.3
Sept. 26	24	3.8	0.1
Aug. 10	52	8.0	0 0
Sept. 19	52	3.9	7.3
July 13	64	9.8	0.0

Osmotic Concentration of Cell Sap.—The investigation of the osmotic concentration of the cell sap of plants yields more constant values which have fewer daily fluctuations and are therefore more useful in plant sociology. The cryoscopic determination of expressed cell sap, so largely employed in America, has been introduced into Europe by Walter (1929, 1929*a*, 1931), who has improved the method and made it serviceable to plant sociologists. This determination of the osmotic value of cells under normal conditions permits an insight into the water balance of plants and leads to a better understanding of the water economy of the community as a whole. Scattering measurements of this type are likely to be of little value. The osmotic values of all the most important members of a plant association should be ascertained at intervals throughout the whole growing period or throughout the entire year, in order to obtain yearly osmotic-concentration curves. These curves are likely to be most instructive.

The data shown on page 130 are from investigations of Braun-Blanquet and Walter (1931) on the range of osmotic values in two associations of theMediterranean region.

The maximum osmotic value for these plants will be seen to coincide with the long, dry, rainless summer, continuing to the beginning of September. September 7 was the hottest day of the year. A month later, after autumn rains, the osmotic value of most of the plants reached its minimum and then rose very slowly and rather steadily until the next summer. *Viburnum tinus*, a species with large leaves, little protected against water loss, gave the highest value of 41.6 atmospheres. This is an example of a very irregular annual curve with a strong maximum in the summer.

TABLE 9.—OSMOTIC CONCENTRATION OF CELL SAP (IN ATMOSPHERES) AT VARIOUS SEASONS OF THE YEAR IN THE *Quercus ilex* SCRUB AND IN THE *Brachypodium ramosum-Phlomis lychnitis* ASSOCIATION

Association	May 17, 1929	June 2, 1929	June 16, 1929	July 14, 1929	Sept. 7, 1929	Oct. 16, 1929	Dec. 11, 1929	Jan. 29, 1930	Mar. 3, 1930
Quercetum ilicis:									
Quercus ilex......	14.2	20.7	22.2	22.6	**24.6**	21.8	21.3	17.9	20.8
Lonicera implexa..	18.0	19.3	....	25.4	**26.4**	15.8	17.1	17.2	
Cistus albidus.....	18.3	23.3	26.2	25.7	**34.5**	14.4	15.8	15.0	15.6
Viburnum tinus...	....	19.9	....	30.3	**41.6**	17.4	17.5	19.1	
Brachypodietum ramosi:									
Brachypodium ramosum......	17.5	....	22.0	**31.5**	24.6	13.4	16.4	18.0	
Thymus vulgaris	13.4	14.5	22.8	.....	**33.6**	12.7	12.2	14.1	13.4

Quercus ilex and *Q. coccifera*, on the contrary, give regular curves with feeble maxima in the winter (not visible in the table). To the same group belong *Pistacia lentiscus*, *Phillyrea angustifolia*, *Smilax aspera*, *Rubia peregrina*, and *Ruscus aculeatus*, that is, the vast majority of the woody species of the ultimate climatic association (climax) of the region.

Annual curves with small minima and maxima appear to indicate that the species in question are in harmony with their environment and do not suffer from lack of water even during dry periods. According to the form of the annual curves, various plants may be designated as belonging to the *Viburnum* type, the *Quercus* type, the *Cistus* type, etc.

Very high values were obtained for halophytes; *e.g.*, *Salicornia macrostachya* from a locality near Montpellier gave 44.9 atmospheres on May 18 and 42.0 on June 10. These figures refer to normal plants in their best development. On the same days and growing on the same soil that was somewhat drier, so that these plants were evidently suffering from lack of water, the following results were obtained: *Salicornia macrostachya*, May 18, 82.5 atmospheres; June 10, 79.6 atmospheres.

The dryness thus increased considerably the osmotic values, and the plants which were incapable of increasing their osmotic value were the first to be eliminated.

On the other hand, plants with milky juice and certain desert succulents do not have, and apparently do not need, high osmotic values. *Cereus*, *Opuntia*, *Umbilicus*, *Sempervivum* and *Sedum* agree in exhibiting low sap concentrations often ranging from 5 to 8 atmospheres. In plants like *Umbilicus pendulinus* the osmotic value rises to 13 atmospheres, at which point the leaves begin to wither.

From investigations by Walter and by Walter and Braun-Blanquet it appears that winter cold acts like desiccation in increasing osmotic values. Walter found during the winter that species with Atlantic affinities like *Hedera helix, Ilex aquifolium, Helleborus foetidus,* and *Sarothamnus* were able to increase the density of their cell sap up to 20 atmospheres but died when the concentration reached 25 atmospheres, while *Buxus sempervirens* was able to increase its concentration from 33 to 72.6 atmospheres without injury.

It is known that concentrated solutions of sugars and of certain salts very greatly increase the resistance of certain plants to cold. Iljin has demonstrated experimentally that the accumulation of sugar in the cell sap is also caused by dryness. He insists on the fact that the action of salts on the resistance of cells depends upon the concentration of the sap as well as upon the specific constitution of the protoplasm. Solutions of both sugar and salts possess the property of plasmolyzing plant cells. Plasmolysis is the first sign, according to Iljin, of the concentration of the cell sap. This explanation does not contradict the observations of the osmotic values in plants.

Osmotic Concentration of the Soil Water.—The osmotic concentration of the cell sap of plants is opposed to the osmotic concentration of the soil water. High osmotic values in the soil prevent the free intake of water by the roots of plants and tend to make the habitat barren of vegetation. Stocker (1930) found that in the sodium soils of Hungary an osmotic concentration equivalent to 28 atmospheres made the acquisition of water by plants impossible. At concentrations equivalent to 28 to 12 atmospheres only steppe plants were able to grow; and only habitats with concentrations of less than 12 atmospheres were open to colonization by non-steppe plants. The osmotic concentration in roots usually exceeds that of the soil water by 2.7 atmospheres or more.

Measurement of Osmotic Concentration in Soil.—Strips of filter paper saturated with a cane-sugar solution of known concentration placed in contact with the soil solution must increase or decrease in weight depending on whether the soil solution has a greater or a lesser concentration than the sugar solution. Strips 4 by 4 cm. are folded once, attached to a small silver or copper wire, and dropped into the sugar solution. They are then taken out, the surplus solution removed with dry filter paper, are then quickly weighed, and hung by a wire in wide-mouthed bottles which contain the soil samples. The wires may be fastened to the corks with sealing wax and a grain of thymol added to the soil to prevent the growth of fungi and bacteria. The bottles are then placed in a compartment maintained at a constant temperature (ice box or fireless cooker) for 24 hr., when the paper is weighed again. If necessary, the experiment may be repeated with a sugar solution of another concentration.

Wilting.—Maximov (1929, 1931) regards the behavior of the plant during wilting as a good indicator of its drought resistance. He defines xerophytes as "plants of dry (or physiologically dry) habitats which are able to decrease the transpiration rate to a minimum under conditions of minimum water supply." The wilting of leaves is accompanied by a great reduction in the rate of water loss due to the closing of the stomata. Wilted corn plants lose by transpiration less than one-tenth the water lost by unwilted specimens, and in highly cutinized leaves the reduction of water loss due to wilting is even greater. Thus in the wilted condition the last water reserves of the plant are retained for a long time.

Humidity of Air and Plant Communities.—The autecological side of the problem of drought resistance offers, as we have just seen, new and unsuspected difficulties. Much more is this true of the synecological side. The aspect of a plant community gives no reliable indication of its water economy. In many cases its growth forms have doubtless come down from earlier geological periods and are genotypically fixed. Only thus can we explain the xeromorphic structure of ericaceous heaths and the Tojal (*Ulex* scrub) of the permanently moist coastal regions of western Europe. The drought-sensitive *Empetrum* heaths of the mountains of central Europe, protected by snow cover, and the ericaceous scrub of high moors probably acquired their xeromorphic character under very different conditions in Tertiary times.

Measurement of Humidity.—The climatologist measures the humidity of the air in grams, or in millimeters, of vapor pressure. Besides this, the relative humidity is also determined, that is, the relation of the actual vapor pressure to that of total saturation at the existing temperature.

The plant sociologist, however, lays greater stress upon the measurement of two other functions of the humidity of the air, namely, saturation deficit and evaporation.

Relative Humidity.—Relative humidity is measured by the well-known commercial hygrometer or psychrometer and is expressed in percentage of the possible humidity (saturation point).

Relative humidity, like vapor pressure, decreases toward the interior of great land masses.

TABLE 10.—DECREASE IN RELATIVE HUMIDITY AND VAPOR PRESSURE IN MORE CONTINENTAL LOCALITIES (48.3 TO 38.6° N. LAT.)
(After Hann)

	Paris, France	Vienna, Austria	Elisavetgrad, Ukraine	Lugansk, Russia	Irgiz, western Siberia
Relative humidity (in summer), per cent...	73	70	63	60	45
Vapor pressure (annual mean), millimeters	7.5	7.1	6.6	6.4	5.1

The general rule is often modified by local influences. For example, Mülhausen, in the rain shadow of the Vosges, has only 67 per cent annual relative humidity, whereas Warsaw has 79 per cent.

There is no immediate connection between humidity and total precipitation. Scanty humidity cannot be inferred from low precipitation. Kola, in Russian Lapland, has but little rain (18 cm. per year) but a mean relative humidity of 80 per cent. The whole southwestern coast of Morocco, the climax area of the *Argania* forest, has an annual rainfall mostly less than 30 cm., but the relative humidity runs between 80 and 90 per cent. On the other hand, the rainy Monte Generoso in southern Ticino (176 cm. rainfall) has a mean relative humidity of only 64 per cent.

Fog.—Fog observations give important information about humidity of the air. The cloud belt of our medium and high mountains is characterized by luxuriant epiphyte communities (mosses and lichens). The lichen association of the Lobarietum pulmonariae, best developed in the Atlantic province, is wholly confined, in central and southern Europe, to the cloud levels of 1,200 to 1,600 m. (Ochsner). Cooper (1919) has demonstrated that the eastern distribution of *Sequoia sempervirens* is determined by the extent of the landward movement of the fog of the Pacific coast of North America.

The cloud belt corresponds to the beech level in southern Europe, to the *Quercus mirbeckii-Q. maroccana* forest in north Africa, and to the laurel forest in the Canaries.

Relative Humidity in Small Areas.—Humidity of the air is subject to sudden and considerable variations, caused by rain, clouds, fog, local winds, and exposure.

Stocker (1923) measured humidity in natural plant communities. He found astonishingly great differences, not only between different habitats but also between the different layers of vegetation in the same habitat. On a quiet sunny day in July in a pasture community of grass, *Trifolium* and *Lysimachia nummularia* near Freiburg, he found the relative humidity and saturation deficit to be respectively 96 per cent and 1.2 mm. at 2 cm. above the soil, in the vegetation; 78 per cent and 6.5 mm. at 13 cm., in the vegetation; and 57 per cent and 12.8 mm. at 100 cm., in the open air.

Relative humidity has been measured by foresters for long periods and has been correlated with forest growth. But the relation of humidity to the transpiration of forest trees seems to remain uninvestigated (*cf.* Burger, 1925). Bühler (1918) found the relative humidity in beech woods lower than in spruce wood. The spruce-wood air was 8 to 12 per cent moister than the air in the open.

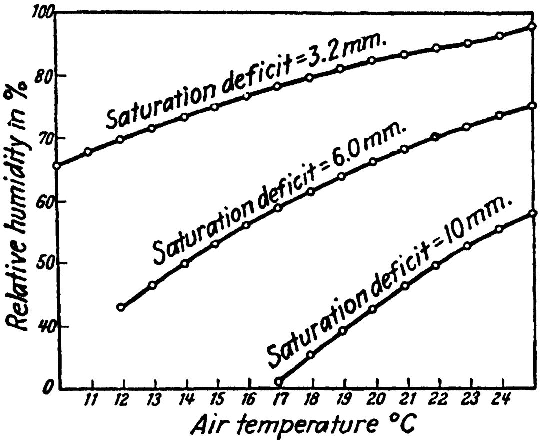

FIG. 71.—Saturation deficit of the air at various degrees of relative humidity with increasing temperature. (*After Bolas.*)

Observations on relative humidity extending over 11 years, in a *Larix decidua* forest at Interlaken, in a spruce forest at Berne, and in a beech forest at Pruntrut in the Bernese Jura gave the following results: larch forest relative humidity 69.5 per cent, excess over the open air outside 4.1 per cent; beech forest relative humidity 78.9 per cent, excess over open air 3.6 per cent; and spruce forest, relative humidity 85.5 per cent, excess over open air outside the forest 9.9 per cent.

C. Saturation Deficit

Saturation deficit is obtained by subtracting the actual vapor pressure from the maximum possible vapor pressure at the given temperature. It is expressed in millimeters of mercury. A relative humidity of 75 per cent at 15°C. corresponds to a vapor pressure of 12.73 mm. by 0.75, or 9.56 mm. The saturation deficit is the difference between the highest possible vapor pressure (12.73 mm. at 15°C.) and the actual vapor pressure (75 per cent), that is, $12.73 - 9.56 = 3.17$ mm. As Bolas (1926) pointed out, the saturation deficit may vary greatly even when relative humidity remains constant, for it rises with the temperature (Fig. 71).

For the measurement of saturation deficit the plant sociologists of Crakow use the commercial Assman psychrometer. The saturation deficit is calculated from the difference between the readings of the wet- and dry-bulb thermometers by means of tables of equivalents.

Ecologically, saturation deficit means more than humidity. Regions with high relative humidity may have the character of desert steppe (southwest Africa). The relative humidity of the coastal belt of southern Morocco between Agadir and Cape Juby continuously shows an enormously high value (90 per cent in summer). Nevertheless the xeric cactoid euphorbia scrub extends to the very shore (Fig. 72). Regardless of the high relative humidity, the saturation deficit, and therefore the evaporation, is large.

FIG. 72.—*Euphorbia beaumierana*, a cactoid euphorbia at Cap Ghir, Agadir. (*Photo by Girardet.*)

Measurement of saturation deficit should be made in the daytime, since stomatal transpiration of higher plants is greatly reduced at night. Also the saturation deficit shows a pronounced daily maximum between 8 a. m. and 6 p. m.

TABLE 11.—MEAN DAILY RANGE OF SATURATION DEFICIT, JUNE, 1901, AT PAWLOWSK (59.41 N. LAT.)
(After Szymkiewicz)

	A. M.						P. M.					
Time of day	1	3	5	7	9	11	1	3	5	7	9	11
Millimeters of mercury	0.3	0.4	1.2	3.3	6.1	7.2	8.6	8.5	7.7	5.2	2.3	0.8

If we compare the lowest values of the dryest months, we find that the polar regions and mountains have the lowest saturation deficit, and steppes and deserts the highest. Hilleh in Mesopotamia, during the period 1908–1910, had a mean deficit of 59.3 mm., measured at 2 p.m. in the driest months. The Schneekoppe in the Riesen-Gebirge (1,603 m.) during the period 1895–1904 had only 1.7 mm. deficit, measured at the same time of day in the driest months (Szymkiewicz).

Saturation Deficit in the Habitat of Plant Communities.—Szafer *et al.* (1923) have studied the saturation deficits for a series of associations in the Polish Tatra. They found very constant and characteristic differences, not only between different associations but also between the different layers of vegetation. Simultaneous measurements in a spruce wood with undergrowth of *Vaccinium* and in a Sphagnetum only 6 m. away gave:

TABLE 12.—SATURATION DEFICIT
(In millimeters)

Vegetation	2.5 cm. above the soil	1 m. above the soil
Sphagnetum	5.6	12.6
Spruce forest	9.3	14.0

The air temperature in both places was practically the same. Figure 73 gives a graph of the saturation deficits in two alternating associations of the crest of the Siwa pass in the Polish Tatra. All the wind-swept western slopes bear the drought-resistant Juncetum trifidi. On the protected eastern slopes the Vaccinietum myrtilli prospers; and on the bottoms of the depressions the Polytrichetum sexangularis spreads its velvety green carpet. The saturation deficit 3 cm. above the ground during a strong wind was 2.6 mm. in the habitat of the Juncetum but only 1.1 mm. in the Polytrichetum.

Müller (1922) measured the saturation deficit in various habitats of the vegetation on eroded chalk.

The distribution of many climax communities is undoubtedly governed by the saturation deficit of the air. This is especially shown by the vegetation maps of Szymkiewicz (1923). *Picea excelsa* holds strictly within moisture limits of 10 mm. (mean saturation deficit of the air in the driest months at 2 p.m. 1895–1904) throughout all of eastern and northern Europe, crossing these boundaries only rarely and in insignificant amounts. The southeastern boundary of the Russian forest region adjacent to the Sarmatian and Aralo-Caspian steppe corresponds exactly with the 15-mm. line.

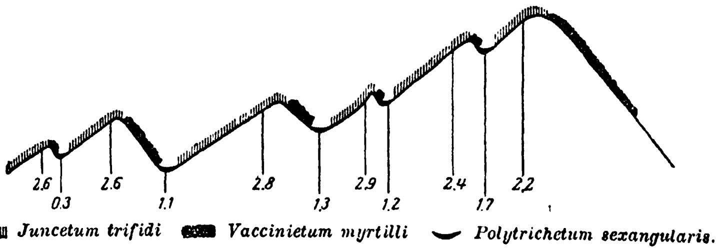

FIG. 73.—The profile of the vegetation and the saturation deficit in the Juncetum trifidi and the Polytrichetum sexangularis, in the Tatra Mountains, 1,900 m. Length of area 200 m.; height 25 m. (*After Szafer, et al.*)

D. EVAPORATION

Without air movement, evaporation is closely proportioned to vapor-tension deficit. The evaporation rate is the combined effect of humidity, wind, temperature, atmospheric pressure, and radiant energy. Temperature far exceeds wind in its influence on evaporation

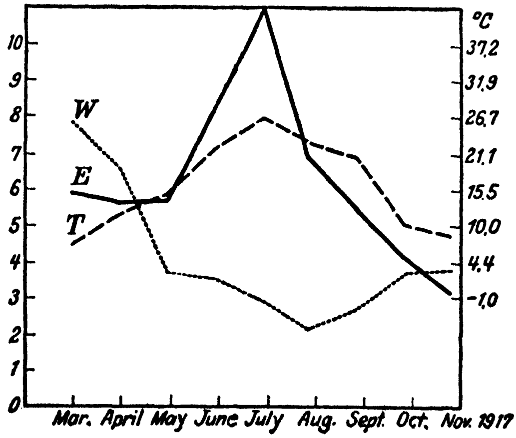

FIG. 74.—Graphs showing the relation between mean monthly evaporation in inches (*E*), wind flow in miles per hour (*W*), and temperature in degrees Centigrade (*T*). (*After Shull.*)

(Fig. 74). It is impossible to deduce the water loss from plants directly from evaporation, although transpiration and evaporation curves will frequently be found to parallel one another rather closely (Fig. 75). However, different plants respond quite differently to the factors controlling evaporation because of the difference in the density of cell sap and colloidal content of the living organisms. Transpiration, however, stands in such an intimate relation to evaporation that measurements of evaporation, along with precipitation, throw much light on the water economy of plant communities.[1]

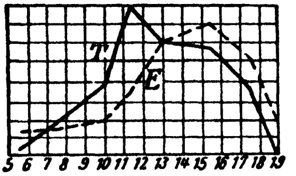

Fig. 75.—Diurnal range of transpiration from *Encilia farinosa* (*T*) and evaporation from an atmometer (*E*) on May 25, dry season, at Tucson, Arizona. (*After Shreve.*)

Measurement of Evaporation.—Meteorologists usually have preferred to measure evaporation from a free water surface of a deep pan, giving the results in the depth in inches or centimeters of water lost within a given time. Evaporation is thus regarded as the inverse of precipitation. Since the water surface reflects the greater part of the incident radiant energy, while colored bodies like plants absorb it, the rate of water loss from the water surface of the pan and from plants is very differently affected by insolation. Then as the water in the evaporating pan is deep, there is a very decided lag in its temperature changes as compared with those of the atmosphere, while the leaves of plants quickly adjust themselves to the same temperature as the air. These difficulties have been largely overcome, however, by the use of a shallow blackened pan from which Briggs and Shantz (1917) found that evaporation closely paralleled the rate of transpiration from *Medicago sativa.*

Ecologists during the last two decades have found that measuring instruments known as "atmometers" react to external factors in a manner somewhat similar to the plant body and that atmometers possess many advantages over the open-pan evaporimeter; that is, the atmometers measure rather accurately that summation of atmospheric factors that tend to make demands upon the water within the plant body. They can take no account, however, of the modification of transpiration by stomatal control or by osmotic concentration of the cell contents.

The evaporating surface of the atmometer is a porous clay cup, preferably of spherical form, fed from beneath from a water reservoir.

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[1] A good account of the physics of evaporation and of the relationship of transpiration to evaporation may be found in Maximov, "The Plant in Relation to Water," pp. 133–155, 1929.

When water is evaporated, the level in the reservoir falls and the amount of water evaporated is read from the changes in the surface level and expressed in cubic centimeters per hour or per day, from the standard atmometer. The atmometers most widely used are those devised and improved by Livingston (1915). As the atmometer cups vary somewhat individually, each one is compared with a standard cup and is given a coefficient of correction. Thus if the coefficient of correction for a given cup is 0.70 and the loss from the cup for the given time is 40 cc., then 40 × 0.70 = 28 cc., which is the rate of evaporation from the standard atmometer for the given place and time.

The improved Livingston-Thone atmometer mounting (Fig. 76 *A*) consists of a broad bottle with rubber stopper through which pass two glass tubes, the one (*a*) for filling the bottle with distilled water, the other (*b*) for connecting the porous cup with the water within the bottle. When the instrument is set up, the bottle is filled to a mark on the tube *a*, and by measuring the water required to refill to the same mark the loss for the period of exposure may be readily and accurately ascertained.

Since all types of porous porcelain atmometers will absorb water from rain or mist, returning it to the reservoir and thereby falsifying the reading, it is necessary to equip the mountings intended for field work with some type of rain-proofing valve. The valve most widely in use is one devised by Livingston and Thone (1920) (Fig. 76 *A*, *c*). This consists of a column of mercury, about 5 mm. high, resting on a plug of wool, absorbent cotton, or other porous material *e*. The mercury acts as a highly flexible yet perfectly sealed check valve, permitting upward movement of water but preventing a reversal. A second plug of porous material *f* higher in the tube prevents loss of mercury when the apparatus is being handled. Other successful rain-proofing valves for atmometers, devised by various workers, are described by Thone (1924).

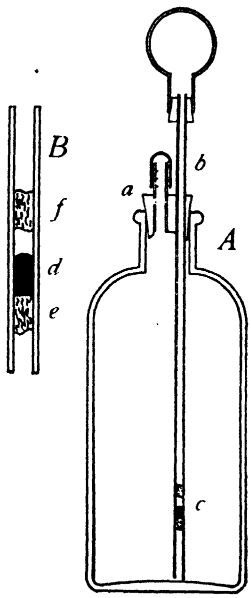

FIG. 76.—*A*, The Livingstone-Thone atmometer mounting; *B*, a detail of the rainproofing valve.

A convenient modification of the above mounting consists in making the valve in a bit of glass tubing about 5 cm. long (Fig. 76 *B*) and attaching this to the lower end of the tube within the bottle by means of a short piece of rubber tubing.

Evaporating cups standardized by comparison with a normal cup may be purchased.[1] Black cups are also available (radioatmometers). These have a higher rate of evaporation in the sunlight on account of the absorption of heat rays.

Convenient mountings have been devised by Johnston and Livingston (1916), Wilson (1928), and Chalkey and Livingston (1929) for making readings from the Livingston atmometers at intervals of one minute or less.

One of the best instruments for obtaining almost instantaneous readings in different plant communities is the Piche evaporimeter, devised in 1872 and much used by meteorologists. It is a simple, easily manipulated instrument and suitable for studies of limited duration. It consists of a graduated glass tube to the lower end of which is affixed a disk of filter paper that may be colored green, more closely to resemble a leaf. As the disk is kept constantly wet from the water in the tube, the loss by evaporation may be read from the graduations at intervals of half an hour or more, and the results expressed in cubic centimeters per hour. It permits simultaneous readings in adjacent communities and easily demonstrates the great differences between the aerial conditions of associations in the open and those in the shade (Fig. 77).

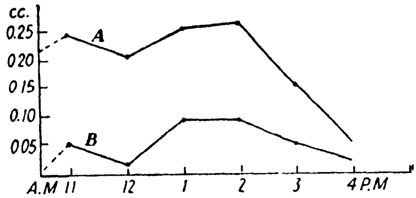

Fig. 77.—Hourly evaporation from a Piche evaporimeter in the open in a *Brachypodium ramosum* garigue association (*A*) and under the *Quercus ilex* scrub (*B*) near Montpellier, France, November 21. Light clouds; temperature 16° to 19°C.

Evaporating Power of the Air as a Habitat Factor.—The measurements of Wetter (1918), Lüdi (1925), Müller (1924), and Walter (1928) in Switzerland and Germany show clearly the importance of the evaporation factor for the ecological differentiation of plant communities. But they were on too small a scale to show the precise relations of evaporation to the individual communities. The investigations of Yapp (1909) in England and of Fuller (1914,) Weaver (1914), Transeau (1910), and Gates (1917) in America have been more extensive and more conclusive.

Fuller (1914) studied evaporation and soil moisture in relation to vegetational succession near Lake Michigan throughout three growing seasons. The evaporation curves of the different years show considerable differences. The maximum in midsummer (July–August) was preceded by a smaller maximum in May. The maxima and

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[1] Atmometer Apparatus Co., Baltimore, Maryland.

minima of the graphs and the general course of the curves are in general agreement for all the communities studied, but the amounts of evaporation and the differences in the evaporating power of the air in the different communities are characteristic.

The development of vegetation in the Lake Michigan dune area proceeds from xeric to mesic conditions. This is clearly shown by the progressive reduction of evaporation from the pioneer stages to the beech-maple climax. The beech-maple climax forest has the lowest evaporation and the least variation in the evaporating power of the air. The *Populus deltoides* pioneer association of the dunes has not only the most intense evaporation but also the greatest fluctuations.

The mean daily atmometer readings throughout the three growing seasons in the lower layers of the forest communities are thus related to the development of vegetation: *Populus deltoides* dunes 22.3 cc.; *Pinus banksiana* dune forest 10.4 cc.; *Quercus velutina* dune forest 11.0 cc.; *Q. borealis* forest 8.8 cc.; *Fagus grandifolia-Acer saccharum* forest 7.0 cc.

The evaporation maximum in May, before the trees leaf out, is very marked and indicates the different conditions to which the vernal and aestival herbaceous plants are exposed.

The investigations of Weaver (1914), in the mesophytic conifer forests of eastern Washington show that throughout the summer the evaporating power of the air is essentially the same as in the beech-maple forests of Indiana investigated by Fuller. In other words, the mesophytism of the two climax types is of the same order; the moisture conditions of their atmospheres, the same.

Striking results are given by the investigations of Weaver, and of Weaver and Thiel (1917, 1918) in the forest and prairie areas of Washington, Idaho, and Nebraska. Their evaporation curves make a valuable complement to the characteristics of the associations investigated, even though these were rather too broadly conceived. The similarity of the course of the evaporation curves in different associations brings out clearly the dominating influence of the general climate (Fig. 78).

The quantitative demands of individual communities are indicated by the intensities of the evaporation measured in their midst. It should be noted, however, that the aerial parts of different plants in the same community may be exposed to very different evaporating power of the air, depending on the height from the ground at which the foliage is displayed. Yapp (1909) found the evaporation in an English fen at 2 cm. above the surface to be 20 per cent of that at 10 cm. and only 5 per cent of that at 20 cm. Similarly, Sherff (1913) in an American Phragmitetum found the daily evaporation at the surface of the soil, at 25 cm., at 107 cm., and at 198 cm. above the surface to be respectively 2.5, 4, 5.3, and 7.5 cc., while Fuller (1912) in the beech-maple forest of Indiana reported the evaporation at 2 m. above the soil to be double that at 25 cm. This leads to the conclusion that plants may grow in close proximity to each other and yet be subject to widely different growth conditions.

Thone (1922) working in Illinois made comparative measurements with the ordinary spherical atmometer and the blackened radio-atmometer. On the forest floor the maximum difference in readings of the two kinds of atmometer was in the first 10 days of May under conditions of high illumination. The rest of the time the readings were about parallel.

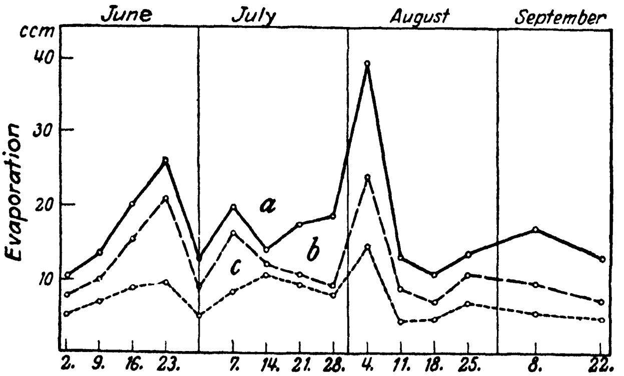

FIG. 78.—Evaporation graphs (*a*) for the *Andropogon* prairie; (*b*) for the Corylus scrub; and (*c*) for the *Tilia americana-Ostrya virginiana* forest near Peru, Nebraska. (*After Weaver.*)

The relative dryness (relative xerophytism) of the habitat may be deduced from the relation between water used by the plant and evaporation. The higher the relative dryness the more open is the ground cover, the fewer the tree seedlings, and the fewer the annuals that persist through summer.

The evaporating power of the air, although greatly underrated by practical foresters (*cf.* Bühler, 1918, p. 150), is undoubtedly an extremely important factor in forest ecology. It is often decisive in reforestation of grassy slopes, in reclaiming alluvial sands, and in the conflict between forest and steppe. Even in the forest areas of northern Switzerland, southern Germany, and eastern France, in the beechwood climax regions, one may search in vain for seedlings of beech in dry grassland (Xerobrometum), and oak seedlings are one and all destroyed in dry summers. Only the drought-resistant Scotch pine, *Pinus silvestris,* can endure long droughts in the seedling stage. The slightest protection by shrub or tree layers alters the evaporation relations and with it the chance for tree seedlings to develop.

Larsen (1922) found the atmometer readings in the *Pinus strobus* forest hardly half as much as in the open. The daily means (from July 13 to Aug. 31), were 16.0 cc. in the forest against 35.3 cc. in the open. Measurements of evaporation made at the German forest reserve research stations, showed that evaporation in beech woods during the summer months is only one-third of that in the open. The annual evaporation in spruce woods and in pine woods averaged 48 per cent of that in the open; in beech woods, 42 per cent.

Finally, we must consider the ability to reduce leaves and stems, to shorten the duration of the life cycle, and to mature seeds in or close to the ground (geocarpy, basicarpy). All of these capacities are adaptations to a dry climate and hence are especially common in communities of arid regions.

E. Ratio of Precipitation to Evaporation

In endeavoring to represent the water relations of the soil by a single unit, Transeau (1905) employed the ratio between precipitation and evaporation. He obtained his ratio (P:E) by dividing the normal annual precipitation for each station in the United States by the corresponding total evaporation from Russell's (1888) record of evaporation data. The ratio values range from 0.4 for parts of California and Nevada to 1.76 for portions of North Carolina and 3.84 for Tatoosh Island, Washington. From these data the United States was divided by isoclimatic lines into four climatic zones which correspond fairly well to the great plant-community types.

Livingston and Shreve (1921) have somewhat extended this idea, but there are yet too few evaporation data to permit this expression of humidity to be very significant.

N. S. Quotient

In seeking a substitute for evaporation, Meyer (1926) argued that air humidity as well as temperature regulates the amount of evaporation. He therefore proposed the so-called "N. S. quotient" (*Niederschlag und Sättigungsdefizit*)—precipitation by saturation-deficit quotient. In spite of its imperfections, appreciated by Meyer, the ratio (quotient) appears to give significant results, and it has the advantage of the abundant air humidity data which are of record. The larger features of the distribution of both vegetation and climatic soil types agree with the results of this factor, as seen in an N. S.

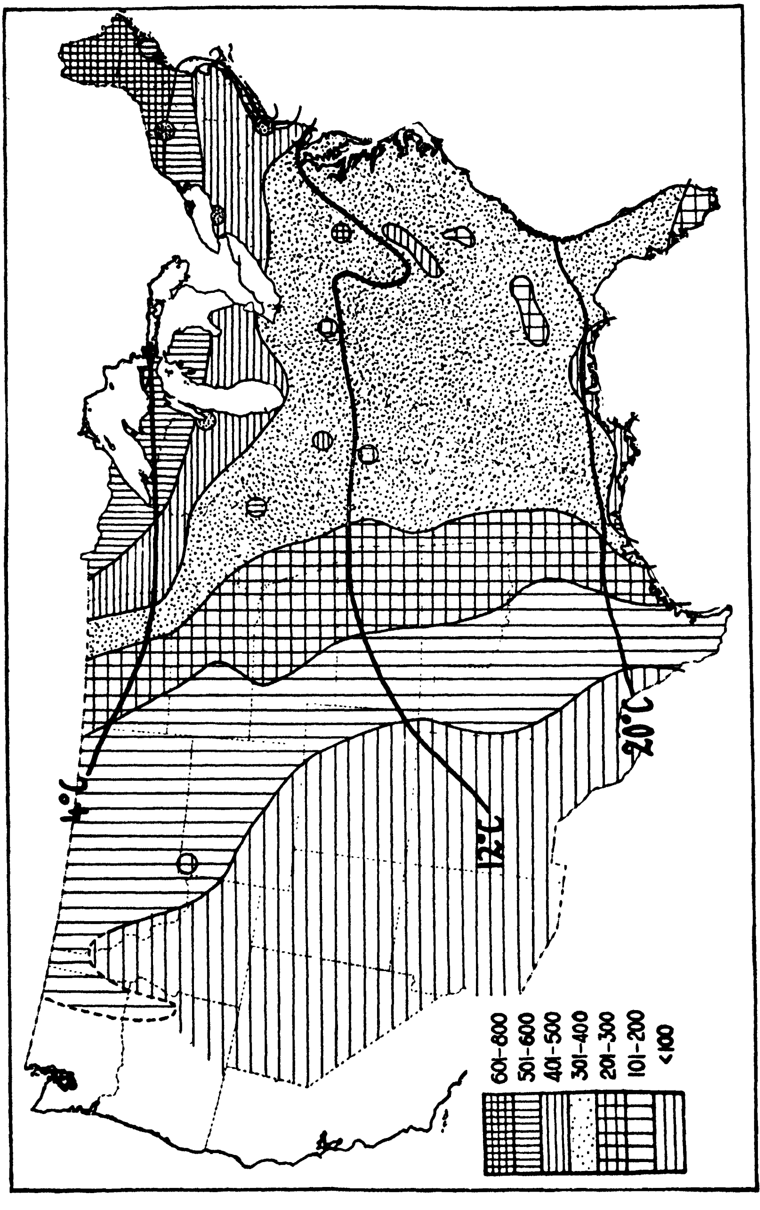

FIG. 79.—A humidity factor (N. S. Quotient) map of the United States, and the annual isotherms of 4°, 12°, and 20°C. (*After Jenny.*)

quotient map of the United States by Jenny (1930) (Fig. 79).[1] Jenny has also taken advantage of this to show graphically the relations between the nitrogen content of the soil and the climate along two isotherms in the United States. The one line (11°C.) belongs to the temperate region and includes territory in Colorado, Kansas, Missouri, Illinois, Indiana, Ohio, and New Jersey; the other (19°C.) passes through the subtropical states of Texas, Louisiana, and Mississippi (Fig. 80).

5. WIND

Wind becomes of importance as a habitat factor on shores, on broad open plains, and on mountain ridges.

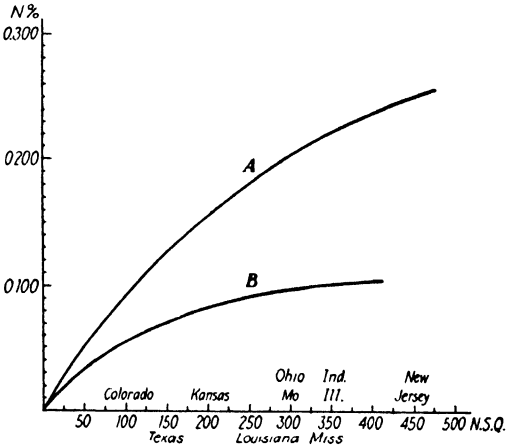

FIG. 80.—The relation of the soil nitrogen content (N) and the humidity factor (N.S.Q.) for grassland soils of the United States; along the annual isotherms (A) of 11°C.; and (B) of 19°C. (*After Jenny.*)

Winds are stronger the farther one goes above ground level. According to Hellmann (*Meteor. Zeitschr.* **32:** 1915), the mean annual velocity of wind in an open field in Nauen was 3.29 m. per second at a height of 2 m.; 4.86 m. at 16 m.; and 5.54 m. at 32 m.; that of the wind-swept coast of southern Ireland has 7.4 m. per second (Valencia). This is almost as much as the alpine summits of Säntis (2,440 m.) with 7.7 m. per second; and Mount Washington, which stands quite alone (1,950 m.), with 15 m. per second (annual means).[2]

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[1] A similar climatic map of North America based on precipitation effectiveness and temperature efficiency has been constructed by Thornwaite (1931).

[2] Since Kihlman's (1890) epochal investigations on the effect of wind upon vegetation, a mass of data has been collected on the wind factor. Among the

The extremes are quite remarkable. For example, at Sonnblick, the mean for one hour was 38.1 m. per second; on the Säntis the anemometer registered on Jan. 27, 1890, a daily mean of 32.3 m. per second, with a velocity between 1 and 2 p. m. of 46.1 m. per second. The maximum in Zurich during 1890–1900 was 24 m. per second. Such winds can snap off or uproot a whole stand of trees and tear off slabs of rock from frozen ground and whirl them aloft (Braun-Blanquet, 1913, p. 53).

Winds act mechanically by their pressure and physiologically by increasing evaporation, *i.e.*, water loss. Continuity of wind action is the factor that most affects the form of vegetation.

FIG. 81.—Wind form of trees. *Cupressus macrocarpa* deformed by ocean winds, Pacific Coast, California.

Mechanical Effects of Continuous Winds.—Winds effect the pollination of anemophilous plants and facilitate the distribution and migration of many plants by increasing the range of dissemination of seeds. Transport of wind-blown seeds over distances of 10 to 20 km. is not unusual. Seeds of *Picea, Pinus silvestris, Larix, Alnus viridis,* and *Acer pseudoplatanus* have been collected on snow fields far above their last outposts and 10 to 15 km. from the nearest seed-bearing trees.

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more important contributions are those of Klinge (1890), Vogler (1901), Früh (1903), Warming (1902–1903), Buchenau (1903), Hansen (1904), Kraus (1910), Skottsberg (1916), Th. C. E. Fries (1913), Braun-Blanquet (1913–1915), Szymkiewicz (1924), Flahault (1925), and Hauman (1927).

It is a significant sociological fact that the regularity in the direction of the wind at seeding time in many places causes a distinct tendency toward distribution and migration of species in the direction of the prevailing wind. Christ called attention to this in speaking of the immigration of rare alpine species into the Säntis Alps. In southern France the natural flight of seeds of isolated Aleppo pines is chiefly in the direction of the prevailing wind (mistral), and in this direction the seeds travel farthest from the mother trees.

FIG. 82. Wind form of *Cedrus atlantica* at the Lalla Kheditscha (2,200 m.) Algeria. (*Photo by K. Müller.*)

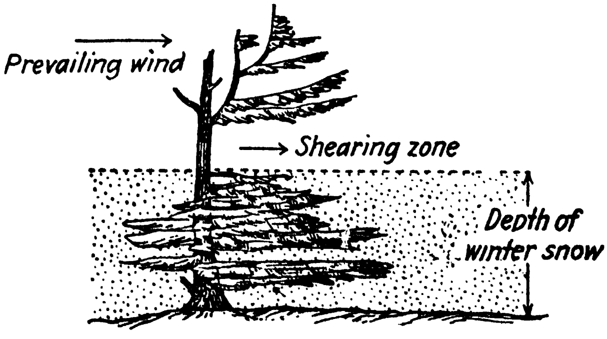

FIG. 83.—The flag form of pine at the wind timber line in the Alps.

Wind pressure causes injury by crippling and deforming trees and shrubs. Injury to young shoots and buds on the windward side is often accompanied by increasing growth on the leeward side, forming those peculiar flag shapes and trimmed-up, smooth-shorn hedge forms

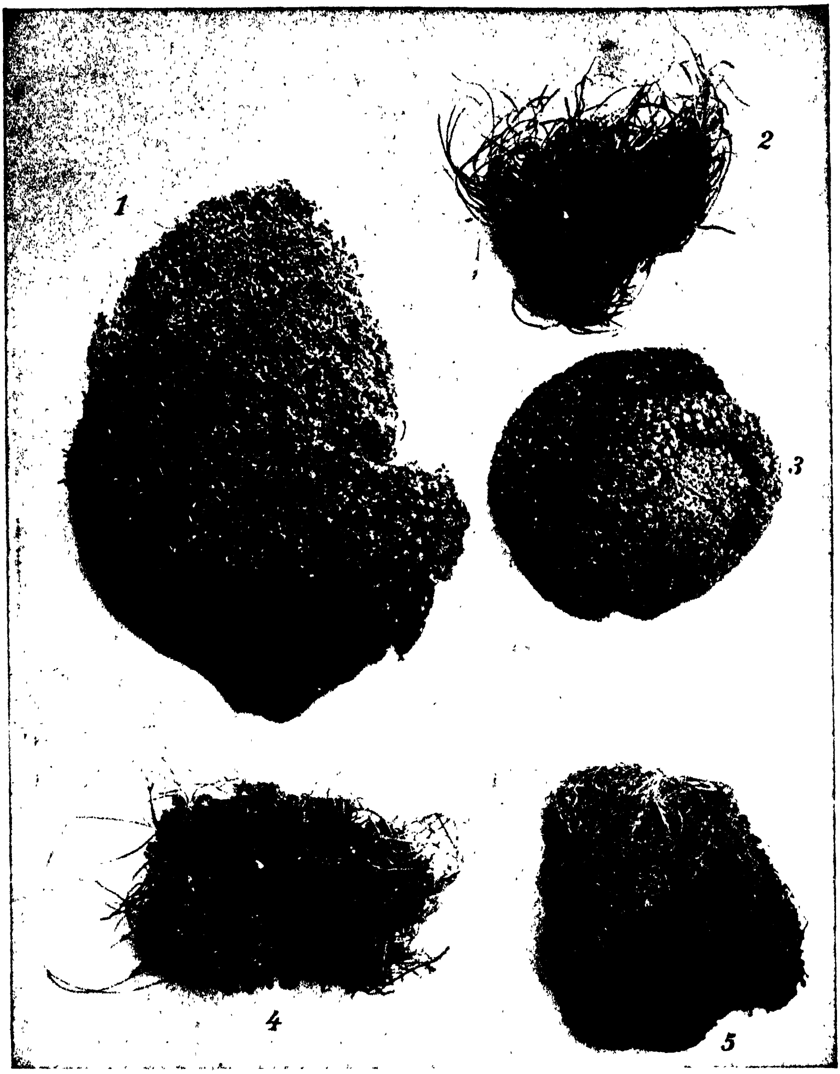

Fig. 84.—Effect of snow blast on exposed ridges in the high Alps. 1. Clump of *Silene acaulis* cut away on one side. Flimerstein, 2,670 m., January, 1911. 2. *Elyna myosuroides* partially eroded. Aelpli Pass, 2,640 m. 3. *Androsace helvetica* cushion killed on one side. Stäzerhorn, snowless rock promontory, 2,500 m. 4. *Elyna myosuroides* from Piz Lagalb, 2,600 m. 5. *Festuca glacialis* cushion cut away on one side. Pyrenees, 2,660 m. (*Braun-Blanquet.*)

which are so characteristic of wind-swept regions (Figs. 81, 82). The direction of the prevailing wind may be clearly deduced not only from trees and shrubs but even from grassland vegetation.

Sand, grit, or crystals of salt or snow acting as abrasives accentuate the mechanical effects of wind. This sand-blast action is strongest a few centimeters above the surface of the ground or snow. This cutting zone is often destructive to trees and shrubs (Fig. 83). Branches and twigs within reach of the wind show, in the danger zone, more or less distinct marks of the sand or snow blast. They are barked and eroded on one side or on all sides and are often partly cut off. Even closely prostrate shrubs like *Dryas*, species of *Salix*, *Loiseleuria procumbens*, and cushion plants bear marks of wind erosion. Sand grains and snow crystals produce similar erosion effects, but sand cuts deeper than snow (Figs. 84, 85). In Finnish grazing districts, according to Häyrén, cushions of *Hedwigia albicans* and *Rhacomitrium* species are especially resistant.

FIG. 85.—Effect of sand blast in the desert. 6. *Stipa tenacissima* (Halfa) from rock ridge of sand dunes. Biskra, Sahara. A dead colony eroded by sand. 7. *Andropogon laniger*, clump eroded on one side. Tolga, Sahara. 8. *Centaurea omphalotricha*, growing plant body, three-fourths of which has been worn away. Rock desert between Tolga and Biskra. (*Photo by Braun-Blanquet*, 1913.)

Wind is of especial importance to plant sociology in its rôle as distributor of sand and snow. The local depth and duration of snow cover depend less upon the amount of snowfall than upon the prevailing wind relations. Every winter it is the same ridges, crests, and peaks that are blown bare and the same depressions and corners sheltered from wind which are overspread with great masses of snow. Hence shrub communities of *Rhododendron*, *Vaccinium*, and *Juniperus*, and in the north *Betula*, *Picea*, and other species exposed to wind, are reduced to the height of the average thickness of the winter snow. Their table-like tops mark the depth of the snow-cover.

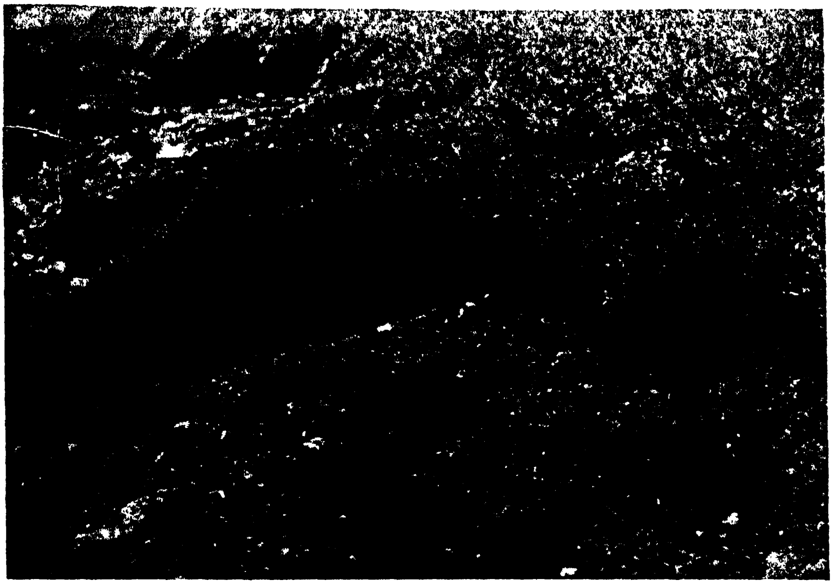

FIG. 86.—Wind attack upon Elynetum at the Piz Padella (2,500 m.). (*Photo by Klika and Braun-Blanquet.*)

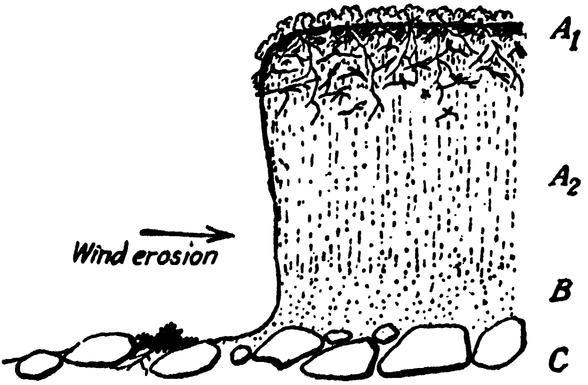

FIG. 87.—Frontal wind erosion and soil profile in the Empetreto-Vaccinietum on limestone in Tatra Mountains.

On wind-swept surfaces the injurious sand-blast effect of wind goes so far as to undermine and break down the sod, especially in the Elynetum and the Caricetum firmae. Using every break in the sod as a new point of attack, the wind digs and gnaws like the breakers on a rocky coast. The soil crumbs are loosened and crumbled, and roots are laid bare. Lichen scales nestle in the dying tussocks, which finally break to pieces and are blown away with the fine soil. The undermining and destroying of the turf goes on until the nature of the soil stops it. By a frontal attack, wind clefts are made (Figs. 86, 87). A lateral attack results in long wind furrows, so that the outline of the ridge looks

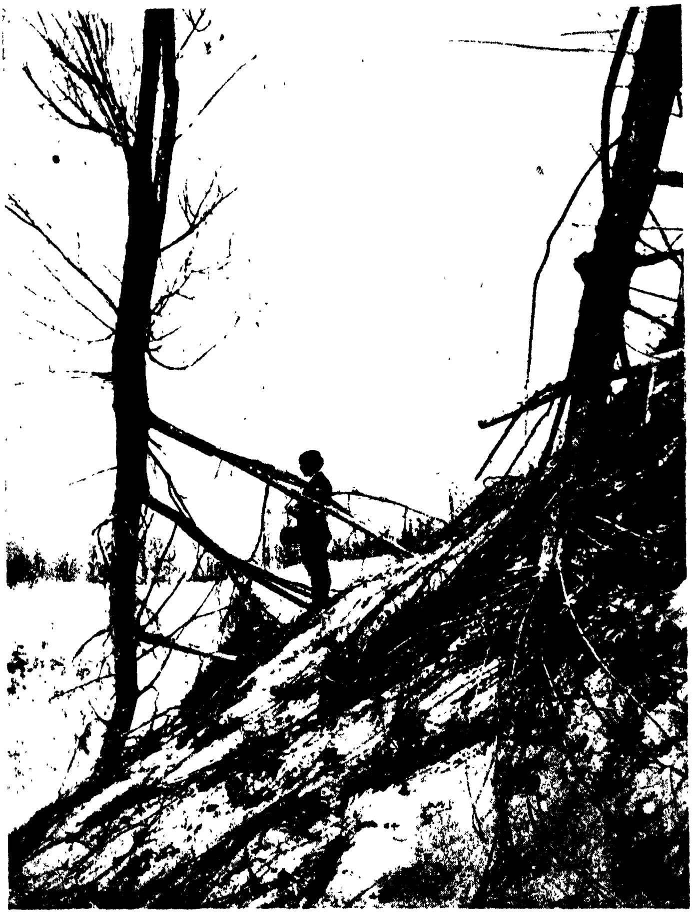

FIG. 88.—Wind erosion uncovering *Populus deltoides* trees that had been buried in dune sand and had put out adventitious roots that are now exposed. Miller, Indiana. (*Photo by Fuller.*)

Wandering Dunes.—The stabilization of truly wandering dunes by natural plant communities is well-nigh impossible without human aid, even where the wandering dunes are separated by wide interspaces. Nevertheless, the behavior of natural plant communities gives most helpful suggestions for the artificial control of the dunes (Fig. 162).

In the great region of wandering dunes between Cape Sim and Cape Ghir, on the south Moroccan coast, there lies between the dunes which are 20 m. or more in height an extremely characteristic succession of communities. The study of this succession has led to rational methods of dune control. It begins on the strips of land most recently left by the dunes. The initial stage is made up of *Ononis tournefortiana* and is followed by a closely crowded association of *O. angustissima.* This is later overgrown by a scrub of *Retama webbii,* but before the last is fully developed the next dune rolls in and buries the scrub.

FIG. 90.—Aestival aspect of the *Ammophila-Medicago marina* association at Carnon, near Montpellier (in the foreground *Echinophora spinosa* and *Euphorbia paralias*). (*Photo by Rübel and Uehlinger.*)

Artificial stabilization of dunes begins with the *O. angustissima* stage, which is planted by the hectare. Seed-bearing shoots are scattered about over the area and anchored with sand. When the Ononidetum has taken hold, *Retama* is sowed in it, or it appears sooner or later naturally and without any help (Fig. 163).

Physiological Effects of Wind.—Along with the mechanical effect of wind goes always the physiological drying effect.

If the water supply of the plant is inadequate, if water movement is slowed up by frozen ground, strong winds produce the same wilting effects as severe drought. The young succulent shoots dry up, the leaves turn brown and often bend or roll up at tips and margins where water loss is greatest. According to Hansen (1904), the vascular bundles lose their conductivity under the influence of wind, which causes drying and death of the mesophyll.

The physiological action of wind determines the polar boundaries of forest. According to Kihlman (1890, p. 75), it is neither the mechanical force of the wind nor the cold nor the salt content nor the humidity of the atmosphere which sets a limit to the forest but rather the uninterrupted drying out of the young shoots, lasting for months, at a season when replacement of the water lost is impossible.

On the limits of tree growth in the north and in mountains the physiological drying effect of wind is always accompanied by mechanical injury, and arboreal vegetation always shows the combined effect.

Total Effect of Wind.—Resistance to wind injury, like resistance to cold and drought, is a specific character, only partly referable to morphological and anatomical modifications. Dense cushion-like growth is often induced by wind action and is always to be regarded as a protection against high winds. Cushion plants are characteristic of windy habitats: coast regions, desert steppes, crests of high mountains, and the arctic. Cushion plants are not only less sensitive to wind but also less sensitive to variations of temperature and intense insolation. It is therefore difficult to estimate wind resistance of plants uninfluenced by other factors. It would be valuable in forestry to know the specific wind resistance of trees and their relation to the wind factor near the timber line. Many mistakes in reforestation might thus be avoided. All of the many attempts at reforestation on the crest of Mont Aigoual and on the Col de Trepaloux in the southern Cévennes (1,520 to 1,560 m.) have come to naught because of underestimation of the wind factor. Similar failures have often occurred in the Alps.

Wind and Plant Communities.—The greatest influence of wind upon the form of vegetation is not by hurricanes which snap off and uproot whole stands of trees but by continuous currents of air. Nowhere is this more readily seen than in mountains, where protection from wind is the necessary condition for the existence of many plant communities. The extremes lie hard by one another and are the more sharply marked, because the wind also controls the distribution of the snow. The vegetation of habitats exposed to wind is totally different from that of protected places, so that even in still weather the wind relations of the habitat can be deduced from the vegetation. These relations have been minutely studied in Lapland and in the Swiss Alps. In Lapland the characteristic associations of wind-swept places are the *Parmelia lanata, Gyrophora proboscidea, Hierochloe alpina, Dryas octopetala, Diapensia lapponica,* and the *Loiseleuria procumbens* association with abundant lichens (Fries, 1913). In the Central Alps the Loiseleurietum cetrariosum covers wind-swept crests and hogbacks. This acidophilous azalea heath with abundant lichens presents several variants, which differ in their resistance to wind.[1] On thin calcareous soils this association is replaced by the Caricetum firmae, with abundant *Dryas*. At the higher mountain levels, the extreme habitats, blown bare of snow all winter, are occupied by the Elynetum, the Curvuletum elynetosum, and the Curvuletum cetrarietosum with abundant mixture of wind lichens (*Thamnolia vermicularis, Cetraria cucullata, C. nivalis, C. juniperina*).

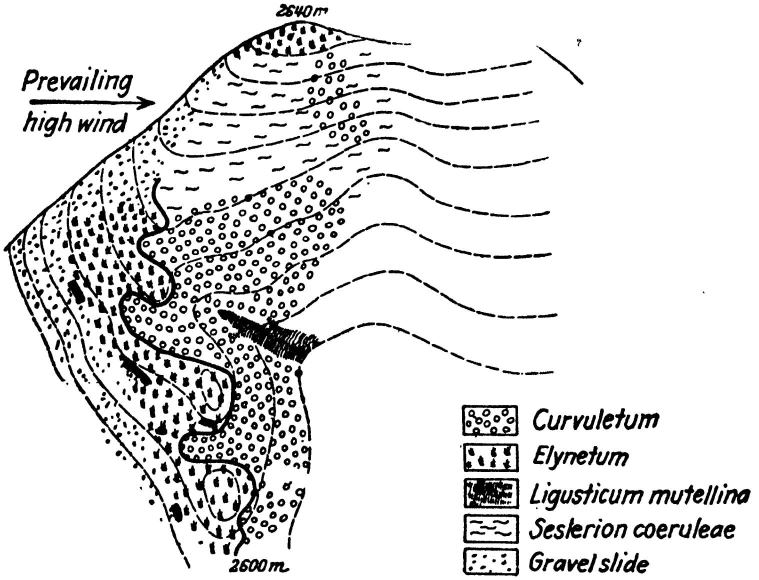

FIG. 91.—Alternation between the Elynetum and the Curvulatum at the Murtèrjoch Swiss Alps, 2,600 m. (*Braun-Blanquet and Jenny.*)

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[1] The most resistant dwarf-shrub community of the greater Alps is the Loiseleurietum alectorietosum, a sub-association of the Loiseleurietum cetrariosum with *Alectoria ochroleuca, A. nigrescens,* etc.

In the Tatra in place of our Elynetum is the Trifidi-Distichetum; in the Auvergne (at 1,700 to 1,850 m.), the association of *Festuca spadicea* and *Chrysanthemum delarbrei* (Braun-Blanquet, 1926); and in the Pyrenees, an association related to the Elynetum, in which *Elyna* often dominates. On the wind-swept crests of the high Atlas (Jebel Ourgouz) are found beautiful examples of wind erosion at 2,500 m. in a *Festuca maroccana-Scutellaria demnatensis* association covering the crests.

FIG. 92.—*Pinus montana* in the Nardetum on the summit ridge of the Aigoual (South Cévennes), 1,500 m. (*Photo by Furrer.*)

Alpine wind communities in the Rocky Mountains of Colorado show splendid examples of the cushion-mat type of vegetation. Characteristic of wind-swept slopes and ridges are the *Paronychia pulvinata, Arenaria sajanensis, Trifolium nanum, Carex rupestris,* and *Sieversia turbinata* associations. Rounded shoulders frequently have all soil and rock fragments stabilized by cushions of *Paronychia, Trifolium,* and other mat-forming species. Gentle slopes and depressions along which rush the powerful descending wind currents, sometimes gathering up and other times depositing the coarse wind-borne fragments, are frequently terraced and more or less stabilized by the dwarf shrub *Dryas octopetala* and its companion *Carex rupestris.* Both these species exhibit remarkable powers of adaptation for combatting either degradational or depositional action which alternates according to the velocity of the wind. The zonation of the vegetation according to the degree of wind exposure is outstanding.

All of these "wind communities" are sharply circumscribed in area and well differentiated from the surrounding turf communities (Fig. 91). They offer a fruitful field for the study of comparative ecology. In addition to direct wind effects, exposed ridges often show indirect influences upon the habitat, by changing the composition of the soil, the soil fauna, the circulation of carbon dioxide, etc. These conditions, however, have not been investigated. The soil on exposed ridges is often less acid than adjacent soils protected from wind. Dense crowding in a community increases the wind resistance of the individual members, be they trees, shrubs, or herbs.

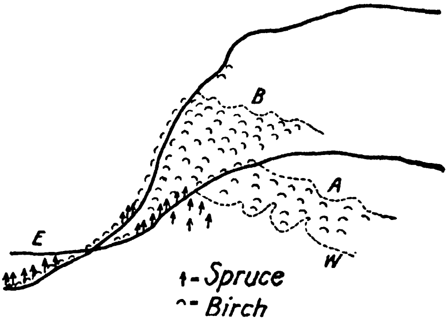

FIG. 93.—*A*, Wind timber line upon a bare ridge; and *B*, a temperature timber line on a steep slope, Lapland. (*After Hannerz.*)

Wind and Boundaries of Forest.—The treelessness of exposed islands and sea coasts is well known. The relation of the polar forest boundary to wind effects has been especially clearly shown by Kihlman (1890). According to Skottsberg (1913, 1914) and Hauman (1926) the treelessness of large parts of southern Argentina is due to the continuous high winds. They cause, in western Patagonia, in Tierra del Fuego, and on the Falkland Islands a maritime "tree line," beyond which only a bare cushion heath exists. Morisson attributes the poverty of southern Patagonia to the destructive force of the west and southwest winds and the consequent impossibility of carrying on agriculture outside the few protected *barrancos.*

Szymkiewicz (1923–1927), from his studies of climate, concluded that the cold regions of the earth must remain treeless wherever the wind, 10 m. above the surface, attains a mean velocity of 6 m. per second.

High winds accompanied by freezing temperatures are especially unfavorable for tree growth. Hence the peculiar course of the forest boundary parallel to the coast on both sides of Bering Strait and in Labrador. Hence also the depression of the timber line on exposed crests of the central Alps, in the Black Forest, in the Vosges, in the Auvergne, in the southern Cévennes (Fig. 92). As a result of these wind-induced timber lines, the beeches growing highest on the slopes of the Black Forest (up to 1,450 m.) are at about the same altitude as those that are highest up in the southern Cévennes, several degrees of latitude farther south. And the high forest on exposed crests is surrounded by a protective belt of creeping beeches, now, however, much broken through.

In Swedish Lapland, wind-induced timber lines are characteristic of the isolated flat mountain summits. They often run considerably below the forest boundary as determined by temperature (Fig. 93).

CHAPTER VI

EDAPHIC OR SOIL FACTORS: CHEMICAL

While man must accept the climate and surface contours of the earth as they are and must confess himself almost powerless to alter them, it is within his power to influence the conditions of the soil considerably, transforming them to fit his needs. Soil problems, therefore, have engaged not only research workers in botany but also farmers, foresters, and gardeners. Indeed, there is no other field where so many different practical and purely theoretical interests coincide. The soil presents a tangled complex of factors. The individual factors are constantly interacting and in their reactions they may more or less displace or even eliminate one another.

The soil problem, therefore, cannot be resolved into simple formulae, as was formerly supposed. In the search for such formulae the soil experts of the nineteenth century have spent a vast amount of effort and labor with relatively little results.

Chemical Soil Theory.—A. P. de Candolle, of Geneva, refused to admit that the chemical composition of the soil had any considerable influence upon the occurrence and distribution of plants. He ascribed prime importance to the presence or absence of organic substances in the soil (1832, p. 1245). Unger, however, placed great emphasis on the dependence of plants upon the chemical nature of the soil. The North Tirolean Alps revealed to him the sharp contrasts which exist between the silicicolous flora of the interior mountain chains and the calcicolous flora of the outer ranges. In his famous prize essay "Über den Einfluss des Bodens auf die Verteilung der Gewächse" (Vienna, 1836) on the influence of the soil upon the distribution of plants, he demonstrated that, besides those plants which thrive in any variety of soil, there are many others which are strictly confined to certain kinds of soil. On this basis he distinguished between plants which are, with respect to soil, constant, preferential, and indifferent.

The constant and preferential species he considered chiefly conditioned by the chemistry of the soil and divided these "soil indicators" into two large groups: lime plants and clay-slate or silicicolous plants. For both groups he cited numerous examples. Shortly afterward (1838) Ruehle published an extensive index of indifferent and soil-determined alpine plants (lime constant, lime preferring, archaean constant, archaean preferring). Unger went so far as to make the chemical composition of the soil responsible for the origin of many plant species. He claimed that they had segregated from the original types under the influence of "very different soils." Closely related species found upon lime and clay slates he called substitute or vicarious forms.

Though it may not be necessary to agree with Unger's statements in every detail, the essence of his views is even now accepted. Limestone formations and calcareous soils are very widely distributed in nature. The dependence of plant distribution and plant grouping upon lime is therefore easily determined. Thus it becomes clear why the behavior of plants in regard to the selective action of lime was used as the primary basis of the grouping of vegetation according to the chemical composition of the soil.

While the importance of soil chemistry for the occurrence and distribution of plants and plant communities is beyond all question, purely chemical investigations alone are incapable of solving the soil problem.

Physical Soil Theory.—Credit must be accorded to the Swiss Jules Thurmann for the first clear recognition of the influence of the physical properties of soil. In his "Essai de Phytostatique" (1849) he gives a summary of the soil theories commonly held and sets over against the chemical soil theory of Unger his own physical theory. The soils are divided by Thurmann according to their physical character into pelitic and psammitic soils. Pelitic soils are fine-grained clay soils of a high degree of dispersity. They are products of the weathering of pelogenous rocks (clay slates, marls, limestones).

Psammitic soils are sandy soils with coarse particles. They owe their existence to psammitic rocks which are rich in quartz, especially granites, syenites, gneisses, and certain granular dolomites.

The native rock is, according to Thurmann, either easily weathered (eugeogenous) or weathered with difficulty (dysgeogenous). Siliceous rocks, such as gneisses, granites, etc., are mostly eugeogenous; limestone rocks are mostly dysgeogenous. According to Thurmann, these fundamental physical differences of rocks and soils, and not chemical conditions, determine the composition of vegetation.

By reason of an enormous, although somewhat one-sided, mass of data, the views of Thurmann were promptly accepted, but they never wholly displaced the chemical soil theory.

With Thurmann and with Unger alternately seemed to rest the victory in the resulting strife that for several decades divided plant geographers into two hostile camps and gave a characteristic stamp to the geobotany of the period. Much later it was recognized that both theories have their justification, indeed, that they are frequently complementary, but that neither the one nor the other in its original form does justice to all the evidence recorded. A special chapter would be required to deal with all the arguments which the followers of the two theories advanced in support of the correctness of their views. Famous names—Lecoq, Sendtner, Kerner von Marilaun, A. P. de Candolle, Christ, Contejean, Fliche and others—are connected with these discussions. Today the discussion is of historic interest only although it certainly stimulated geobotanical research for several decades. Advances in chemistry have made the original hypotheses obsolete.

The development of colloidal chemistry and the electrolytic dissociation theory of acidity gave a decisive turn to the soil question. With the discussion of these new aspects of the subject we pass from the older to the modern phases of soil science.

A. Colloid-chemical Viewpoint

Colloid or, better, dispersoid-chemistry, the link between physical and chemical soil research, aims to discover the laws of the relation between the degree of dispersion of substances and their physical and chemical properties.

According to Wiegner (1926), who was the first to base the investigation of soils wholly upon dispersoid chemistry, the soil as a whole is conceived to be a colloidal system. In this system the grains of the soil are the dispersed phase; the soil atmosphere and soil water represent the dispersion medium. The dispersed phase shows an extremely large surface and is the seat of a special form of energy (surface energy). Upon this fact rests the common distinction between light (coarsely divided) and heavy (finely divided) soils. According to their degree of division, their dispersity, substances can be divided into two large groups differing in their physical state and general properties: crystalloidal and colloidal.

Crystalloids are substances whose external, regular form stands in definite relation to the special physical and chemical properties of the substance. As the name indicates, they can be obtained in crystal form. Furthermore, they are capable of passing through thin membranes (parchment) out of a solution into pure water: they dialyze. Colloids (Gr. *colla,* glue) are characterized by their amorphous consistency, their great amount of surface and hence their surface phenomena, their poor diffusion and low osmotic pressure, and the fact that they do not dialyze. An important rôle is played by the surface phenomena, especially by adsorption.

However, crystalloids as well as colloids, while maintaining their chemical composition, may change their physical condition; many crystalloids may be transformed into colloids, and *vice versa.* They pass into one another, often without distinct boundary lines, and are really the same substances in different degrees of division. The degree of division of crystalloids is greater than that of colloids. In colloids the individual particles have a diameter of 1 to $100\mu\mu$,[1] while the individual particles of crystalloids are molecular or ionic and have a diameter of less than $1\mu\mu$. Crystalloids, although highly dispersed systems made up of molecules and ions, do not exhibit active surface phenomena.

The phenomena of adsorption, the most important phenomena of colloid chemistry, are due to the surface action of the extremely fine particles.

Saturated and Unsaturated Colloids.—With progressive division of the particles the effect of the surface forces increases. Colloidal particles are therefore capable, to a high degree, of attracting foreign substances, *i.e.*, of adsorption. A distinction is made between saturated colloids, which have gathered a maximum of foreign substances, and unsaturated colloids, which have not reached their limit of adsorption. Important changes of properties occur when saturation is reached. In the case of soils, these changes are clearly reflected in the vegetation. The behavior of the humus colloids in the soil is of special importance. According to their more minute division they are characterized by greater capacity for adsorption. If soil-alkali cations are present (magnesium, calcium) in ample quantities, they bring about the coagulation of the humus substances; the product is a saturated humus (*cf.* p. 250).

In the absence of bases, in high moors and upon sandy forest soils, the humus colloids remain adsorptively unsaturated and contain exchangeable hydrogen ions. Then the soil is densely packed, poorly aerated, poor in food substances and in electrolytes, and, because of its

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[1] The classification of dispersed systems used in colloid chemistry is based upon the size of the particles (*cf.* Wiegner, 1926, p. 9):

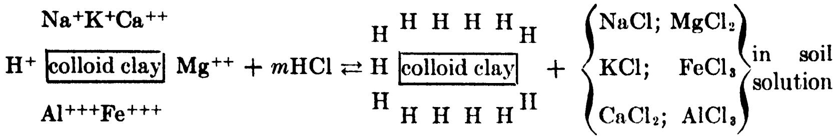
1. Coarsely dispersed systems (dispersions); diameter of particles over $100\mu\mu$ (microns).
2. Colloid-dispersed systems (dispersoids); diameter of particles 1 to $100\mu\mu$ (ultra-microns).
3. Maximal-dispersed systems (true solutions); diameter of particles less than $1\mu\mu$ (amicrons, molecules, ions).

lack of sensitiveness toward electrolytic effects, it gives an acid reaction.

Protective Colloids.—Adsorptively unsaturated, highly disperse humus is, because of its lack of sensitiveness toward electrolytic effects, an efficient protective colloid. Iron hydroxide, aluminum hydroxide, silicic acid, etc., are much more sensitive toward coagulating electrolytes. When the particles are protected by the enveloping colloid particles of the less sensitive protecting colloid of the highly dispersed humus, they themselves are no longer sensitive toward electrolytic effects, so that changes of dispersion are retarded and precipitation may be stopped completely, under certain circumstances. Even very small quantities of protective colloids may prevent changes in the dispersity of the disperse phase. Unsaturated humus, for example, keeps various soil colloids ($Al(OH)_3$, $Fe(OH)_3$, etc.) in soluble, highly dispersed condition. It protects them from precipitation, and renders them highly mobile, susceptible to leaching out. The dark waters of regions of crystalline rocks and of moors owe their color to the protective colloid action of the acid humus. The color is due to leached humus colloids.

The formation of podsol also depends upon the ready displacement of protected colloids ($Fe(OH_3)$, $Al(OH_3)$ sols), which are washed out and disappear from the upper horizons of the soil, to be flocculated below and to enrich the lower horizons where the electrolytic content is greater.

Ionic Exchange.—The phenomena of exchange in many soils, especially significant in the study of fertilizers, are classed as "ionic (or basic) exchange." The various soil colloids are the carriers of the interchange, where the negative particles show basic exchange while the electropositive particles show an exchange of anions. The exchange of bases in agricultural soils has long been known but is properly interpreted only through colloid chemistry. The gels of aluminum hydroxide and silicic acid, important components of clay, bind the ions of ammonium and potassium more strongly than those of sodium and even calcium at certain concentrations. The latter can for this reason be displaced by the former and substituted adsorptively. While ammonium and potassium remain insolubly combined in the soil, the dissolved sodium and calcium ions flow away, and the soil is decalcified by the addition of potassium. Similar phenomena of exchange also occur in natural soils and are of the greatest importance to the development of vegetation. Jenny (1926) explains the leaching of the rendzina soils of the Alps and their transformation into podsol and alpine humus soils, from the viewpoint of base exchange. The H ions displace the cations on adsorbed humus and clay colloids of the rendzina soil according to the following graphic formula:



$$\begin{matrix} & \text{Na}^+\text{K}^+\text{Ca}^{++} & \\ \text{H}^+ & \boxed{\text{colloid clay}} & \text{Mg}^{++} \\ & \text{Al}^{+++}\text{Fe}^{+++} & \end{matrix} + m\text{HCl} \rightleftarrows \begin{matrix} \text{H} & \text{H H H H} & \text{H} \\ \text{H} & \boxed{\text{colloid clay}} & \\ \text{H} & \text{H H H H} & \text{H} \end{matrix} + \left\{\begin{matrix} \text{NaCl; MgCl}_2 \\ \text{KCl; FeCl}_3 \\ \text{CaCl}_2\text{; AlCl}_3 \end{matrix}\right\} \text{in soil solution}$$

The displaced, soluble cations are washed out by rain and melting snow and migrate to greater depths, while the H ions, in spite of continuous additions of bases (from decaying plants, drifting dust particles, animal remains), gather in the upper horizon (Fig. 94).

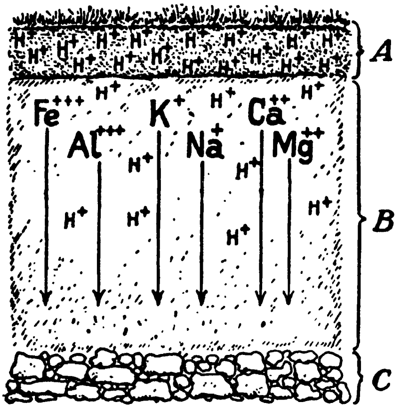


Fig. 94.—Diagram showing hydrion accumulation in the humus horizon (*A*), and the leaching of the products of weathering from horizon (*B*) into the subsoil (*C*).

The exchange of bases here effects a thorough change in physicochemical soil properties, which, as described elsewhere (p. 311), certainly reacts upon the vegetation.

Gola's Osmotic Theory.—The first application of the results of colloid-chemical research to geobotanical problems was attempted by Giuseppe Gola, professor at Padua. His work on this subject, dating back to 1905, was summarized in 1910 in the important "Saggio di una teoria osmotica dell' edafismo."

According to Gola, the prime factor in the relation between the plant and the soil is the osmotic concentration of the soil solutions which come in contact with the root system. The osmotic pressure of these solutions is conditioned by their degree of concentration. The concentration of the dissolved salts in the soil is either stable (eustatic) or rapidly changing (anastatic). The rapidly changing concentration of anastatic solutions exerts upon many plants a particularly harmful influence.

According to their degree of concentration, soil solutions are divided into slightly and highly concentrated solutions. The peculiarities of soils with slightly concentrated salt solutions are due to their colloidal nature. On the other hand, in the soils of highly concentrated solutions the crystalloidal properties predominate. Gola therefore divides soils into two great classes:

1. Geloid soils, characterized by low salt content, slightly concentrated solutions, with colloid properties dominant; dissolved crystalloids less than 0.5 part per 1,000.
2. Haloid soils, marked by rich salt content, highly concentrated solutions with more than 0.5 part per 1,000 of dissolved crystalloids; the concentration, as a rule, rapidly changing, *i.e.*, anastatic.

Plants and plant communities are divided into two major groups according to the following system:

1. Plants of geloid soils:
   - *a.* Pergelicole species. Growing in soils which contain less than 0.2 part per 1,000 of dissolved crystalloids; saprophytes, epiphytes, humus plants.
   - *b.* Gelicole species. In soils with from 0.2 to 0.5 part per 1,000 of dissolved crystalloids; including the species which avoid lime, characteristic of most of the raw silicate soils.
2. Plants of haloid soils:
   - *c.* Halicole species. In soils with dissolved crystalloids from 0.5 to 2 parts per 1,000; plants of soils rich in lime, and denizens of fence rows and roadsides.
   - *d.* Perhalicole species. Growing in soils which have more than 2 parts per 1,000 of dissolved crystalloids; nitrophilous ruderal plants, species of the saline soils of the seaboard and of arid lands.

This classification of soils according to the concentration of nutritive solutions suggests a division according to dispersion and acid content. The geloid soils are more or less identical with those which are acid and highly dispersed; the haloid, with the basic and less dispersed.

B. Soil Acidity

The more modern doctrine of acidity rests upon the electrolytic dissociation theory of the Swedish investigator Svante Arrhenius. The words of Arrhenius are: "Entirely independent of an electric current every electrolyte in solution is wholly or partially split into electrically charged atoms or groups of atoms, which are called ions."

To this must be added the following considerations: Pure water, H_2O, will conduct an electric current to a very slight degree only, and the fluid gas hydrochloric acid, HCl, insulates completely. It might therefore be expected that pure H_2O and HCl mixed together would be equally non-conductive. Strangely enough, however, this mixture proves to be a good conductor of electricity. The HCl gas in aqueous solution really enters into a new state or condition. The solvent, H_2O, splits the neutral molecules into their electrically charged positive and negative ions; *i.e.*, it effects their dissociation. The fraction of a salt which is divided into ions is called the "dissociation gradient" and is measured in the percentage of ionization. The ions, as the smallest particles, move separately from one another within the solution. When an electric current flows through such a solution, the positive ions migrate to the cathode (hence the name cations for these particles), while the negative ions collect at the anode (hence the name anions).

The degree of acidity of any solution depends upon its content of positively charged hydrogen ions (H^+). The preponderance of these H^+ ions gives acids their common characteristic properties, while in bases the negatively charged hydroxyl ions (OH^-) always predominate. In every solution, however, an enduring equilibrium exists between the H^+ and OH^- ions in such a manner that an increase of the H^+ ions is always accompanied by a corresponding decrease of the OH^- ions, or *vice versa.* The more H^+ ions there are present the more strongly acid, the more OH^- ions, the more basic, is the solution. When H^+ and OH^- are present in equal numbers the solution is neutral. This is the case in chemically pure H_2O.

In one liter of pure H_2O, at 18°C., there are 0.0000001 gram-ion of H or, briefly expressed, 10^{-7} gram-ion of H^+ and 0.0000001 gram-ion of OH^- or 10^{-7} gram-ion of OH^-. Since the total number of H^+ and OH^- ions always remains the same, the total mass of ions in pure water is always 10^{-14}. If the solution is acid, the H^+ ions predominate ($H^+ = 10^{-1}$ to 10^{-7}); if it is basic, the OH^- ions are in excess ($H^+ = 10^{-7}$ to 10^{-14}). Thus one can state the degree of acidity of an acid as well as of a basic solution by the quantity of H^+ ions per liter of solution.

Expression of Hydrogen Ion Concentration.—The inconvenience of writing the actual H ion concentration of a solution that is exactly neutral as $\frac{1}{10,000,000}$ gram-ion of H or as 0.0000001 gram-ion of H led Sörensen (1909) to propose the use of the negative logarithm of the H ion concentration as the expression of the degree of acidity, preceded by the sign "pH." When the H ion concentration of a solution is 10^{-6}, by the use of the reciprocal the negative exponent is avoided and it is expressed, according to Sörensen, as pH 6. The pH value of a solution is therefore the logarithm of the reciprocal of the H ion concentration. For the sake of brevity, the pH value is called the hydrogen number.

It must always be remembered that large hydrogen numbers (pH 7 to 14) correspond to a low H ion concentration; small hydrogen numbers, to a high concentration of H ions.

In the language of the plant ecologist, the hydrogen numbers with reference to the behavior of individual species and communities have the following significance:

1. Acidophilous species and communities (calciphobes); soil reaction pH 6.7 to 3.8:
   - *a.* Plants extremely acidophilous, soil strongly acid, pH 5.0 to 3.8.
   - *b.* Plants moderately acidophilous, soil moderately acid, pH 6.2 to 5.0.
   - *c.* Plants weakly acidophilous, soil slightly acid, pH 6.7 to 6.2.
2. Neutrophilous species and communities, soil neutral, pH 7.0 to 6.7.
3. Basophilous species and communities, soil reaction, pH 8.5 to 7.0.
   - *a.* Plants basophilous to neutrophilous, soil basic to neutral, pH 7.5 to 7.0.
   - *b.* Plants distinctly basophilous, soil basic, pH 8.5 to 7.2.
4. Indifferent species and communities on soils that range from basic to highly acid.

Active or Specific Acidity.—The logarithmic H number has the disadvantage that it does not bring into adequate relief the considerable differences in the active H ion concentrations. To remedy this, Wherry (1922) has proposed a method which, starting from neutrality (pH 7 = 1), gives the active acidity or alkalinity. The active or "specific acidity" indicates the quantity of H ions in one liter of solution, referred to the approximate H ion concentration of pure water (0.0000001 g. per liter). The "specific alkalinity" means the corresponding number of OH^- ions. Wherry's method was promptly accepted by North American plant ecologists but is little used in Europe. In European literature it is mentioned by Christophersen (1925), who, however, prefers the indication of acidity by Sörensen's H numbers. In order to facilitate a direct comparison of Sörensen's H numbers with active acidity, the corresponding acidity numbers are given on page 168 with their pH equivalents.

Measurement of pH.—Several methods are in use for the measurement of the H ion concentration of the soil solution, and new and very satisfactory apparatus for its determination are constantly appearing. The colorimetric method is one of the simplest, and equipment for it is least expensive and most portable. When used according to the directions accompanying the testing sets, the results are accurate to 0.1 to 0.2 pH unit, especially on the acid side. Olsen (1927) has expressed the opinion that the colorimetric method is the most satisfactory and that properly used it yields results that are quite sufficiently accurate for all ordinary soil investigations. In Europe the "Folien colorimeter" after Wulff and in America the "La Motte-Morgan soil-testing set" have proved themselves satisfactory, simple, and easily manipulated. They are well adapted for use in the field and, when it seems desirable, may be checked against more elaborate apparatus in the laboratory.

The most accurate method is probably the electrometric. The equipment is here more elaborate and more expensive, but both in Europe and in America portable sets are available that are accurate to

0.02 pH unit. Accurate directions for use always accompany these instruments.

TABLE 13.—SPECIFIC ACIDITY EQUIVALENTS FOR pH VALUES
(After Wherry)

pH	Specific acidity	pH	Specific acidity	pH	Specific acidity
4.0	1,000	6.1	8	8.1	0.08
4.1	800	6.2	6.3	8.2	0.063
4.2	630	6.3	5	8.3	0.05
4.3	500	6.4	4	8.4	0.04
4.4	400	6.5	3.15	8.5	0.032
4.5	315	6.6	2.5	8.6	0.025
4.6	250	6.7	2.0	8.7	0.020
4.7	200	6.8	1.6	8.8	0.016
4.8	160	6.9	1.25	8.9	0.013
4.9	125	7.0	1	9.0	0.010
5.0	100	7.1	0.8	9.1	0.008
5.1	80	7.2	0.63	9.2	0.0063
5.2	63	7.3	0.5	9.3	0.0050
5.3	50	7.4	0.4	9.4	0.0040
5.4	40	7.5	0.32	9.5	0.0032
5.5	31.5	7.6	0.25	9.6	0.0025
5.6	25	7.7	0.20	9.7	0.0020
5.7	20	7.8	0.16	9.8	0.0016
5.8	16	7.9	0.13	9.9	0.0013
5.9	12.5	8.0	0.10	10.0	0.0010
6.0	10				

It has been shown recently by Pallmann (1930) that the inversometric method agrees with the electrometric.

Treatment of Soil Samples for pH Determinations.—The samples are examined as soon as possible after collection, although Gustafson (1928) has shown that they may be kept for weeks in air-dried condition without effecting any appreciable change in their H ion concentration. To 20 g. of fine soil 50 cc. of distilled water are added, and the mixture left in a stoppered flask for 24 hr., shaking frequently.[1] From this solution a required amount is taken after thorough shaking. This precaution is necessary in order to obtain a uniform concentration in the suspension. Pallmann (1930) and others have shown that such suspensions have, in general, a different pH value from the clear solution. Suspensions of acid systems react more acid, while suspensions of alkaline systems are more alkaline than the dispersion medium itself.

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[1] Peat soils which take up much water may be diluted with more water. Indeed, according to Gustafson, the amount of dilution usually makes little difference to the result.

For similar reasons, in the determination of the acidity of peat a prepared suspension and not an extract from fresh peat should be used, since the latter is subject to considerable variations.

Significance of Hydrogen Ions.—The H ion, a simply constructed and most active ion, affects the physiological processes within plants to a high degree. It greatly influences enzyme actions so important in the life cycle of a plant. The concentration of the cell sap of a plant must maintain a certain relation to the ionic concentration of the soil solution. When this relation is interfered with, by change of the concentration of the solution, morbid phenomena soon appear in the plant, and even death may occur. Certain pathogenic bacteria can grow only upon media of very definite H ion concentration. Ulehla (1923) proved that the apical cells of certain algae (*Cladophora, Basidiobolus*) burst when they are transferred into an acid medium. Apparently adsorptive effects of H ions upon the colloidal material of the cell membrane are involved, and not osmotic phenomena.

The harmful effects of parasitic fungi can be diminished or completely counteracted by changes of pH values. According to Fischer (1925), the effect of the potato-scab organism (*Actinomyces scabies*) at pH 8 is strong, at 7.2 weak, at 6.8 near zero, and at pH 5.2 to 5.0 the organism is entirely destroyed. Gäumann (1925) showed that an infection of garden beets by *Phoma betae* produces the heart disease of the roots only in strongly alkaline soils. Attempts to induce the infection in weakly acid soils failed. The decisive influence of pH values upon the vitality of mycorhizal fungi, and thereby upon the vigor of conifers, has recently been demonstrated by Melin (1924).

The higher plants have a more or less wide pH tolerance, with a distinct region of optimum, which may be taken to express the soil preference of the species. The pH optimum of wild species, examined in natural habitats, results in a more or less steep, one-peaked (unimodal) or possibly occasionally in a two-peaked (bimodal) curve.

Pearsall (1926) and more recently Volk (1931) have criticized the two optima of Salisbury and others. These optima seem to have resulted from a very unequal distribution of samples of the soils with respect to their chemical composition, or else they may have resulted from the fact that the species studied belonged to different ecotypes. When associations are concerned, the causes of errors are evidently less, and there are probably no bimodal curves for one and the same association.

Perfect unimodal pH curves were obtained from soils of the root layer of *Ammophila arenaria* at Blakeney Point, England (Salisbury), and of *Carex curvula, C. firma,* and *Elyna myosuroides* from the Alps (Fig. 95).

This curve is based upon 125 soil samples from the Swiss, Italian, and Tirolean Alps, taken from the root region of *C. curvula* (5 to 10 cm. deep). It illustrates the pH tolerance of the species but depends to some extent upon the number of the samples examined. The pH optimum of the species lies between pH 5.4 and 4.6. *C. curvula* is thus a distinctly acidophilous plant. Within the optimum boundaries of the species the acidity seems unimportant for the welfare of *C. curvula;* but in the minimum region (below pH 5.4) acidity becomes the deciding factor. So also in the equally injurious maximum. Here even a small excess or shortage determines the survival and competitive power of the species.

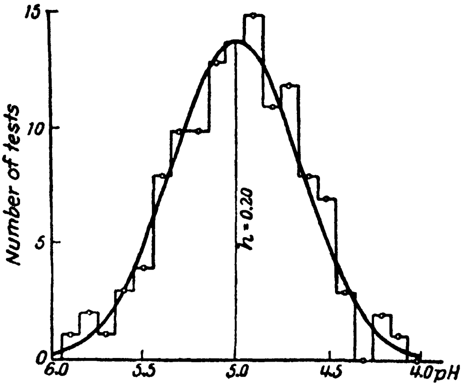

Fig. 95.—Theoretical and experimental curve for the pH values for *Carex curvula;* 125 tests in the Central and Eastern Alps. (*Braun-Blanquet and Jenny.*)

Plant Communities and pH Values.—Each plant community has its own definite tolerance of pH values, with a more or less distinct optimum. This, of course, does not exclude the possibility of other associations having about the same pH optimum. Very extensive communities, for example, the *Quercus pedunculata* and the beech woods of southern England, examined by Salisbury (1925) may show two pH optima. This, no doubt, is due to the fact that two different associations, or at least two different societies, are involved. The researches of Wlodek and Strzemienski (1924), Christophersen (1925), and Braun-Blanquet and Jenny (1926) on more narrowly delimited communities of one or several layers give harmonious unimodal curves, with often a very narrow pH optimum.

For example, the pH range of the *Carex firma* association in the Central Alps (from 100 samples) lies within a range of 0.4 pH unit.

The optimum in the Curvuletum, however, lies within 0.6 pH unit and in the Elynetum within 0.9 pH unit (Fig. 96).

In order to interpret the changes in vegetation caused by changes in the H ion concentration of the soil, the pH curve is indispensable. The points of intersection of the pH curves of the different associations which lie adjacent to one another are of especial ecological importance. They mark the region of sharpest struggle between the established community and the invading species which are favored by the pH change. From such curves (Fig. 96) it may be seen that this keenness of competition between the Elynetum and the Firmetum occurs in soils of pH 7.0 to 6.5; and between the Curvuletum and the Elynetum, in soils of pH 5.5 to 5.1. In these transition regions of the Elynetum the pH value of the soil is the deciding factor for the existence of the association.

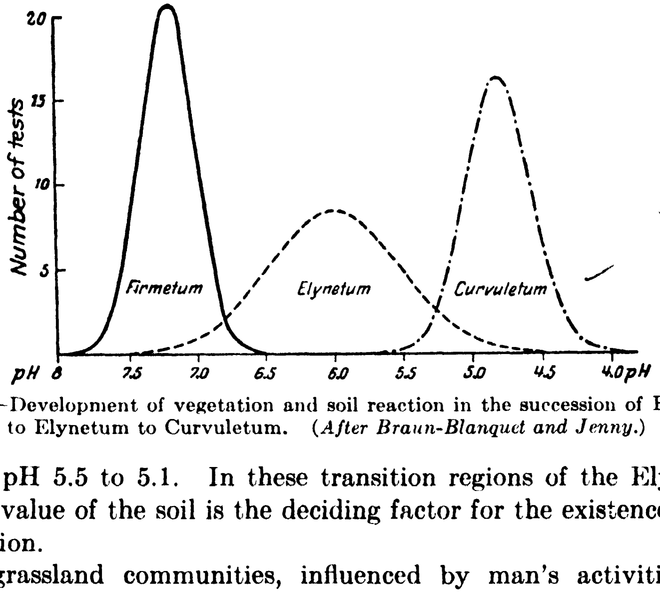

FIG. 96.—Development of vegetation and soil reaction in the succession of Firmetum to Elynetum to Curvuletum. (*After Braun-Blanquet and Jenny.*)

In grassland communities, influenced by man's activities, the importance of the H ion concentration is often obscured by other factors. Klapp (1930), however, insists that the presence of a certain association is a better indicator of the soil reaction than the occurrence of any individual species.

The opinion has been expressed that associations of strongly acid soils have a narrower pH amplitude than those of neutral or alkaline soils (Wlodek and Strzemiensky, 1924, p. 811; Christophersen, 1925, p. 566). This generalization, however, is hardly tenable. It is true that in young calcareous soils in humid climates the enrichment of the soil with humus and the leaching process lead quickly to the acidification of the uppermost soil horizon; thus considerable variations in the pH value of the surface soils arise, depending upon whether the samples are taken from the disintegrated rock itself or from the highly organic cover. In places around springs and especially near running water, soil acidity decreases. Hence, in such places weakly acidophilous and even neutrophilous or basophilous species may appear, in the midst of a strongly acidophilous community (see also Szafer *et al.*, 1927).

Lines of pH Values.—In order to determine the average pH value and the pH variations within an individual stand, soil samples must be taken in several places. The concept of the soil line used by Jenny (1925) is useful in this case. The soil line gives a graphic representation of the horizontal variations of soil properties within a selected area. Through a homogeneous plant community a straight line is laid out, and along it at certain intervals (2 m. in large communities) samples of soil are taken and tested. The pH soil lines of the Firmetum, Elynetum, and Curvuletum are shown in Fig. 97. These soil lines reflect the pH variation within an individual stand and also serve as indicators of the pH range of their respective associations. The great variations in the Elynetum are worthy of note. They are due to different degrees of enrichment by humus and the resulting acidification of the originally strongly alkaline virgin soil. The pH lines of the Curvuletum and Elynetum were run very close together upon the same substratum of Rhetic marl at the Murtërjoch (lower Engadine valley). Physiognomically, the two communities look very much alike, but a floristic analysis reveals fundamental differences which receive an adequate ecological explanation by reference to the soil lines.

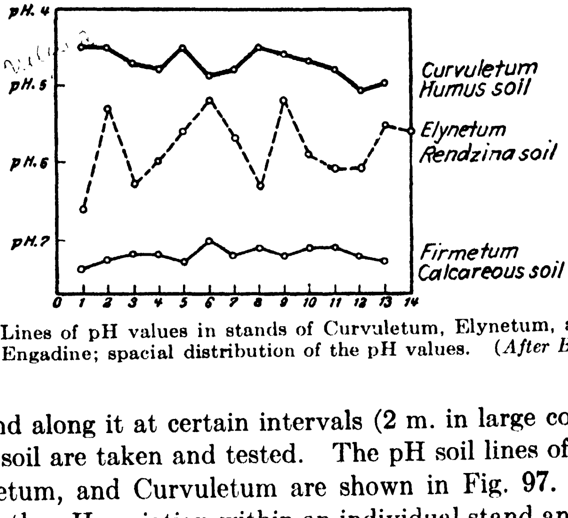

FIG. 97.—Lines of pH values in stands of Curvuletum, Elynetum, and Firmetum in the Lower Engadine; spacial distribution of the pH values. (*After Braun-Blanquet and Jenny.*)

Profiles of pH Values.—With increasing depth the soil reaction usually changes rapidly. Deep-rooting species, particularly trees, therefore often draw their nourishment from soils of very different H ion concentrations. Nevertheless, it must be remembered that germinating seeds and young plants are always dependent upon the topmost soil layer. Accordingly, the pH value of the uppermost horizons of the soil is of particular importance. In this very top layer (1 to 2 cm.) the H ion concentration is notably dependent upon the predominant plant species or, more exactly, upon their decomposition products (see p. 245).

With increasing depth the influence of dead plant matter upon pH values diminishes, in favor of the climatic influences of water and the effect of the underlying rock. On consideration of a soil profile in its entirety the climatic influence upon pH values stands out very clearly.

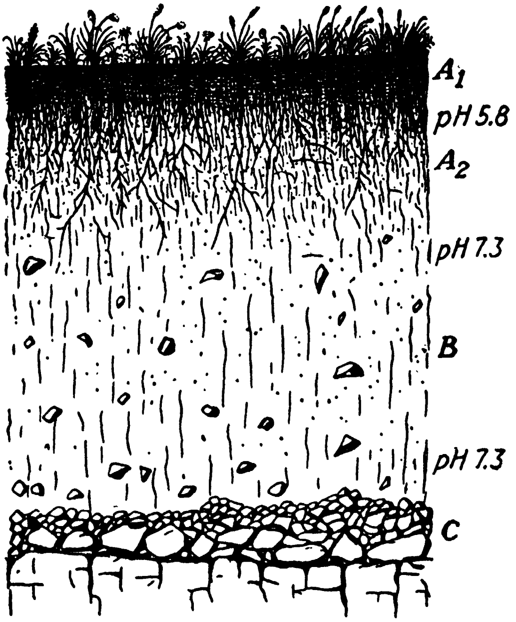

FIG. 98.—Soil profile in the Curvuletum on dolomite in Central Alps, 2,500 m. showing 2 cm. black humus (A_1); 6 cm. fine soil with some humus (A_2); light gray disintegrating soil material (B); and dolomite fragments (C). (*After Braun-Blanquet and Jenny.*)

In the very humid climate of the Alps, the H ion concentration usually decreases with increase of depth in soil. This applies to podsol and podsolic soils, as well as to alpine humus and rendzina soils. The production of H ion is greatest in the acid raw humus horizon and decreases slowly in the case of deep soils, more rapidly in shallow soils. Above calcareous substrata a very sudden pH reversal often occurs between the humus layer and the mineral soil, a fact which is brought out in Fig. 98. The extent and layering of roots of plants of acid raw humus reflect distinctly this acid reversal in the soil.

In podsolic and podsol soils of the Alps, of northern Europe, and of the northern United States the raw humus layer (horizon A_1) always shows a high H ion concentration; the leached, light earth or sandy soil layer (horizon A_2), a somewhat lower; and the accumulating layer (horizon B), the lowest H ion concentration. Examples are shown in Table 14.[1]

TABLE 14.—VARIATIONS IN pH VALUES IN NORTHERN AND ALPINE PODSOL PROFILES
(After Braun-Blanquet and Jenny, and Christophersen)

Vegetation	Horizon A_1 raw humus		Horizon A_2 leached		Horizon B enriched		Horizon C disintegrating soil material	
	pH	Depth, centimeter	pH	Depth, centimeter	pH	Depth, centimeter	pH	Depth, centimeter
Curvuletum on rendzina-podsol; Central Alps	5.0	0 to 35	5.7	35 to 38	6.5	33 to 45	7.8	45
Curvuletum on humus-podsol; Central Alps	5.5	0 to 3	5.4	3 to 13	5.4	13 to 18	6.3	18
Empetrum-Vaccinium uliginosum heath; Central Alps	4.2	2 to 5	5.0	15				
Larix-Pinus forest; Central Alps	6.0	0 to 15	6.4	15 to 30	6.8	30 to 50	7.2	55
Calluna-Cladonia heath; Sylene, Norway	4.3	.....	4.4	....	4.7			
Vaccinium myrtillus-Betula pubescens forest, Sylene	4.0	......	4.0	....	4.7			

Only sparse data now exist regarding the pH changes in the soil profiles of definite plant communities of other climatic regions. In the arid portions of central Bohemia, Firbas and Sigmond (1928) found the upper 2 cm. of the soil always less acid than the 4 to 10 cm. immediately below. This also appears to be the situation in the red soils of the Mediterranean region (Table 15). Under the dry climate of Bohemia and in the hot, dry Mediterranean region it appears that the acidity of the soil increases with depth or remains constant. The litter of the woody evergreen plants is, on the contrary, somewhat acid (*Pinus halpensis* litter pH 4.5; *Quercus ilex* pH 6; *Myrtus* pH 6.4), but these organic acids are very quickly neutralized.

Buffering of Soils.—As far back as Gola (1910) it was known that the constant or rapidly changing concentration of soil solutions affects the composition of the vegetation in greatly varying degrees. Upon

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[1] Soil profile studies on podsols of the Black Forest by Frank (1927) and on soils in Michigan by McCool *et al.* (1923) give similar pH data.

TABLE 15.—VARIATIONS IN pH VALUES IN RED-EARTH PROFILES IN THE MEDITERRANEAN REGION

Vegetation	Horizon with little humus		Reddish earth, rich in Fe, Al.				Disintegrating soil material	
	pH	Depth, centimeter	pH	Depth, centimeter	pH	Depth, centimeter	pH	Depth, centimeter
Brachypodietum ramosi on Jurassic; Montpellier	6.8	1 to 5	6.5	15	6.5	60		
Quercus ilex young forest; on Cretaceous limestone; Pont-du-Gard	7.4	1 to 2	7.3	5	7.2	25	7.2	50
Q. ilex scrub with *Calluna* on siliceous gravel; Montpellier	6.9	1 to 2	6.6	10	6.3	20 to 25	6.2	40 to 50
Q. ilex primeval forest; volcanic substratum; Atlas Mountains 1,500 m	7.2	2	7.2	10				
Q. suber open forest on Pliocene sand; Morocco	7.2	2	7.0	10	6.9	20	6.9	30

this fact rests his distinction of anastatic and eustatic soils. Our question, then, is: Is the acidity of a soil constant, or does it change from time to time?

Soil studies of recent years have brought out the important fact that most soils have the capacity of maintaining a very nearly constant H ion concentration. Each soil has its characteristic pH value, its "reaction constancy," which normally is little changed by external conditions. This is analogous to the capacity to maintain its physical condition to a large extent regardless of the surrounding temperature. This property of tenaciously maintaining a "reaction constancy" is called buffering (see Baver, 1931).

The buffering substances in the soil are weak acids, salts of weak acids with strong bases, amphoteric electrolytes, clay and humus compounds capable of base exchange, and colloidal hydroxides of iron and aluminum. Humus soils are especially highly buffered against additions of acid and even more so against additions of alkali. Raw calcareous soils are very highly buffered against acids. Thus these soil types have a very persistent reaction constancy. Sandy soils, on the other hand, are very poorly buffered. Their pH value changes rapidly on the addition of acids or bases; the reaction constancy is negligible; these soils are "flexible" or non-resistant. In podsol soils, therefore, the leached fine-grained middle horizon is much more feebly buffered than the organic and accumulation layers. A clear idea of the permanency of the reaction constancy in humus soils and the "flexibility" or lack of resistance of fine loam may be gained from Table 16.

TABLE 16.—AMOUNT OF BUFFERING IN SOME ALPINE SOILS
(After Braun-Blanquet and Jenny, 1926)

Soil	Reaction constancy	Buffering against acid		Buffering against alkali		Remarks
	pH	pH	Change	pH	Change	
1. Humus:						
Curvuletum	5.3	4.8	0.5	5.6	0.3	Well buffered, relatively constant pH values
Elynetum	5.5	5.3	0.2	5.7	0.2	
Firmetum (with limestone)	7.2	7.2	0.0	7.3	0.1	
2. Light soil:						
Podsol under Curvuletum	5.5	< 4.1	> 1.4	6.6	1.1	Little buffering, easily changed pH values
Podsol, upper Engadine	6.0	< 4.0	> 1.9	7.0	1.0	
Podsol under fir forest, Cluoza	6.4	4.8	1.6	6.9	0.5	

Of the soils listed above, the most highly buffered is the calcareous soil with abundant humus of the *Carex firma* association. The acid organic soils of the Curvuletum also are well buffered against the addition of alkali. Large amounts of alkali may be added without effecting a change in their reaction constancy; yet on addition of 1 cc. of $N/10$ HCl the acidity rises from pH 5.3 to 4.8. By this experiment the tendency of climax alpine soils to become acid is clearly demonstrated.

Measurement of Buffering.—The flexibility of soils is determined by observing the pH changes of the reaction constancy on the addition of 1 cc. of $N/10$ HCl or 1 cc. of $N/10$ NaOH to 10 g. of soil dissolved in 30 cc. of pure water.

Buffer Effect and Plant Communities.—The ability of most soils to maintain their reaction constancy favors the stability of plant communities and retards changes in vegetation. In weakly buffered soils with fluctuating H ion concentration the vegetation must be able to withstand considerable pH changes. The pH tolerance of the invaders of such soils is wide; the factor loses its selective importance. This may be assumed to be the case in many sandy soils and in siliceous gravel soils.

How large an addition of alkali is borne by the humus soils of the central alpine *C. curvula* association without effecting a change in its reaction constancy is shown by researches in the Rhetic Alps. Measurements of wind-borne dust have shown that in the region of the Alp Murtèr (Val Cluoza) large amounts of calcium carbonate are deposited annually. It must, therefore, be due to the strong buffering action of the humus soils that the Curvuletum as the climax association of the Swiss alpine survives even in regions with large deposits of drifting alkaline dust.

Salisbury (1922, p. 237) discusses buffer curves of lime soils of southern English beech woods. Owing to high humus content the surface layer (2 to 3 cm. deep) showed good buffering. At 6 cm. depth the flexibility to acid was increased; that is, the buffering was poorest there, because of decreasing humus and carbonate content. In the deeper soil strata (15 to 25 cm.) buffering was found to be on the increase again, owing to a large increase of carbonate.

The following table 17 illustrates buffering of the various layers of alpine rendzina (lime) soils and rendzina podsols.

TABLE 17.—RESISTANCE AGAINST CHANGE FROM ADDITIONS OF ACID OR ALKALI IN THE ELYNETUM AND IN THE CURVULETUM PROFILES IN THE CENTRAL ALPS (After Braun-Blanquet and Jenny, 1926)

A. Elynetum on Rendzina Soil

Soil horizon	Alp Murtèr 2,450 m.				Alp Murtèr 2,250 m.			
	Depth, centimeters	pH	Buffering		Depth, centimeters	pH	Buffering	
			Against alkali pH	Against acid pH			Against alkali pH	Against acid pH
A..........	0 to 10	5.8	0.3	0.3	0 to 25	6.0	0.1	0.2
B..........	10 to 14	6.6	0.1	2.0	25 to 65	6.9	0.3	1.4
C..........	14	6.7	0.4	0.0	65	7.6	0.2	0.0

B. Curvuletum on Rendzina Podsol at Murtaröl (Cluoza), 2,570 m.

Soil horizon	Depth, centimeters	pH	Buffering	
			Against alkali pH	Against acid pH
A_1................	0 to 35	5.0	1.3	0.4
A_2................	35 to 38	5.7	0.8	>1.6
B................	38 to 45	6.5	0.1	1.2
C................	45	7.8	0.0	0.0

Strong buffering in the surface soil stratum is also responsible for the fact that neither an increase of carbonic acid, H_2CO_3, in the soil by action of soil organisms nor the formation of nitric acid, HNO_3, by nitrifying bacteria causes a material change in the reaction constancy of many soils.

Soil Types and pH.—Both organic content and H ion concentration can be used for the characterization of soil types. The pH value should not be taken at random but should be restricted to the ectodynamomorphic climax soils. In the upper soil layer of warm arid regions values of more than pH 7 (*i.e.*, alkaline soils) occur almost exclusively. In warm semiarid regions (red-earth region) more or less neutral climax soils are the rule. In beech-wood regions the climax soils maintain a pH 6.5 to 4.5. In spruce forest it is around pH 6.0 to 3.6.

In the moist, cool climax regions of the Curvuletum in the Central Alps the pH values of the climax soils lie between pH 5.0 and 4.0. The extreme pH values of soil solutions that have been ascertained are pH 2.9 and 11 (the latter in Egypt).

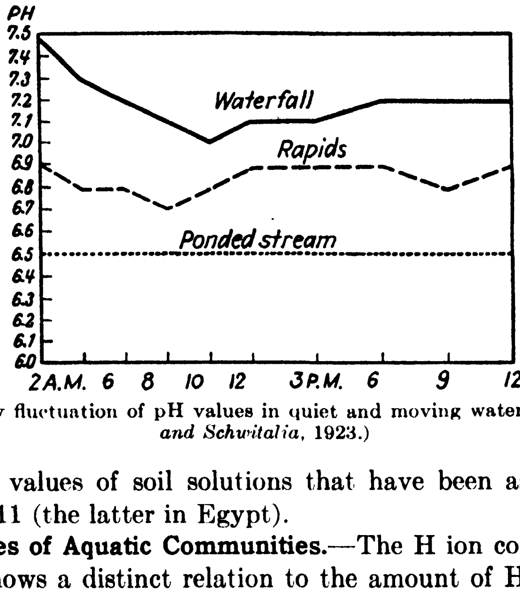

FIG. 99.—Daily fluctuation of pH values in quiet and moving waters. (*After Cowles and Schwitalia*, 1923.)

pH Values of Aquatic Communities.—The H ion concentration of the water shows a distinct relation to the amount of H_2CO_3 present. The same stream may show greatly varying pH values in quiet spots and in places of considerable movement. While no pH changes may be shown in quiet spots during the course of the day, such changes may be very considerable in waterfalls (Fig. 99). The photosynthesis of floating species has a decided influence on the pH value of the water. Thus Iversen (1929) has stated that in a pond in Denmark, at a depth of 50 cm., the reaction of the water was pH 6.8; at 40 cm., pH 7.0; at 30 cm., pH 7.6; at 20 cm., pH 8.2; and at 10 cm., pH 8.8. The vegetation was very dense (*Elodea*, etc.), and in the upper stratum photosynthesis was very active but decreased with depth on account of diminishing light.

C. NUTRITIVE SALTS AND PLANT COMMUNITIES

Nutritive substances are taken up by the roots of plants in the form of ions. Very probably exchange reactions on root colloids are of prime importance in this process. H ions may act in a regulatory capacity, but they are of no food value for plants. Under the influence of hydrolysis in combination with the carbon dioxide, CO_2, and other (especially organic) acids, the slightly soluble mineral substances in the soil are brought into solution. In the absorption of nutritive substances an antagonistic effect of the ions is often evident, in that certain ions minimize or offset the effect of other ions.

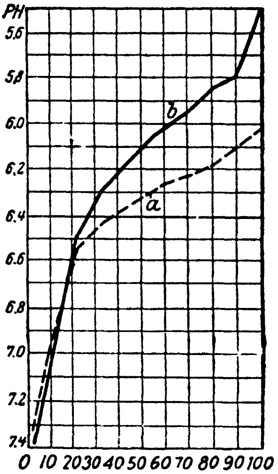

FIG. 100.—The regulation of the pH of water by an *Oedogonium* grown in a mixture of pure water and water saturated with CO_2. The abscissae show the percentage of CO_2-saturated water in the mixture and the curves the resulting pH values (*a*) with and (*b*) without the Alga. (*After Ulehla.*)

In the absorption of mineral nutrients the plant shows a pronounced selective power. In fact, the permeability of plant cells for certain ions appears to be a property characteristic of the species. The investigations of Pantanelli (1915), Lundegårdh, and others show that sometimes the anions and sometimes the cations are absorbed in greater quantity. For example, sugar beets absorb the cations of most chlorides more strongly (with $CaCl_2$, seven times more strongly) than the anions (Stiles, 1923). Conversely, the Gramineae appear to prefer the anions rather than the cations (Stoklasa, 1924). The capacity of selective absorption explains the earlier known fact that the plant itself is able to change the acidity or alkalinity of its nutritive solution from pH 6.6 to 11.0 (Bode, 1925–1926). Ulehla (1923) gives very striking graphs of the pH regulation of the water by an *Oedogonium* (Fig. 100).

In culture experiments with the root fungus *Rhizoctonia silvestris* upon nutritive media of various degrees of acidity the following pH changes resulted under the influence of the fungus, according to Melin (1924, p. 45):

Before experiment.....	pH	3.4	4.1	4.4	4.9	5.7	6.0	7.0
After experiment......	pH	3.2	3.5	4.1	4.2	4.4	4.5	6.0

The possibilities of ionic exchange and the maintenance of the ionic equilibrium within the plant cell have been discussed in detail by

Stiles (1923). The absorption of nutritive matter from the soil solution by roots calls for an electroequivalent exchange of ions or molecules from the root to the soil solution.

The dissolved mineral matter is, in part, indispensable to the plant (as potassium, magnesium, sulphur, phosphorus, iron, and for higher plants calcium) and, in part, exerts a favorable influence upon the growth of the plant or, again, it may be of no effect at all or even be harmful. Highly concentrated solutions are injurious to most plants. The capacity to endure certain ions in large quantities is a specific property of the species or genus (*cf.* also Iljin, 1925).

Toxic Effects.—The farmer knows the harmful effect of large quantities of fertilizer added to the soil. Analyses by Chauzit (see Russell, 1921) showed that *Vitis vinifera* began to suffer seriously as soon as 35 per cent or more lime was added. Calcium ions also have a toxic effect upon fungi (*e.g.*, *Citromyces*) under neutral and basic conditions. In the grapevine, the chestnut tree, *Calluna*, and other plants lime chlorosis occurs with excess of calcium. A small excess of iron induces iron chlorosis in soy beans. The same metabolic disease, however, is also caused by a shortage of iron (Marsh and Shive, 1925, p. 79). The poisonous nature of aluminum is affected by H ion concentration, being intensified by an increasing H ion concentration of the soil. Below pH 5 the solubility of Al_2O_3 rises rapidly. In soils of more than pH 5, however, according to Magistad (1925, p. 20), lucern, red clover, and oats suffered little from the poisonous effects of aluminum. Kaho (1926) has discussed the harmful effect of soil alkalies upon the protoplasm of plants. He was able to prove that the toxic effect depends upon the penetrating power of the ions where the anions enter the plant more abundantly than the cations. The permeability of protoplasm seems to change under the influence of different ions.

Antagonistic Effect of the Ions.—The classic investigations by Loeb (1906) have shown that certain salts such as sodium chloride, when alone, have a poisonous effect upon plants but that with the addition of magnesium or calcium the poisonous nature of the sodium chloride solution may be decreased or entirely neutralized.[1] In this antagonistic action the concentration of the solutions doubtless plays an important rôle (see also p. 186).

Law of Relativity.—According to Lundegårdh (1931, pp. 204–209), three phases of the action of nutritive salts may be distinguished:

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[1] Instructive examples of the antagonistic action of different ions are also cited by Iljin (1925).

1. The simple, chemical effect of nutrition.
2. The osmotic effect of higher concentrations of salts.
3. The colloid-chemical effect of the ions.

Of these three phases, we are best informed concerning the nutritive effects, thanks to investigations upon cultivated plants. The third phase is almost untouched. For the chemical nutritive effect of salts and their significance in building up the plant body, the "law of relativity" (Mitscherlich-Lundegårdh) is of value. It has replaced the time-honored "law of the minimum" of Liebig. The latter is no longer tenable in its original form (Romell, 1926). Lundegårdh (1931) has given the law the following ecological expression:

> The more nearly a factor is in minimum in relation to the other factors acting upon the organism the greater is the relative influence of a change of that factor upon the growth of the organism. As a factor increases in intensity, its relative effect upon the organism decreases; and when the factor is in the region of its maximum, the effect of a change upon the organism is nil.

We have shown elsewhere that this law applies to the pH factor in the Curvuletum of the Alps. In the minimum regions, or in the harmful maximum, the pH is decisive, while in the optimum other factors such as soil humidity, snow cover, and wind determine the survival of the association.

While the following pages are an attempt to illuminate the significance of the most important nutritive substances of the soil in their ecological effects upon the structure of vegetation, it must be admitted that very few precise investigations are on record in this field. The whole section, therefore, is only a general survey.

1. Calcium.—In its effect upon the distribution and grouping of plants the bivalent calcium ion (Ca^{++}) is second only in ionic effect to the hydrogen (H^{+}). Calcium, whose manifold importance in plant structure is well known, is found extensively in nature as humate in organic combination, as a sulphuric salt (gypsum), as a silicate, but most abundantly in the form of a carbonate. Certain limestone rocks, such as marble, consist of as much as 99 per cent of $CaCO_3$. Even some siliceous rocks, as syenite, plagioclase gneiss, and diorite, contain considerable quantities of calcium. The effectiveness of the calcium content for plants is determined by its solubility rather than by the absolute amount of calcium present. For, according to Klochmann, in water saturated with CO_2, calcium carbonates dissolve in the proportion of 9 to 12 parts per 10,000, while the dolomitic carbonates dissolve in the proportion of 3 to 10 per 10,000.

For a better understanding of the relations between lime content of the soil and vegetation it will be necessary to distinguish between direct and indirect action of calcium.

Indirect Action of Calcium.—Calcium affects in large measure the physicochemical conditions of the soil and thereby, indirectly, the vegetation. Lime affects the coagulation and aggregation of the soil colloids whereby coarse crumby structure, water conduction, temperature, and aeration of the soil are favorably influenced.

Soils rich in lime nearly always have a neutral or alkaline reaction, since $CaCO_3$ neutralizes acids.[1] This affords favorable living conditions to such soil organisms as bacteria and worms, while the food supply for higher plants increases and is converted into a more assimilable form.

Upon this indirect action of calcium ions depend a number of phenomena which have not always been adequately distinguished from the direct action of lime.

Anyone from northern or central Europe who observes the soil constancy (adherence of a species to a type of soil) of certain, apparently obligate, lime plants in northern Europe will discover to his astonishment that many a lime-constant species of the north grows in the south upon soils with little or no lime. In such cases basophilous or neutrophilous species may be concerned, which find their soil preferences in the north upon lime only but in the south grow upon limeless soils. We are then dealing with a conditioning effect of H ions. If a neutral or basic reaction prevails, many of these species thrive upon practically limeless silicate soils. Similarly, the Sphagnaceae, described as calcifugal, seem much more sensitive to OH^- than to Ca^{++} ions (in low concentration) (Paul, 1908; Mevius, 1921). Iljin (1925, p. 349) was able to prove that *Vincetoxicum officinale*, a plant which endures Ca^{++} ions very well, is extremely sensitive to OH^- ions.

Plants which thrive in a dry climate are more and more confined to calcareous soils as they approach the northern limits of their ranges, since these soils alone can afford them favorable physical conditions of temperature, water supply, and soil aeration. Frequent reference has been made to this situation since Flahault called attention to it in 1893. Only in this respect is it proper to speak of physical factors acting as a substitute for lime.

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[1] The alkalinity, however, does not rise proportionally with the amount of lime present, as one might expect, the H_2CO_3 being a determining factor. In a soil solution a mixture of $CaCO_3$ and CO_2 will have a pH value of 7.8 to 7.2 (Wiegner, 1926, p. 154).

Of the species which have been described as lime-constant by Contejean (1881, p. 125), the following occur also upon non-calcareous soils in southern France: *Melica ciliata, Carex halleriana, Hippocrepis comosa, Coronilla emerus, C. minima, Prunus mahaleb, Euphorbia seguieriana, and Vincetoxicum officinale.*

Flahault (1893) gives a list of species which are considered lime-constant in northern France but are found in the Cévennes also upon soils poor in lime.

A similar ecological relation is shown by *Fagus silvatica, Quercus pubescens,* and *Bromus erectus,* which thrive in the south of Europe upon any kind of soil—chalk, acidic gneiss, granites—and also form extensive communities upon soils poor in lime. But in central Europe *B. erectus* is considered a lime plant, and from the close interrelation of chalk and the distribution of beech woods in England, many authors have arrived at the conclusion that *Fagus* is directly dependent upon the chemical nature of the substratum.[1]

Direct Action of Calcium.—The direct action of Ca ions, determined by the amount of soluble calcium, seems unaffected by acidity or alkalinity. According to Magnin (1886), Contejean (1881), and others, soils with at least 2 to 3 per cent of soluble calcium are to be considered lime soils. Under particularly favorable external circumstances, with no competition from better adapted species, many calciphobous species endure this amount of lime. On the other hand, mere traces of lime (0.2 to 0.3 per cent) enable calcicoles to survive. Large quantities of $CaCO_3$ drive out the indifferent plants, and the calcicoles or lime-constant species gain more and more monopoly over an area. Magnesium carbonate, $MgCO_3$, has a similar effect and may partially take the place of $CaCO_3$.

As we speak of lime-constant species and calcicolous colonies, so we may speak of lime-constant associations.[2] Many communities of arid regions and of mountains are lime-constant in the strictest sense. Among these the Festucetum glaucae of central Europe from the Jura to Poland; the Caricetum firmae, the Caricetum ferrugineae, the Petasitetum nivei, and the Thlaspeetum rotundifolii on the talus of the Alps; the Schoenetum nigricantis of central Europe; the *Schoenus*

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[1] Fine earth from the root layer of the Bromion upon chalk in central England contained, according to V. Anderson (1927), at a depth of 15 to 20 cm. an average of 70 to 80 per cent; at 30 to 40 cm., 90 to 95 per cent of carbonates, mostly $CaCO_3$.

[2] It is surprising that in the work of Lundegårdh (1931, p. 215) we read that only very few markedly lime-avoiding species (*Sarothamnus, Castanea vesca, Pinus pinaster*) are known. Anyone taking the trouble to look through the voluminous literature on the subject will find evidence to the contrary.

nigricans-Plantago crassifolia association, the Deschampsietum mediae, and the *Rosmarinus-Lithospermum fruticosum* association of southern France; and all the rock-crevice associations of the Potentillion alliance and related communities of northwestern Africa have been rather minutely investigated.

Many cryptogamic communities are perhaps even more strictly limited to the occurrence of highly saturated calcium solutions. The lime-encrusting tufa builders, *Eucladium verticillatum*, *Gymnostomum calcareum*, *Cratoneuron irrigatum*, form broad carpets on rocky slopes and walls which are constantly wet with waters rich in lime. The *C. commutatum-Arabis bellidifolia* association in all its facies is one of the regular phenomena of cold, calcareous springs in the Alps. Motyka (1926) describes a number of lime-constant lichen communities of the Tatra, such as the *Lecanora lamarckii* association, the *Verrucaria calciseda* sub-association, and the *L. reuteri* association. He stresses particularly the unusually sharp line of division between the lime-constant and lime-avoiding lichen associations. Similar communities inhabit the dolomite of the Swabian Alps, such as the *V. calciseda* community with its several variants of central Germany (Kaiser, 1926) and the Alps.

That aquatic vegetation, including plankton, reacts sharply to the lime content of the water is very well known. The calciphobous, oligotrophic association of *Isoetes echinospora* (with *I. echinospora*, *I. lacustris*, *Subularia*, etc.) of the lakes in the Vosges and Black Forest is entirely missing in the calcareous waters of the northern foothills of the Alps and reappears (without *Subularia*) only at the southern slopes of the Alps in the Ticino valley.

To summarize briefly: The lime-avoiding species are in part such as are harmed or are hindered in their development by saturated lime solutions; in part, acidophilous species, which thrive only upon acid soils with an excess of H ions, and whose absence upon lime is readily explained by their relation to the soil reaction.

To what extent the indifferent and lime-favoring species can tolerate lime it is at present impossible to state. In one essential the observed facts and experimental investigations tally; the Ca ions (and perhaps Mg ions) seem to be the decisive factor in regard to lime constancy; the direct action of the supply of calcium ions cannot be replaced by the physical properties of the soil. The occurrence of calcicolous (lime-constant) communities is strictly dependent upon solutions rich in calcium.

Calcium Determination.—Calcium carbonate, being an easily soluble compound, is always accessible to plants. Instead of laborious

Ca analyses, therefore, very simple carbonate determinations are performed. It must not be overlooked, however, that calcium may be present in the soil in other combinations than the carbonate and, furthermore, that in making the carbonate determinations other carbonates, as of magnesium and iron, are included in the results. The fact remains, however, that magnesium carbonate, present in large quantities in dolomite, closely resembles calcium carbonate in its effect upon vegetation.

Simple, calibrated calcimeters are commercially available in various finishes, makes, and sizes. In Switzerland and in Germany the calcimeter of Passon is most used; for soils poor in carbonate the small, and for those rich in carbonate (more than 1 per cent) the large, Passon apparatus is recommended.

An estimate of the lime content of a soil may be obtained by wetting a fresh soil sample with a few drops of dilute hydrochloric acid ($HCl : H_2O = 1:1$). Soils with less than 1 per cent of $CaCO_3$ cause no bubbling, those with 1 to 4 per cent effervesce weakly and for a short time, while soils of more than 5 per cent effervesce strongly and for some time.

Instructions for the determination of the calcium content as calcium oxide, CaO, are given by Wiegner (1926) and by Mitscherlich (1923).

Gypsum Vegetation.—Gypsum, $CaSO_4 + 2H_2O$, and its anhydrite ($CaSO_4$) bear exclusively calciphilous flora; the Ca ion here proves its effectiveness. Fossil gypsum deposits of Paleozoic and Tertiary origin exist in southern Europe in the Alps, in central and northern Germany, northern France, Poland, and in numerous other places. The gypsum islands of the Alps with their blinding brilliancy contrast sharply with the adjoining sedimentary strata. Their vegetation is exceedingly meager and consists of basophilous prostrate pioneer shrubs (*Dryas*, *Salix serpyllifolia*), a small number of pronouncedly lime-constant and lime-loving species, and a few indifferent species. Gypsum-constant, or even merely gypsum-loving, species are missing here, as they also are in the steppe associations of *Stipa capillata* and of *Carex humilis* and *Inula ensifolia* on the gypsum soils in the high plateau of Little Poland examined by Dziubaltowski (1915, 1925) and Kozlowska (1925). These gypsum soils are rather rich in carbonates; their H ion concentration varies between pH 7.6 and 6.8. However, the same associations are found on calcareous loess. From the soil analyses of Miklaszewski (cited in Dziubaltowski, 1925) it follows, incidentally, that the gypsum bed rock contains no $CaCO_3$, while in weathered gypsum rock 10 per cent or more of $CaCO_3$ may be present.

The gypsum soils of the Harz mountains are remarkable for the poverty of their vegetation. The *Festuca glauca* association with *Gypsophila fastigiata, Alyssum montanum, Teucrium montanum,* and a few other species is spread over the dry slopes on soil containing little fine material. More sharply distinguished from the lime vegetation is the gypsum vegetation of the Spanish mesa. This is emphasized by the fact that Del Villar (1925, p. 18) describes a special successional series for the gypsum area. Indeed, the *G. struthium-Lepidium subulatum* association which he describes appears to be unique. Del Villar names as characteristic gypsum plants *G. struthium, L. subulatum, Herniaria fruticosa, Frankenia reuteri, Vella pseudocytisus, Agropyrum curvifolium, Sedum gypsicolum, Narduretia gypsacea, Centaurium gypsicolum,* and others.

On the high Algerian plateau the gypsophilous plants form an upper zone of scanty vegetation bordering some shotts at Le Kreider. The dominant plant is *Frankenia thymifolia* with which are also found *L. subulatum, Schismus marginatus, H. mauritanica,* and *Erodium glaucophyllum.*

2. Magnesium.—Magnesium occurs in numerous compounds but usually in small quantities in rocks and soils. There are two important magnesian rocks. Dolomite, $MgCO_3 + CaCO_3$, with 54 per cent Ca and 46 per cent Mg, forms great white shining mountain chains (the Dolomites of southern Tirol). Serpentine, $2SiO_2MgO2H_2O$, has a dark greenish luster, weathers into sheets and jagged pieces, and forms an unusually sterile residual soil. The serpentine ridges of the Alps, in their dark, deathly hardness, are among the most depressingly lonely phenomena of nature, and the popular reference *tote Alp* (dead Alp) is quite appropriate.

Saline soils of dry regions and large salt-water basins have their magnesium mostly in the form of chloride and sulphate.

Physiological Effects of Magnesium.—Willstätter and his students have discussed the importance of magnesium in the molecular structure of chlorophyll. Canals (1920, p. 33) has given a good digest of our knowledge of the physiological effects of magnesium. By a number of experiments he confirmed André's view that the Mg ion, in small doses, favors the development of plants. Concentrations of less than 0.0001 mg. of Mg were beneficial to the plants used, while at higher concentrations a toxic effect appeared. The addition of calcium, as mentioned, reduces the toxic effect of magnesium, and considerable amounts of magnesium may accumulate in plant tissues. The ashes of the leaves of *Ilex aquifolium* contain 12.34 per cent Mg; those of *Stellaria media,* 13.08 per cent; those of *Solanum tuberosum,* 17.08 per cent.

Dolomite Vegetation.—Dolomite, a compound of soluble $CaCo_3$ and rather insoluble $MgCO_3$, supports, in general, the same type of vegetation as compact limestone. The effect of Ca ions is of supreme importance upon dolomite substrata. But whether the exclusively dolomite species (and without doubt there are such) need considerable quantities of magnesium in combination with calcium or are strictly confined to dolomite soils for other reasons cannot now be decided. Perhaps it is only in such places that favorable physical conditions of the soil are found. In future studies of vegetation closer attention will have to be paid to whether or not the soil is dolomitic.

Numerous dolomite species inhabit the Spanish Sierras, the southern Cévennes, and the southern Alps. In some individual cases their limitation to dolomite substrata may be explained as due to their relict nature. Several of them are relicts of the Tertiary, with narrowly delimited occurrence such as *Armeria juncea, Saxifraga cebennensis,* and *Arenaria hispida* of the Cévennes and *Asplenium seelosii* and *Draba ladina* of the southern and central Alps.

These are exclusively denizens of the raw dolomitic soils; that is, they are rock or talus plants. As soon as humus is formed upon dolomitic rock or gravel, its specific characteristics are lost, and the resultant soil scarcely differs from the adsorptively saturated, mild humus of lime soils. In humid regions the leaching of carbonates sets in upon dolomite as upon limestone, and acidophilous plants follow in the train of the progressive acidification of the dolomite soil. This occurrence of silicicolous plants on dolomite substrata was first noticed by Sendtner (1854, p. 330).

As examples of plant communities of raw dolomitic soils we may enumerate the rock-crevice association of *Potentilla caulescens,* var. *cebennensis* and *Saxifraga cebennensis* and the South Tirolean facies of the *Androsace helvetica* association; also, the richly colored, unique association of the endemic *Armeria juncea,* accompanied by *Arenaria capitata, Alyssum montanum,* var. *psammeum,* etc., so characteristic of the dolômite vegetation of the southern French Causses. Certain rock-clinging communities seem also to be pronounced dolomite specialists. According to Motyka (1926, p. 198), dolomite, lime, and marl are colonized by entirely distinct lichen associations in the Tatra. The lichen vegetation on dolomite is much more sparse and made up of fewer species than that upon lime. Diels's (1914, p. 524) researches in the Dolomites of southern Tirol showed this. Furthermore, the vitality of many species is considerably diminished on dolomite. In part, this may have some connection with the manner of weathering of the rock. But, according to Motyka, the chemical factors are decisive. Among the lichen associations of the Dolomites in the Tatra are the *Thelidium* association of wet dolomite rocks and the *Opegrapha saxicola* association. The latter may possibly occur also upon limestone, but the former is dolomite constant.

The epilithic and endolithic algal communities of the south Tirolean dolomite cliffs, first described by Diels (1914), are notable dolomite associations. On the steep walls of the Schlern these communities of cryptogams are distinctly stratified according to their light requirements. The rock surface is covered with an association of *Scytonema crassum* and other species of *Scytonema* in tufts up to 0.5 mm. in length. Below the coating of *Scytonema* comes a Cyanocapsetum, which is really a stage preliminary and preparatory to the Scytonemetum. Aside from these epilithic or surface communities, which can bear intense light and drought, there are also very peculiar endolithic algal groups penetrating as much as 0.8 mm. into the finest capillary crevices invisible to the naked eye. Those immediately under the surface of the rock consist of an orange-red *Trentepohlia*. Deeper in the rock, with very weak light, occur extremely minute transparent *Gloeocapsa* forms, which appear as green bands when the rock is broken with a hammer. The question of the dependence of these algal associations upon $MgCO_3$ needs further examination.

Serpentine.—Raw serpentine soil supports plants which are indifferent to lime as well as many lime-favoring and even lime-constant species, such as *Trisetum distichophyllum, Ranunculus parnassifolius, Oxytropis montana, Rhododendron hirsutum, Doronicum grandiflorum,* and *Leontopodium alpinum.* The occurrence of lime plants may be connected with the presence of calcium in the serpentine. A substitution of Ca by Mg ions may also be possible. According to Angel, an analysis of serpentine from Steiermark gave these percentages:

Serpentine	SiO_2	MgO	Fe_2O_3	FeO	CaO
Of Kraubat	40.81	37.09	12.98	5.02	1.32
Of Oppenberg	36.41	36.79	11.60	2.7	0.18

The rather high CaO content in the serpentine of Kraubat is reflected in the floristic composition of the vegetation. Serpentines of the region of Bruck, on the other hand, contain no CaO.

Serpentine has a limited number of characteristic plant forms, which are confined exclusively to magnesium silicates or carbonates (serpentine, magnesite) and may be considered strictly serpentine species. Among these are the ferns *Asplenium adulterinum* and *A. cuneifolium*. These are widely distributed in Europe, very local in their occurrence, and their distribution coincides exactly with the occurrence of serpentine.

Novak (1928) has studied the serpentine problem and added to the list of plants peculiar to serpentine and magnesium substrata. He cites among others certain paleoendemic species of the Balkan Peninsula, such as *Halacsya sendtneri*, *Potentilla visiani*, and *Fumana bonapartei* together with various subspecies and varieties. He considers that the serpentine vegetation is controlled by the Mg:Ca ratio, which must be greater than unity; that is, there must be in the soil an excess of Mg ions. Most of the facultative serpentine plants have an extraordinarily developed root system, whereas the surface parts of the plants are rather meagerly developed, and frequently their flowers and fruits are quite sparse. Little is known about the plant communities of immature serpentine soils. In contrast to communities peculiar to the saline soils of arid regions, the serpentine vegetation presents a purely local, edaphically controlled phenomenon.

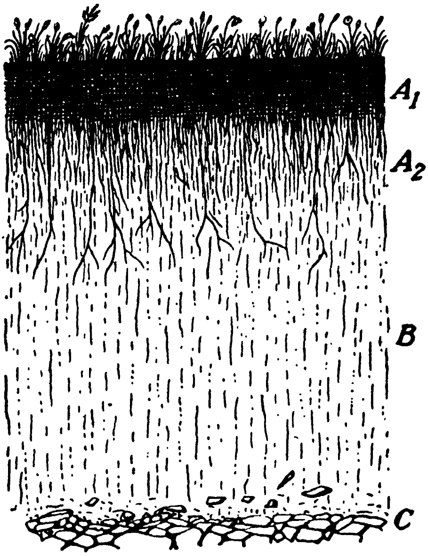

FIG. 101.—Soil profile above serpentine rock upon the Ochsenkopf near Parpan, 2,400 m., showing 2 to 3 cm. black humus (A_1); 4 to 5 cm. grayish brown organic loam, pH 5.4 (A_2); 18 to 20 cm. yellowish brown weathered soil, pH 5.8 (*B*); and serpentine rubble, pH 6.8 (*C*). (*After Braun-Blanquet and Jenny.*)

Soil development upon serpentine substrata proceeds slowly. On steep slopes the dark-green immature serpentine soil, with few plant inhabitants, is everywhere exposed to view. Only on slightly inclined or flat places can the soil and the vegetation reach a true climax. In the alpine zone, the soil-forming process upon serpentine results in a rather finely dispersed, clay-like upper layer of decalcified rendzina soil (Fig. 101), which, in contrast to the raw serpentine soil, bears an acidophilous vegetation (Fig. 102).

3. Iron.—The presence of iron oxide in the soil is indicated by a reddish or brownish-yellow coloration. It is iron sesquioxide, Fe_2O_3, which gives the characteristic red or red-brown color to the so-called "red soils" of southern Europe, southern United States, and climatically similar regions. The deep-red bauxite concretions embedded in the upper layers of limestone are especially rich in iron (bauxite is considered to be chiefly amorphous $Al(OH)_3$ – gel). In the large deposits of southern Europe bauxite appears to be in no wise detrimental to plant growth. Upon exposure of these deposits the species of the immediate environment soon establish themselves, lime plants as well as indifferent species. Among the abundant species are *Spartium junceum*, *Dorycnium suffruticosum*, *Euphorbia nicaeensis*, *Helichrysum stoechas*, and *Inula viscosa*. The vegetation of the immediate environment of the Jurassic iron pits is composed solely of indifferent and lime-favoring species (Contejean, 1881). The vegetation is quite different near the deposits of iron blende and pyrites of upper Italy. Large areas are entirely barren. The first pioneers of this soil, heavy with oxides of iron, are calciphobous plants, such as *Calluna*, *Agrostis canina*, *Silene rupestris*, and the indifferent *Molinia coerulea* (Gola, 1910), all somewhat dwarfed and chlorotic.

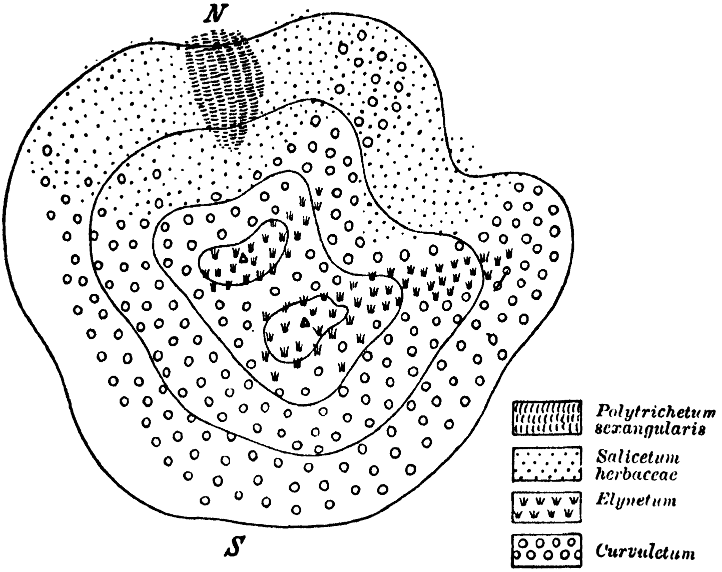

FIG. 102.—Acidophilous associations upon the Ochsenkopf. Central Alps, 2,400 m., upon serpentine. (*After Braun-Blanquet and Jenny.*)

Iron species are unknown,[1] with the exception of a peculiar iron-favoring community of microorganisms (Molisch, 1910). In moor

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[1] According to Vieillard, the red soils of New Caledonia, rich in iron, are said to exhibit an entirely characteristic flora, which includes *Dammara ovata*, *Eutassa intermedia*, and *Dacrydium caledonica*.

tussocks iron bacteria (*Crenothrix polyspora, Chlamydothrix ferruginea,* etc.) live on the finely divided humus releasing iron hydroxide. This product is precipitated as an intensely reddish-yellow, flaky substance, while the moor water itself appears to be covered by an iridescent, oily film. In a similar manner, it is believed, *Crenothrix manganifera* is active in the precipitation of manganese.

4. Zinc, Copper.—Soils which contain zinc, although of rather limited extent, claim a few strictly characteristic elementary species such as *Viola calaminaria,* which is related to *Viola lutea,* and several elementary species of *Thlaspi.* According to Douin, a few liverworts are favorable to heavy metals, especially copper, while of central European species only *Mielichhoferia nitida* is stated to be copper favoring. In the Andes, however, according to Herzog, numerous species of *Mielichhoferia* are said to exist as copper favorites.

The vegetation on soils rich in zinc has recently been studied by Libbert (1930) in the Harz and by Schwickerath (1931) near Aix-la-Chapelle. In addition to the very specialized *Viola calaminaria,* the latter lists *Armeria elongata* and *Thlaspi calaminare* and varieties of *Minuartia verna, Silene vulgaris,* and *Festuca ovina,* as occupying the thin sod (Violetum calaminariae) over extensive areas. The soil here has always considerable zinc amounting to 0.78 per cent in the upper horizons and 0.73 per cent in the lower. One slope at Breininger Berg where the soil has 8.69 per cent of zinc is entirely bare of vegetation, this amount of the metal being apparently quite toxic.

5. Chloride, Sulphate, Soda (Salts of "Saline Soils").—In the plant geography, as also in the agriculture and forestry, of coastal lands, desert, and steppes "saline soils" play an important rôle. They are in part climatic and in part edaphic and show accordingly different physical and chemical compositions.

The edaphically limited saline soils owe their origin chiefly to the world's salt-storage basin of the seas. Consequently they are strongly influenced by the chemical composition of the sea water, and they are rich in sodium and chlorine. Of the salts dissolved in sea water about 80 per cent is sodium chloride.

The climatically conditioned saline soils of deserts and desert steppes are distinguished from edaphically conditioned saline soils by greater dryness and by predominance of sulphates and carbonates, especially the sulphates of sodium and magnesium (Na_2SO_4,$MgSO_4$). The amount of table salt, $NaCl$, falls off somewhat in desert soils, while soda, Na_2CO_3, sometimes appears in large proportions.

The floristic distinctions between sodium chloride, sodium sulphate, and sodium carbonate soils are yet to be ascertained. No doubt, there are distinct differences, even though it is customary to lump the vegetations of all three together under the term "halophyte vegetation" because of their similar external appearance.

The Halophyte Problem.—A fierce feud continuing through many decades concerning the relation of habitat, structure, and manner of life of "salt plants" is summed up in the expression "the halophyte problem."

As is commonly known, the majority of the "salt plants" are succulents, distinguished by their water-storage tissues. The classical theory of Schimper sees herein a protection against transpiration, that is, a xeromorphic adaptation to the so-called "physiological dryness" of the saline habitats. Schimper assumes that salt plants are able to meet their water requirements only with great difficulty on account of the highly concentrated soil solution and that for that reason they are dependent upon mechanisms for the decrease of water loss.

This attractive idea found considerable favor for a time, but doubts soon arose, for it was demonstrated that many halophytes lack xeromorphic adaptations and that many of them not only have a high absorptive power but also transpire vigorously. According to Stocker (1925, p. 13), the loss of water from typical halophytes, such as *Aster tripolium* and *Salicornia herbacea*, calculated for equal time and surface units, amounts to twice that of *Fragaria vesca* and from four to five times that of *Erica tetralix*. At an earlier date Delf (1912) showed that the transpiration from *Salicornia* per unit of area exceeds that from *Vicia cracca*. Thus the cause for the high resistance of *S. herbacea* (and of several other halophytes) against desiccation does not rest upon a decrease of transpiration; rather, it is to be looked for in the increased suction force of the root cells.[1] Keller (1925, p. 234) has further proved that the osmotic concentration of *S. herbacea* rises sharply with

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[1] Recent investigations by Braun-Blanquet, Bharucha, and Meier show the transpiration rate of most of the obligate halophytes of the Salicornion of the lagoons near Montpellier, France, to be excessively low. Among the many plants of the garigues, dunes, and saline soils which were examined, in their own habitats, *S. macrostachya* exhibited the lowest transpiration rate, but *S. fruticosa*, *Inula crithmoides*, *Atriplex portulacoides*, and *Juncus maritimus* showed similar daily transpiration curves. It would be wrong, however, to venture any broad generalizations, since in the same habitat and at the same time *Tamarix gallica* behaved very differently and showed a high rate of transpiration, higher than most of the plants of the dunes and higher than *Quercus ilex*. It has been held that Schimper's hypothesis of "physiological dryness" of saline soil has no general validity, but the studies mentioned above indicate that much caution must be exercised in criticizing this hypothesis. Saline soil may not be "physiologically dry" for every species. Further investigations of the phenomena of halophytic vegetation are necessary before any broad generalizations can be made.

increased salt supply. The researches of Harris *et al.* (1924) on *Atriplex confertifolia* showed extraordinarily high values of osmotic concentration.[1] The osmotic concentration attained no less than 150 atmospheres, the electric conductivity 0.129 mho.; the chloride content exceeded 100 g. per liter of cell sap. On mangroves of the Indian coral islands, Faber (1925) measured at the end of ebb tide 148.4 atmospheres in the leaves of *Rhizophora* and 163.2 atmospheres in the leaves of *Avicennia officinalis*. Besides, most of the halophytes are equipped with an unusually high regulative power against osmotic changes. According to Gola, these are anastatic species. The mangroves, as facultative halophytes, thrive in ordinary soil, but they can stand a salt solution of 8 to 12 per cent.

Juncus subulatus of the Mediterranean coast, one of the species which tolerates the highest concentrations of salt, develops only in a humid habitat. When the soil dries, it begins to suffer and increase its osmotic concentration from 19.6 to 50 atmospheres, at which point the plant yellows and dies. These species can by no means be regarded as xerophytes, as Schimper assumed. In Faber's experiments the mangroves gave evidence of the fact that the increase of osmotic pressure in plants grown in highly concentrated nutritive solutions ($NaCl$, $MgSO_4$, KNO_3) is alone sufficient to cause an increase of water-storage tissue and thereby a thickening of the leaves. Accordingly, the succulence of the mangrove would be a case of hypertrophy caused by high turgor pressure. Keller (1925) arrives at similar results in experiments with *S. herbacea*. An addition of very small quantities of sodium and potassium chloride to the nutritive solution brought about a more vigorous growth as well as an increase of succulence. Sodium sulphate has a similar effect, while magnesium sulphate, according to the experiments of Batalin (cited in Keller, 1925), caused no noticeable increase of succulence as compared with plants of unsalted soils.

The experiments of Lesage (1890) have shown that sodium chloride soils induce a certain degree of succulence in many species. Numerous observations on the conduct of non-halophytic, inland species in shore regions agree with this. Upon saline soils quite a few non-halophytic species develop special, more or less succulent varieties: *Tetragonolobus siliquosus* var. *maritima, Plantago major* var. *carnosa, P. coronopus* var. *màritima*, etc. Crossing between genotypes of a population of salt-favoring species, with extinction of unfit descendants, seems to have

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[1] In their studies in Tooele valley, Utah, Harris *et al.* (1924) found distinct relations between soil conditions and the physicochemical behavior of cell content (osmotic pressure, electric conductivity, chloride content) of the most important indicator plants.

led to the genotypical fixation of the ecologically advantageous structure of succulents, favored by the salt soil. Succulence, however, need not necessarily be xeromorphic, even though it actually is so in numerous cases, as was demonstrated by Duval-Jouve (1868) in the case of *S. macrostachya.*

Salt Constancy.—As in the case of lime plants, so also for the halophytes, a gradation may be shown from the absolute salt-avoiding, through the salt-enduring, to the salt-obligate species. In the last group are numerous Gramineae of such genera as *Spartina, Glyceria, Atropis, Distichlis,* and *Sphenopus* and the succulents of the genera *Salicornia, Arthrocnemum, Salsola, Suaeda,* and *Atriplex.* There are also the sea plankton and the coast vegetation sprayed with sea water. True halophytes may, however, be grown artificially without salt, according to Contejean, Gräbner, and others. Their growth remains dwarfed, however (*cf.* Keller, 1925), and only such species as *Salsola kali, Suaeda fruticosa, Hordeum maritimum,* and *Aster tripolium,* which are not to be regarded as absolute halophytes, are able to persist for any considerable time. Nevertheless, the optimum for the growth of *A. tripolium* seems to be at a very low salt concentration. The distribution of such species upon places of low salt content is chiefly a question of competition.

The experiments of Paris with *Atriplex halimus* (Bequinot, 1913, p. 101) indicate that there are species which thrive normally and continuously only upon sodium chloride soils. Such species have not only a high suction force but require also the specific ionic effects of the components of the salt. From the investigations of Iljin (1925) this fact may now be accepted for Na ions as well as for Ca ions.

It has been known for a long time that some marine algae and such seed plants as *Zostera* and *Posidonia* can live only in highly concentrated salt water. They show toxic symptoms following dilution. The accompanying curves show the NaCl optima for some marine and terrestrial halophytes (Fig. 103). The optima for the narrow curves agree with the concentration of sea water ($\frac{3}{4}$ to $\frac{1}{1}$). The terrestrial halophytes show optima at lower concentrations but with wider tolerance. For further details concerning the present status of the halophyte problem see the work of Montfort and Brandup (1927) and of Stocker (1928, 1930).

According to this interpretation, the obligate halophytes are plants which for their normal development need certain ions of the alkali metals and halogens, and which, therefore, can exist and bear seed only in soils containing salt. They also can live in soils where the respective salts have accumulated in such quantities as to be fatal to most other plants. Halophytic vegetation taken as a whole should permit of classification into various types according to the presence or absence in the soil solution of certain of the ions of sodium chloride, or of sulphates of potassium, calcium, or magnesium. The specific ionic effect should be reflected by the floristic composition of the vegetation, even though, as Gola (1910) states, a partial substitution of NaCl by $MgCl_2$ or $CaCl_2$ may be possible.

Vegetation of Sodium Chloride Soils.—Few reliable facts are known in regard to the limitation of plant communities to certain types of saline soils, but the vegetation of sodium chloride soils has received most attention. High concentrations of pure sodium chloride are deadly to all plants. In mixed solutions the harmful effects of the Na and Cl ions are counteracted by the antagonism of the Ca ions, and along with Na and Cl the soil usually contains a considerable quantity of $CaCO_3$ and $MgCO_3$ together with varying amounts of sulphates in dry areas. In places the sodium chloride soils of the Mediterranean are rich in ferric oxide. A sample from the lagoon of Venice near Mestre, according to Beguinot (1913, p. 46), gave these figures: NaCl 1.10 per cent; $CaCO_3$ 6.08 per cent; $MgCO_3$ 6.87 per cent; Fe_2O_3 + Al_2O_3 11.25 per cent; organic matter 3.00 per cent; and insoluble residue 69.62 per cent.

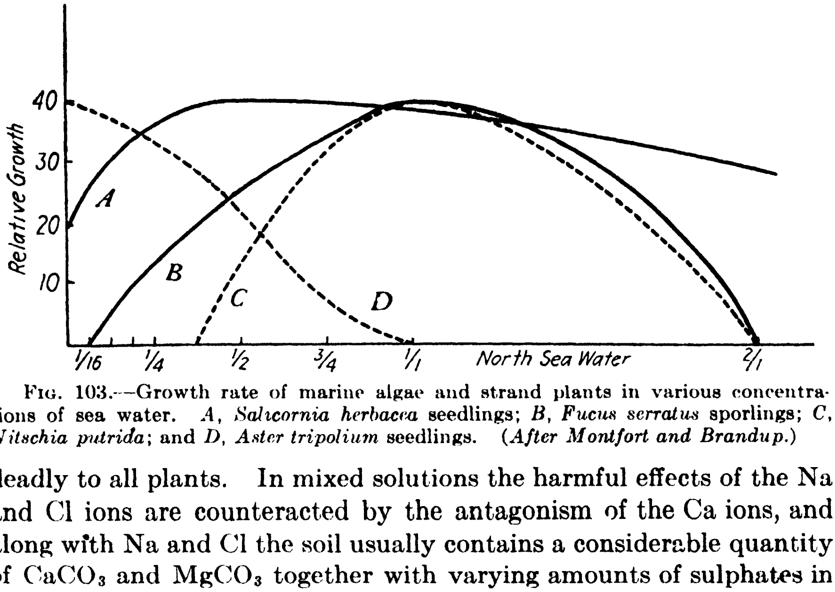

FIG. 103.—Growth rate of marine algae and strand plants in various concentrations of sea water. *A*, *Salicornia herbacea* seedlings; *B*, *Fucus serratus* sporlings; *C*, *Nitschia putrida*; and *D*, *Aster tripolium* seedlings. (*After Montfort and Brandup.*)

The average sodium chloride content of the Mediterranean Sea ranges around 3.8 per cent and is subject to only minor variations. But the salt concentration of lagoon water and of soils which are occasionally flooded will vary greatly. During the summer drought sodium chloride concentrations of 8 to 10 per cent in the uppermost layers of the soil occur frequently, while after the autumn rains the soil is almost completely leached out (0.15 per cent of NaCl). The sodium chloride content of soils which are not continuously overflowed with sea water depends upon the amount of atmospheric precipitation. The effect of this is greatest in the uppermost layers of the soil, that is, in the region of the roots of the halophytes. Investigations on the seasonal fluctuations of salt concentration in the soils of southern France were made by Lagatu and Sicard (1911). They have reference to dry and moist soil as well as to the aqueous soil solution.

The *Salicornia* vegetation of these soils can stand sodium chloride concentrations of 8 to 10 per cent; the seasonal fluctuations in the topmost soil layers approximate 8 to 9 per cent. Below depths of 50 cm. they are rather insignificant (Fig. 104). The sodium chloride concentration of the ground water at 1 to 2 m. shows only small changes in the course of a year. This soil water is the permanent storage reservoir which constantly gives off salt in solution to the upper soil layers as water evaporates.

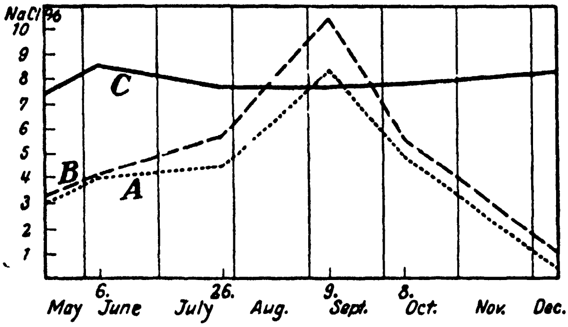

FIG. 104.—Annual fluctuation in the NaCl content of the soil solution (percentage by weight) at (*A*) 0 to 15 cm., (*B*) 15 to 25 cm., and (*C*) 25 to 100 cm. depth in a lagoon soil, with stands of *Salicornia*, near Montpellier, France. (*After Lagatu and Sicard.*)

In the classification of floating and submerged plant communities of the sea which live in the constant salt optimum, physicochemical factors other than the sodium chloride content, such as light, wave motion, and temperature, become decisive habitat factors. This seems to be the case also on steep rocky coasts where the nature of the rock, the exposure, wave motion, wind, and light often become of greater importance to vegetation and to its zonation than the salt content.

It is quite different in the case of low shores, which are subjected to periodic flooding and are therefore characterized temporarily and locally by great fluctuations of the sodium chloride content of the soil. The researches of numerous investigators show the sodium chloride content of the soil solution to be the most decisive factor in the distribution of plant species and communities on low-level coasts. Belt transects by English investigators clearly demonstrate this principle.

Similar belt formations are also to be observed near the lagoons of the Mediterranean Sea, where, however, the decrease of sodium content inland runs parallel to and simultaneous with declining moisture of the soil (Fig. 105).

Where wet saline areas are in immediate contact with dry saline soils, a very different zonation occurs. This may be seen around the shotts of high Algerian plateaus, where the following zonation obtains:

1. A salt-water belt of *Juncus subulatus* and *Scirpus maritimus*.
2. A little above water level a belt of *Salicornia fruticans*.
3. Small elevated hummocks formed by a belt of *Halocnemum strobilaceum*.
4. A gypsum border of the shott with a belt of *Frankenia thymifolia* and *Lepidium subulatum*.

The maximum concentration of salt is found in the *Halocnemum* belt.

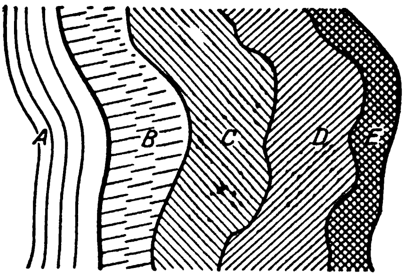

Fig. 105.—Belts of vegetation of the Lagoon of Palavas (southern France) according to decreasing NaCl content of the soil at a depth of 10 cm. *A*, Open water; *B*, Salicornietum herbaceae, pH 7.3, Chlorides 1.136 per cent; *C*, Salicornietum fruticosae, pH 7.2, chlorides 0.948 per cent; *D*, *Atriplex portulacoides*, pH 7.4, distinct traces of chlorides; *E*, *Atriplex* and *Agropyrum elongatum*, pH 7.4; no traces of chlorides.

The salt plants of the lagoons germinate in the winter and spring. Their major development occurs in the period following the heaviest precipitation and therefore with the smallest salt concentration. In the late summer, when under the influence of the burning rays of the sun, the capillary rise of the soil salts has reached its maximum, the annuals are already withered, and shrubs have reached their fruiting stages. Their root hold is generally very weak and superficial, thus avoiding the salt concentration of the soil at depths of 25 to 50 cm. Tall bushes, as *Salicornia macrostachya*, root only to a depth of 10 to 15 cm., and it is easy to remove the entire upper layer of the soil with the roots.

The following may be cited as extremely perhaloid-anastatic associations of the sodium chloride soils of southern Europe: the *Suaeda maritima-Kochia hirsuta* association of the small lagoons in coastal dunes; Salicornietum radicantis (resists the longest flooding); Salicornietum fruticosae, which, with *Atriplex portulacoides*, covers many square miles (Fig. 106); and the Salicornietum macrostachyae (see p. 231). This last characteristic association endures the greatest and most continuous salt concentration. It covers the otherwise plantless salt pans, which are flooded in winter and in summer crack into characteristic polygonal columnar structures (Fig. 118).

Algal communities of *Microcoleus chthonoplastes* and *Lyngbya* appear as pioneers upon bare, occasionally flooded (by sea water) muddy and sandy soil on northern European coasts as well as about the Mediterranean Sea. Warming and Gräbner (1918) mention communities of blue-green algae and diatoms on the sandy coasts of Denmark, which, with their mucous sheaths and membranes, glue together the grains of sand into crustlike masses just beneath the sandy surface. These pioneer associations contribute to the development of the uppermost soil layer and afford favorable germinating beds for higher plants.

Fig. 106.—Winter aspect of the *Salicornia fruticosa* association in the Camargne, France.

On low shores the sweeping advance of natural vegetative and soil changes ("sweetening of the soil") affords a great number of sociological problems, whose vast practical significance have not received the recognition and consideration which they deserve, especially in the regions about the mouths of such great rivers as the Po, Ebro, Rhine and Mississippi.

The saline soils on the shores of the large inland lakes are also rich in sulphates. Thus the salt crust on the shore of Lake Jugar Kul near Chiwa, in Transcaspia, according to Paulsen (1911), contains NaCl 79.9 per cent; $MgSO_4$ 21.5 per cent; and Na_2SO_4 1.6 per cent. The soil is overgrown with *Salicornia herbacea.*

On the strands and in many of the *playas* of the Great Salt Lake region, Utah, the concentration of salts often exceeds the limits of toleration of vascular plants. *Salicornia rubra* and *S. utahensis* are commonly found in soil containing 2 to 3 per cent of salt. In areas subject to summer desiccation they may be found in soil bearing as high as 6.5 per cent. *Suaeda erecta* grows best in soils of 1.5 to 2.0 per cent of alkali but has been found in soil with concentrations of 3.3 per cent. *Distichlis* generally favors soils of about 1 per cent but has been found in those carrying 2.6 per cent. *Allenrolfea occidentalis* is common on barren salt flats, growing in 1 to 1.5 per cent salt. Being a perennial it will grow in dryer soils. By far the commonest association is that of greasewood and shad scale (*Sarcobatus vermiculatus* and *Atriplex confertifolia*). It occurs on rather mildly saline plains where the salt content amounts to about 0.8 per cent. This varies, however, widely, and it grows abundantly in lower concentrations (0.2 to 0.4 per cent) and also in slightly higher concentrations (1.1 per cent).

The following table shows the analysis of soils taken from representative plant associations:

TABLE 18.—SALT CONTENT IN THE SOILS OF VARIOUS HALOPHYTIC PLANT ASSOCIATIONS NEAR GREAT SALT LAKE, UTAH, JULY, 1929
(After Flowers)

Association	NaCl	Na_2CO_3	$NaHCO_3$	Na_2SO_4	Total
Salicornia rubra	5.81	0.005	0.05	0.401	6.26
Suaeda erecta	·2.60	0.005	0.672	Trace	3.31
Distichlis spicata	2.21	0.053	0.141	Trace	2.60
Allenrolfea occidentalis	1.20	0.005	0.08	0.112	1.39

The relation of the depth of the ground-water level to the percentage of NaCl in the soil within the basin of the Great Salt Lake has led to the following generalization (determinations during July):

Depth of water below the surface, meters	Percentage of salts
1 or less	3 or more
2	1 to 3
3 or more	0.25 to 1

Water brings salt to the surface so that in areas of shallow water table are found the highest concentrations. The contour of the land also has much to do with the salt content. The *playas* being depressional areas are naturally closer to the ground water and have the highest salt concentration.

Determination of Chloride Content.—According to Lagatu and Sicard (1911), the fluctuations of the chlorine content of the soil calculated on the basis of 100 parts of air-dried or moist soil give consistent results. Calculated on the basis of dry or moist earth, the sodium chloride content of the lagoon soils near Montpellier increases constantly down to a depth of 2.5 m., as is shown in the accompanying figure (107).

However, these two authors rightly call attention to the fact that plant roots absorb their nutrition from the soil solution. For this reason the sodium chloride content of the solution must be examined, and in each sample the amount of soil moisture must also be determined. Soil samples for the determination of sodium chloride content are placed in closed containers at the collecting places. The determination of moisture (see p. 213) should be performed as soon as possible. Then 50 g. of soil are dried, and the determination of chlorine is made in the usual manner by leaching out the chlorides with distilled water and titrating the dissolved chlorides with accurately standardized silver nitrate, with potassium chromate as indicator.

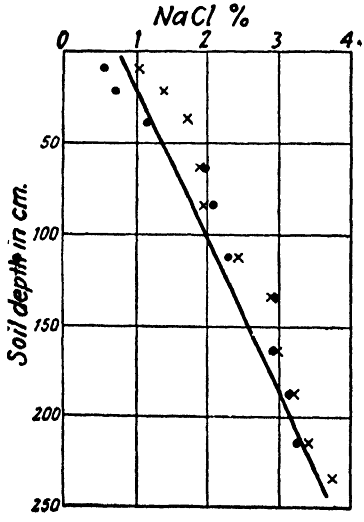

Fig. 107.—Increase of NaCl content with increasing depth of the soil, near Rieucoulon, France, on June 6 (●) and on Sept. 9, 1907 (×). (*After Lagatu and Sicard.*)

Should the soil contain organic admixtures, the filtrate is to be evaporated to dryness, and the residue carefully heated until all carbon is burned off. The sodium chloride content is calculated by multiplying the weight of chlorine by the factor 1.648 $\left(\frac{\text{NaCl}}{\text{Cl}} = \frac{58.5}{35.5} = 1.648\right)$. If the moisture of the soil and the NaCl content of the dry soil are known, it is easy to calculate the quantity of NaCl dissolved in the soil.

Example.—100 g. of dry earth contains 0.53 per cent of NaCl; the moisture in the soil is determined as 20 per cent. Thus the moist earth contains dissolved in it

$$\frac{0.53 \times 100}{20} = 2.65 \text{ per cent NaCl.}$$

The mere notation of the sodium chloride content, on the basis of a dry soil, is not very significant ecologically, without the simultaneous determination of the moisture in the soil.

Vegetation of Sulphate Soils.—Sulphate soils cover vast areas of the dry regions of southeastern Europe, Persia, Central Asia, the western states of North America, Northern Africa, and other regions. In places they have a desert-like character, and often they are covered by a snowy-white crust of salt.

The sulphates occur mostly as sodium sulphate, Na_2SO_4, or as magnesium sulphate, $MgSO_4$; calcium sulphate, $CaSO_4$, occurs more rarely, and sometimes the chlorides predominate.

The solontschak soils of southeastern Russia and Transcaspia have been studied by the Russian soil specialists. B. Keller (1923, 1926) deals mostly with the vegetation. In this region succulent Chenopodiaceae of the genera *Suaeda*, *Salsola*, *Anabasis*, and *Halimocnemis* display the greatest number of species. Characteristic among nonsucculents are *Statice*, *Frankenia*, and *Cressa*, whose glands give off large quantities of highly soluble salts (Na_2SO_4, NaCl). Similar discharges of salts have also been observed on leaves of *Statice*, *Limoniastrum*, *Frankenia*, *Tamarix*, and *Cressa*, of the south European and north African salt steppes and in species of the mangrove, such as *Avicennia* and *Aegiceras*, as well as in *Armeria*, *Statice*, and *Glaux maritima* of the north German coast. Fitting (1911, p. 267) observed this "salt lye" upon leaves in the morning and explained it as due to osmotic action by the solid salts already excreted. The experiments of Ruhland (1915), however, show that it is due to nightly secretions of aqueous solutions which are supposed to free the living cells from a harmful excess of salts. The osmotic value of the epidermal cells of *S. gmelini* rises as high as 165 atmospheres. Montfort (1922, p. 156), who has closely followed the salt secretions of *S. limonium* and *Armeria maritima*, sees in this function an indication of uninterrupted absorption of water by strong osmotic action of the roots.

The dominant succulents of the solontschak soils of western Asia and along the Mediterranean Sea are arranged in various communities, frequently in belts, according to salt concentration and moisture.

B. Keller (1923, p. 38) recognizes three associations of annuals in the desert steppes near Sarepta arranged in accordance with decreasing salt and moisture content of the soil: the *Salicornia herbacea, Suaeda maritima,* and *Petrosimonia crassifolia* associations and two half-shrub associations: the *Halocnemum strobilaceum* and the *Atriplex verruciferum* association. The two first occur, with approximately the same composition, on NaCl soils of European coasts.

The solontschak associations of the arid steppes of Turkestan are more peculiar. According to Sprygin and Popow nine communities (or associations) are distinguished with decreasing moisture and salt content of the soil.

Community

Decreasing NaCl content ↓

Salicornia herbacea
Halocnemum strobilaceum
Halostachys caspica
Kalidium caspicum
Suaeda arcuata
Salsola crassa
S. lanata
Artemisia maritima
Anabasis salsa

Halocnemum strobilaceum forms an important constituent of the halophytic vegetation on the shore of the north African shotts, while the *Anabasis salsa* association of Central Asia is represented upon the sulphate soils of northern Africa by the *A. aphylla* and the *A. articulata* associations of the arid desert. These deserts represent very extreme xerohalophytic habitats. Stocker (1930) has found the concentration of the soil solution in the upper layer of soil (1 to 10 cm.) of a wadi in the Lybian desert to be 51 per cent, the osmotic concentration being 336 atmospheres. At a depth of 25 cm. the salt content of the soil solution is 7.8 per cent, with an osmotic value of 39 atmospheres. Still the spot possesses vegetation!

Kearney (1914, 1918) is conspicuous among the American investigators who have examined the vegetation of the sulphate soils of that continent. Upon soils with a predominance of chlorides but also with considerable quantities of sulphates an association of the desert salt bush, *Atriplex polycarpa,* prevails on moderately inclined slopes of southern Arizona and in the dry regions of California. These receive occasional light rains. Large areas are covered with the pickleweed, *Allenrolfea occidentalis,* which can endure salt concentrations that admit only a few grasses and shrubs but no annuals. In the region of the Gila river on sulphate soil the composite *Pluchea sericea* (arrow weed) forms impenetrable thickets as tall as a man.

Solfataras, Fumaroles.—Whereas the halophytic vegetation of deserts and steppes consists chiefly of xerophytes, the plant communities of *solfataras* and fumaroles show a mesophytic character throughout. The vegetation of the sulphur springs of Java has been given much attention, even to the structure of tissues. There the soil surface is covered with a yellow and whitish coating of sulphur and sulphur compounds. The steaming springs are rich in alum. The beautiful fern, *Pteris incisa,* nowhere thrives better than upon these soft sulphurous soils; *Polypodium vulcanicum* even ventures upon rocks which are occasionally flooded by water reaching a temperature of 75°C. According to Holtermann (1907, p. 78), the dominant shrubs, *Agapetes vulgaris* and *Rhododendron retusum,* are completely covered with a yellowish precipitate from the sulphurous fumes. In spite of it, however, the leaves retain a rich green color, and even in the warm mud, surrounded with boiling solfataras, the shrubs bloom and bear fruit. The leaf anatomy of all the species examined is remarkable for the absence of xerophytic structures.

Sulphur Formation by the Action of Bacteria.—The sulphur bacteria (purple bacteria, *Beggiatoa, Thiothrix, Thiovolum, Thiophysa* spp., etc.) which oxidize hydrogen sulphide are widely distributed in nature. Their communities live chiefly in sulphur springs and on the shores of brackish waters. The sulphuric acid resulting from oxidation of H_2S is neutralized by carbonates (mostly $CaCO_3$): ($H_2SO_4 + CaCO_3 = CaSO_4 + CO_2 + H_2O$) and deposited as sulphate, in this case as calcium sulphate.

All sulphur bacteria require sulphur compounds for their development. These are furnished as hydrogen sulphide by the decomposition of plant and animal remains in water. Such bacteria are abundant in quiet waters rich in sulphates, as described for the Danish coast and the Kiel Fiord by Warming (1875) and Engler (1883).

In the spring purple bacteria form communities upon the mud bottom of the lagoons near Montpellier. When the inch-thick algal mat of species of *Ulva* and *Enteromorpha* is removed, large areas of the moist soil appear covered with an intensely wine-red, ill-smelling carpet of bacteria. A survey of the sulphur bacteria, with extensive references, is given by Düggeli (1919).

Determination of Sulphates.—A soil extract is made with slightly acidulated water (HCl 1 per cent). In the filtrate the sulphate is precipitated with barium chloride, $BaCl_2$. The barium sulphate, $BaSO_4$, is washed carefully and dried. Its weight, multiplied by 0.4114, gives the amount of sulphuric acid: ($1\,g.\,BaSO_4 = 0.4115\,g.\,SO_4$) (see also Wiegner, 1926, p. 39).

Soda Soils.—In less arid regions, in the northern part of the black-earth zone of Russia, in Rumania, Hungary, also in the United States (California) and Central Asia, soda soils rich in carbonic acid, take the place of sulphate soils. The principal soluble salt is sodium carbonate, Na_2CO_3.

In contrast to the sulphate soils which are due to climatic conditions it seems that soda soils are due to rather local edaphic conditions occurring in medium to semiarid climates.[1]

According to investigations in California by Hilgard (1914) and in Hungary by Treitz (1908), these soils are found only upon loess and marl.[2] The deciding factor for their formation is, according to Treitz, whether or not precipitation water drains off from the soil. If the water does not drain off, the alkali salts collect as a residue in the soil depressions. When the sulphates and chlorides in solution penetrate the porous lime soil (sodium formation is possible only upon soils rich in lime), the calcium goes into solution as bicarbonate; this reacts with the sodium salts forming alkaline salts of carbonic acid, while the lime unites with the sulphuric and hydrochloric acids.

> During the rainy season the sodium carbonate dissolved in the soil water passes from the upper layers of soil to the lower. Here it meets with crystallized gypsum and is changed to sodium sulphate. When the dry season comes on, the soil moisture rises toward the surface again. On reaching the calcium carbonate resulting from the former reaction, the sodium sulphate changes back to carbonate and rises to the uppermost layers of the soil [Treitz, 1908, p. 119].

This salt migration is responsible for the fact that the soda soil is free from sodium in the spring and rich in sodium sulphate in the deeper layers, while in the fall sodium is abundant in the upper stratum and but little sodium sulphate remains deeper in the soil. Soda soils (Hungarian *szek*) contain the halides in the unflocculated form and are therefore finely divided, densely packed, and often crust-like. Owing to the dispersion of organic material the soil solution is colored black. In North America these soils are called "black-alkali" land, in contrast to the "white-alkali" land (chloride and sodium sulphate soils). Thus soda soils are distinguished not only chemically but also physically from the other saline soils which have a coarser and more granular structure.

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[1] In desert regions soda appears only with increased soil moisture, especially in old stream beds and in marshy places (see Dimo, 1925).

[2] The formation of the North America soda soils, according to Breazeale, is due in many cases to the presence of a lime crust in a sodium chloride soil (*cf.* also Dorsey, 1906).

Determination of Soda.—A 50-g. sample of the soil is boiled with 500 cc. distilled water, filtered, and diluted to 500 cc. This solution is titrated with tenth-normal HCl, with methyl orange as indicator ($Na_2CO_3 + 2HCl = 2NaCl + H_2CO_3$). The sodium content may be calculated from the amount of tenth-normal HCl used in the displacement of the carbonic acid.

Vegetation of Soda Soils.—In his studies of the halophytic vegetation of sodium soils in the Hungarian lowlands Bernatsky gives an account of the plant communities. Kerner in his work on the plant life of the Danube countries (1863) had already outlined the salt vegetation of the great Hungarian Alföld. In large areas *Statice gmelini* predominates. Moist sandy saline soils are characterized by great masses of *Achillea crustata* along with *Aster pannonicus*, *Scorzonera parviflora*, *Erythraea linarifolia*, *Carex divisa*, and other salt-favoring species. Deeper depressions in the soil with high sodium content, often plantless in the center, are surrounded by a belt of dark reddish-brown *Kochias* and *Salicornias*, adjacent to the ashy-gray *Atriplex* and *Artemisia salina* belt. The companion floras of these communities are characteristic and richly varied, containing *Crypsis aculeata*, *C. schoenoides*, *C. alopecuroides*, *Pholiurus pannonicus*, *Cyperus pannonicus*, *Lepidium cartilagineum*, *L. ruderale*, and *L. perfoliatum*. The osmotic concentration of the soil solution in the Hungarian sodium soils has been examined by Stocker (1930). All sodium plants are able to put out new absorbing roots in a few hours, as soon as the soil is sufficiently moistened, but these roots dry up again as soon as the osmotic concentration goes above 28 atmospheres.

Gypsum swamps of large extent occur in Australia, according to Osborn (1925). In floristic composition they resemble those of sodium chloride and sodium sulphate soils. The identical halophytic genera which are spread over the European, north African, and central Asiatic salt regions are also found in Australia. The *Mesembryanthemum australe* association of the gypsum swamps of Flinders island are surrounded by the grass *Lepturus incurvatus*, which is also widely distributed upon the Mediterranean saline soils

All saline soil solutions have high osmotic concentrations. The osmotic value of the soil solution often acts as a limiting factor quite aside from its specific composition. This makes quantitative determinations of decided ecological value, and since such determinations of the concentration of the soil water may be made easily and quickly, they are desirable parts of any ecological investigation. If possible, they should extend through the whole vegetative period or, better, throughout the entire year. They can be made with the cryoscopic apparatus used for cell-sap determinations and expressed in atmospheres.

The following determinations made about salt pools near Montpellier, France, in October, 1930, show that the concentration of the water corresponds exactly with the zonation of the vegetation:

	Atmospheres
1. Scirpeto-Phragmitetum, in a fresh-water canal emptying into the pond	0.4
2. *Phragmites isiacus* sub-association with *Scirpus maritimus*	0.6
3. *Cladium mariscus* community	1.7
4. *Scirpus maritimus, S. littoralis* association	8.8
5. *Scirpus maritimus* mixed with *Salicornia radicans*	22.4
6. Salicornietum radicantis	27.4
7. The salt water without vegetation	77.8

CHAPTER VII

EDAPHIC OR SOIL FACTORS: PHYSICAL

1. TEXTURE OF THE SOIL

The colloid chemist deals chiefly with finely divided systems and their smallest particles: the microns, molecules, and ions. On the other hand, the physical study of soils has to do mainly with the coarser particles. There is, however, no fundamental distinction between the two fields of research.

The importance of the degree of division of the soil particles for plant life has long been recognized. Thurmann (1849) expressed it clearly in his classification of soils. His pelitic soils correspond to finely divided clay soils; his psammitic soils to the sandy, coarsely divided ones. Schlösing proposed a classification based upon the quantitative determination of the amount of the various sizes of grains in the soil. The division of soil particles according to size-classes, adopted officially in France in 1898 and in Great Britain in 1928, was based upon the work of Schlösing. Slightly different size-classes are used in North America, but it is hoped that the classification proposed by Atterberg, and internationally adopted in 1914, will lead shortly to a unification of the methods of classification (Fig. 108).

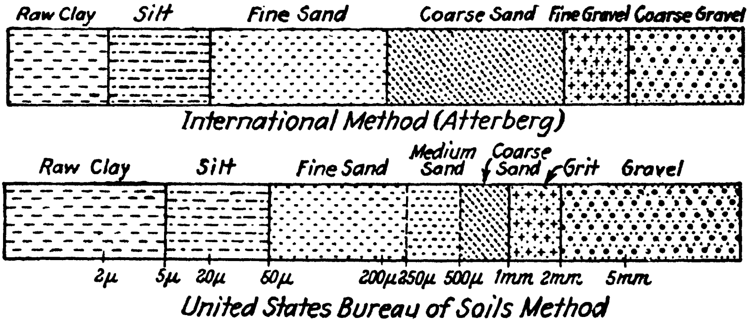

FIG. 108.—Classification of soil particles on the basis of size.

Soil Granulation.—The diameters of the grains of the various classes according to the international method (Atterberg, 1912) are: coarse gravel (rubble) more than 20 mm.; gravel 20 to 2 mm.; coarse sand 2 to 0.2 mm.; fine sand 0.2 to 0.02 mm.; dust or silt 0.02 to 0.002 mm.; and fine silt or clay less than 0.002 mm. (2μ).

The degree of division of the soil determines the most important physical soil properties, such as absorptive capacity, aeration, and water conduction. The activity of the plant roots is also greatly affected by the size of the soil particles.

The upper limit of capillary water movement and water storage is reached when the particles are 2 mm. in diameter. If the grains are less than 0.02 mm., the root hairs are no longer able to penetrate through the spaces between them, if the soil is of single grain structure. All particles of this size, even quartz grains, assume claylike properties (Ramann, 1928). Between 0.02 and 0.002 mm., electrolytes, particularly the H ions, effect flocculation; OH ions, by contrast, maintain the fine dispersity.

Coarse, sandy soils are good conductors of water but are also subject to intensive leaching and therefore are poor in nutritive substances. Finely divided raw clay soils are impervious, subject to little leaching, therefore rich in nutritive substances; but root activity is impeded in these tough soils. Raw clay (grain diameter less than 2μ) is said to stop the movement even of bacteria.

Determination of Particle Size: Mechanical Analysis of Soils.—While none of the customary methods can be called precise (see Mitscherlich, 1923, pp. 51–58), they are regularly used and give practical results (Fig. 108).[1]

For the segregation of the coarser soil particles the sieve methods can be used (see Ramann, 1911, p. 287; Mitscherlich, 1923; Burgevin, 1925). For the determination of stone and gravel content, the soil is dried at 100°C. and then sifted. But air drying is preferable for the analysis of the finer parts of the soil (Burgevin, 1925, p. 480; Russell, 1927).

The medium-fine soil particles may be determined by the elutriation method of Schöne, Kopecky, etc., but the sedimentation methods are better because by them the finer particles may also be measured. At present the sedimentation methods are used almost exclusively in many government institutions. They are based upon the principle that the rate of settling of the various soil particles in a mixture depends chiefly upon the size of the grain, the largest particles settling first. There is a definite ratio between the rate of settling and the size of the soil particles. According to Stokes's formula, the size of the particles may be calculated by this method (see Wiegner, 1926; Burgevin, 1925,

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[1] A full description of the various methods employed in the mechanical analysis of soils has been given by Keen (1931) together with a bibliography of the subject.

p. 457). Numerous apparatus have been constructed for the determination of the rate of settlement of the soil particles. Burgevin (1925) and Russell (1927) enumerate and discuss the advantages and disadvantages of the various devices. For a simple and inexpensive instrument Wiegner's sedimentation apparatus (*Schlämmapparat*) may be recommended (Fig. 109).

Soil Dispersion and Vegetation.—Many soil properties and the related phenomena of plant life may be explained by the influence of the various grain sizes in the composition of a soil. Mechanical analysis separates not only different physical groups but in most cases also chemically different groups of substances. At present, however, too few mechanical analyses of soils from natural plant communities are on record to give a clear picture of the conditions of interdependence.[1] It is known, of course, that a heavy clay soil, without much sand or stone, supports plant communities which are never found upon sandy, gravelly soils (Deschampsietum mediae in southern France, Anthoceretum in central Europe), while coarsely divided sandy soils have their characteristic specific plant communities such as Corynephoretum, Ammophiletum, Crucianelletum. Quantitative relations between degree of dispersion and plant communities have not been worked out.

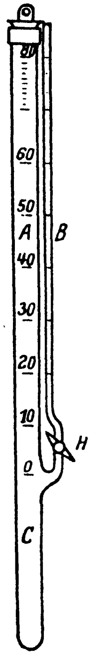

Fig. 109.—Sedimentation apparatus of Wiegner. *A*, Drop tube; *B*, small tube with distilled water; *C*, settling chamber; *H*, stopcock.

Rough determinations of degree of dispersion with the aid of the sieve method have been made by Gregor Kraus (1911) in the soils of the Bromion erecti alliance near Würzburg. It was shown that the distribution of the coarser particles in soils of one and the same plant community may be subject to considerable variations. In the Bromion erecti upon loess Kraus (p. 78) found 89.2 per cent fine earth below 0.5 mm. but only 28.7 per cent in calcareous gravel (*Kalkschotter*). In the same samples the coarser particles (the so-called soil skeleton), with grain diameters exceeding 5 mm., made up of 10.8 and 71.3 per cent respectively of the soil.

More significant glimpses into the matter are afforded by the determinations of dispersity made by Gessner and Siegrist (1925) on soils of some of the brookside plant communities of the Aar in Switzerland.

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[1] *Cf.* Gessner and Siegrist (1925) and Braun-Blanquet and Pawlowski (1931).

A profile in the *Alnus incana* forest showed the following soil granulations:

TABLE 19.—SOIL PARTICLES IN AN *Alnus* FOREST (I), IN A RECENTLY DEPOSITED SAND BANK (II), AND IN THE AAR DUNES (III)

Depth, centimeters	Coarse sand 2 to 0.2 mm., per cent	Fine sand 0.2 to 0.1 mm., per cent	Very fine sand 0.1 to 0.05 mm., per cent	Silt 0.05 to 0.02 mm., per cent	Raw clay less than 0.02 mm., per cent
I:					
0 to 10 sand and humus	2.6	10.1	19.8	29.0	38.3
15 to 25 sand	2.6	20.4	19.3	14.5	41.4
30 to 45 sand	40.5	54.0	2.0	0.8	2.8
II:					
Sand bank	57.5	32.7	3.5	1.0	5.7
III:					
Aar dunes	12.8	82.1	0.9	0.9	3.8

The predominance of the coarse and fine sand in the lowest, and of silt and raw clay in the topmost strata shows the process of soil formation and the accompanying development of vegetation. The lowest stratum represents an old sand bank upon which, after a gradually progressive process of soil formation, the recent *A. incana* forest has established itself, with rich herbaceous undergrowth. Newly deposited sand banks, without any vegetation at all, showed a composition very similar to the lowest stratum (Table 19, II). It is noteworthy that these river deposits contain mostly coarse sand, while the derived dunes, built up by wind, consist (like loess) of fine sand as seen in the Aar dunes (Table 19, III).

These river sand dunes in the Rhine, Aar, and Limmat valleys are stabilized at an early stage of their development by *Calamagrostis epigeios* colonies (geophyte), an association replaced later by a mixed deciduous forest. Coarse gravel banks are first covered with a loose Mesobrometum sod in which, as a rule, *Pinus silvestris* soon gains a foothold.

Basic gravel soils, poor in clay, near the large alpine rivers are exceedingly porous and poor in nutritive substances.[1] These soils are dry, and therefore in the pioneer stages of the development of their vegetation they are invaded by unspecialized pioneers, among which the plain turf moss, *Tortella inclinata*, and species of *Sedum* play an especially important, constructive rôle. These *Sedum-Tortella*

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[1] The most important bearer of nutritive substances is raw clay.

inclinata initial stages, with a rich intermingling of transported alpine plants and of xerophytes from dry, neighboring slopes such as *Oxytropis pilosa* and *Carex nitida*, are driven out in the Swiss Rhine valley, in one or two decades, by impenetrable thickets of *Hippophaë*, which in turn give way to the *P. silvestris* forest.

Soil Crumbing.—The habitability of a soil depends not only upon its dispersion but quite as much upon the relation of the particles to each other. The finer the grain of a soil the greater the importance of these conditions. In this respect two conditions are recognized: single-grain structure and aggregate or crumb structure (Fig. 110).

After prolonged, heavy rainfall finely granular soils appear doughy or sticky: they are "muddy." Rain water with small mineral content passes between the soil particles and decreases their cohesive force. They shift their position under the effect of the beating raindrops and fill up the vacant spaces. The soil changes to single-grain structure. The converse effect is produced by heat and especially by frost.

The sudden expansion of the soil, caused by freezing of the soil water, cracks up the densely packed soil particles. This expansion extends into the minutest chinks. The smallest soil particles collect in groups; they form aggregates or "crumbs" (Fig. 110*b*). Crumbing of the soil is brought about also by the action of soil organisms, by tillage of the soil, and especially by the influences of various soluble salts (salts of carbonic acid, sulphuric acid, chlorides, etc.). On the other hand, neutral carbonates and soluble salts of silicic acid tend toward deflocculation. For this reason soils deposited in pure water (glacial Dryas clay) are very densely packed.

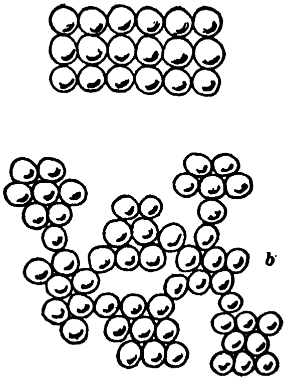

FIG. 110.—Single grain structure (*a*) and aggregate or crumb structure (*b*) of soil.

The farmer and the forester combat the single-grain structure of their soils and endeavor to maintain a crumb structure which is essential to good tilth. For the plant sociologist, the relation of root layering to structure of the soil offers a fruitful field for research. In such work, water content, water conduction, and aeration of the soil should be included as controlling factors.

2. SOIL WATER

According to the manner in which it occurs in the soil, the soil scientist distinguishes between attached water, *i.e.*, water fixed in the soil, and gravitational water, which can drain off. The attached water is fixed either hygroscopically or by capillary forces; hence the terms hygroscopic and capillary water. Vegetation is almost exclusively concerned with capillary water the occurrence and distribution of which depend mainly upon the structure of the soil. The capillary water of the soil forms a thin, coherent water film around each solid particle. This capillary water may move from particle to particle, such movements tending to establish and maintain a uniform supply in all adjacent portions of the soil. Atterberg's experiments with sands of various grain size show that the height and rate of the rise of water increase with a decrease of the grain size, reaching a maximum in the case of soil particles of 0.02 to 0.05 mm. Finer grains are a hindrance to water movement.

Inasmuch as hygroscopic water cannot be taken up by the roots of plants, and gravitational water flows off more or less quickly, only the capillary water remains a permanent source of moisture for vegetation and as a solvent and vehicle for mineral plant foods. Because of these several functions, the capillary water plays an outstanding rôle in the vital competition of plants and plant communities. The more favorable the water supply the more intense is the competition; and the less favorable the water supply the smaller the number of communities which are able to avail themselves of that supply. As a vegetational factor the water content of the soil often reaches a minimum and exercises thereby a decisive effect upon the composition of vegetation. The harmful effects of soil water when in maximum quantity are discussed in the section on soil aeration.

The water which is available for the vegetation is called "chresard" by Clements and "growth water" by Fuller, in contrast to that which remains fixed in the soil, which is called the "echard." The intermediate stage between echard and chresard at which the wilting of the plants sets in is known as the "wilting point," and its numerical equivalent as the "wilting coefficient." Fuller (1914) has termed the water above the wilting coefficient the "growth water," recognizing that most plants continue to absorb small amounts of water from the soil when it contains less moisture than that indicated as the wilting coefficient.

Available Water.—Determinations of soil moisture in order to be of ecological significance should refer to the water available for the use of plants; that is, the chresard or the growth water should be determined. The total water content may be calculated by collecting samples of soil in closed containers and noting the loss of weight after drying at 100° to 105°C. Then

$$\text{Total water content} - \text{wilting coefficient} = \text{growth water.}$$

Determinations of soil moisture should be made at intervals of a week throughout the entire vegetative season and plotted graphically. Their ecological significance is much greater when records for a series of consecutive years are available.

Water Capacity.—The determination of the water capacity of the soil is somewhat more complex than the measurement of the actual water content, but it is more significant ecologically. The water capacity is the amount of water which a soil is capable of retaining against gravity (Ramann, 1911; Hilgard, 1914). Methods for such determinations are described by Ramann, Hilgard, Siegrist (1930), and others. Burger (1922, p. 47) gives the following directions:

> With a 1,000-cc. steel measuring cylinder a sample of undisturbed mature soil is carefully removed and saturated in the water bath for 24 hr. After saturation, any soil protruding over the mouth of the cylinder, due to expansion, is leveled off and the sample is weighed after excess water has been permitted to drip off for 2 hr. Then the sample is broken in pieces and dried at 100° to 120°C. until a constant weight is reached. The difference in weight represents the water content of the saturated soil.
>
> $$\frac{\text{Water content}}{\text{Dry weight}} \times 100 = \text{water capacity percentage by weight.}$$

The best expression for the water-holding power of a soil is given by the statement of water capacity in percentage of volume.

The water capacity is not identical with the pore volume of the mature soil. The larger pores contain gravitational water which is not included in the determination of water capacity.

Interesting comparisons between the pore volume and the water and air capacity of the soil of different dry grasslands of Bohemia are given by Klika (1929). The water capacity of the soil of the Festucion vallesiacae is always high, hardly ever falling below 50 per cent, while the air capacity is low.

Water capacity is a function of grain size and structure, on the one hand; and of the expansible substances (humus, clay) present, on the other. Humus soils have an extraordinarily high water capacity. From Nitzsch's (1925) investigations it appears that water capacity increases with increasing pore volume, *i.e.*, with increasing looseness of the soil, up to a certain maximum determined by local conditions. Beyond this maximum it decreases very noticeably.

While the available water actually present in the soil is dependent upon precipitation and evaporation, and therefore subject to considerable fluctuations, the water capacities of the various soil layers of a plant community are very constant. Their values may usually be established rather accurately by a single examination. In a dry meadow (probably Mesobrometum) near Zofingen, according to Burger (1922, p. 106) in seven determinations spread over all seasons, a maximum deviation of only 2.2 per cent of volume from the mean was recorded; in the mixed deciduous forest the maximum deviation amounted to 3.3 per cent of the volume. With depth the water capacity of the soil examined was found in most cases to decrease.

In the ecological characterization of plant communities the water (and air) capacity of the soil will in the future demand more attention.

TABLE 20.—WATER AND AIR CAPACITY OF THE SOIL OF A 100-YEAR-OLD DECIDUOUS FOREST AT ZOFINGEN
(After Burger)

Depth, centimeters	Volume percentage	
	Water capacity	Air capacity
0 to 10	51.6	14.0
40 to 50	42.9	6.3
80 to 90	40.3	3.1

Coefficients of Soil Moisture.—We have seen that water capacity, along with granulation, is especially affected by the expansible colloid complexes of the soil. Their quantitative distribution in the soil thus affords the best data for the estimation of its water capacity. Basing his calculations upon this assumption, Crump (1913) has computed a soil-moisture coefficient which he calls the "standard index of soil moisture." The soil-moisture coefficient is expressed in terms of the percentage of water content of the air-dried soil (around 15°C.), divided by the humus content $\left(K = \frac{\text{water content}}{\text{humus content}}\right)$. Since the

TABLE 21.—COEFFICIENT OF SOIL MOISTURE IN DIFFERENT FACIES OF OAK FORESTS

Facies of the forest floor	Water, per cent	Humus, per cent	Coefficient of soil moisture, per cent
Scilla non scripta	24.4 30.5	6.9 9.3	3.5 3.25
Carex pendula	281.2 248.3	30.3 26.7	9.3 9.28
Holcus mollis	31.2 28.6	12.9 12.1	2.4 2.36

quotient in humus soils always gives quite corresponding values, Crump views the resultant average value from several determinations as the most important constant for plant communities on humus soil whose occurrence and distribution are conditioned by soil moisture. Various striking edaphic facies of the oak woods in Yorkshire examined in February gave the moisture coefficients shown in Table 21 on page 214.

The following data seem to show that the season of the examination has no particular effect upon the results:

TABLE 22.—COEFFICIENT OF SOIL MOISTURE IN THE *Sesleria coerulea* TURF ON LIMESTONE

Time of examination	Water (air dried), per cent	Humus, per cent	Coefficient of soil moisture, per cent
April	31.4	37.7	0.80
April	15.4	17.0	0.90
August	22.3	19.0	1.17
Average	...	....	0.96

Wilting Point and Wilting Coefficient.—Vegetation responds to an inadequate water supply by wilting. This means that, although the plants still may be taking up water, the amount of moisture drawn from the soil is not sufficient to cover the loss by transpiration. The water which remains in the soil at permanent wilting marks the critical point in the water supply that has been termed the "wilting coefficient" by Briggs and Shantz (1912). With the same soil structure the wilting coefficient is approximately the same for practically all plants. As might be expected, however, it changes with the degree of division of the soil particles and varies directly with the water capacity of the soil. In densely packed fine-grained soils the wilting point is reached at a higher water content than in loose sandy soils which retain water poorly. In dune sand the wilting coefficient often lies below 1 per cent; in clay loam, however, it reaches 17 to 20 per cent.

In determining the wilting coefficient it is often difficult to tell when a plant is permanently wilted. Briggs and Shantz define the condition of permanent wilting thus: "Without the addition of water to the soil the leaves are unable to recover turgidity even in a saturated atmosphere."

According to Maximov (1929) and Knight (1922), wilting is clearly shown by the loss of turgor before there is any visible indication of the condition. The amount of water that leaves may lose without visible wilting is a useful indicator of xerophytism, and the ability to recover from wilting is one of the most reliable indicators of drought resistance. Numerous American investigators such as Fuller (1914), Weaver (1914), Thone (1923), and Shantz and Piemeisel (1925) have come to regard the wilting coefficient as a most useful constant by which to relate the availability of the soil moisture to the plant community.

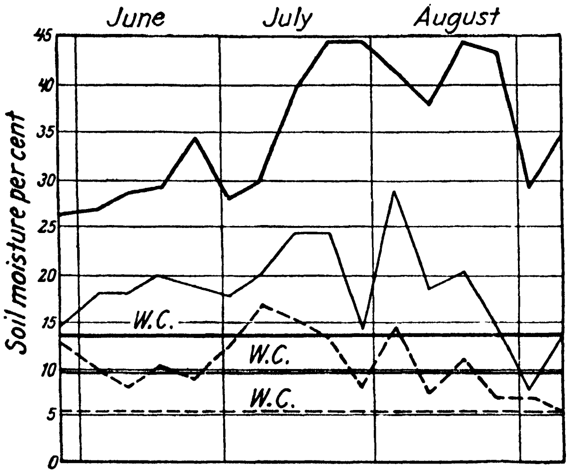

FIG. 111.—Range of soil moisture and corresponding wilting coefficients (*W.C.*) in three different associations in Nebraska. (*After Weaver.*)

The differences in the wilting point of various plant communities may be considerable. Communities requiring a large amount of available water usually have a higher wilting coefficient than those with lesser demands upon soil water (Fig. 111). In other words, the more mesophytic communities usually develop on soil with high water capacity.

The wilting coefficient rises in the course of mesophytic successions with the changes which accompany soil development (the enrichment of the soil with humus, etc.), as Fuller (1914) was able to prove in the Great Lakes region of North America (Table 23).

The determination of the wilting coefficient may be made directly, according to the directions given by Briggs and Shantz, or indirectly through the moisture equivalent, using the equation:

$$\frac{\text{Moisture equivalent}}{1.84} = \text{wilting coefficient.}$$

TABLE 23.—WILTING COEFFICIENTS AND GROWTH WATER IN THE FOREST SUCCESSION NEAR LAKE MICHIGAN, INDIANA
(After Fuller)

	Populus deltoides association	*Pinus banksiana* association	*Quercus velutina* association	*Q. borealis* association	*Fagus grandifolia-Acer* association
Wilting coefficient:					
At 7.5 cm	0.8	1.1	1.1	9.0	13.5
At 25 cm	0.8	1.0	0.9	9.5	9.5
Growth water, mean per cent	2.15	1.15	1.27	3.3	4.4
Evaporation, cubic centimeters	25.2	10.3	10.1	6.7	5.3
Ratio between evaporation and growth water	11.7	10.7	9.37	2.78	1.81

The "moisture equivalent" is the percentage of moisture remaining in the soil when it has been uniformly wetted and subjected, in a centrifuge, to a force of 1,000 gravities (Briggs and McLane, 1907).

The contention of many investigators that the wilting of plants, and hence the value of the wilting coefficient, depends not only on the regulation of the water absorption from the soil but also on atmospheric influences (humidity and movement of the air, etc.) has led Lundegårdh to propose a determination of the permanent wilting point at a certain moisture content of the air. It is doubtful, however, if this would make an appreciable difference in the wilting coefficient, since the investigations of Shull (1916) have shown that the wilting coefficient is really a function of the rate of movement of the capillary water in the soil.

Ground Water.—The level of the water table determines the nature of vegetation, especially in areas where topographic changes are in progress. Artificial changes in the ground-water level, by drainage for the production of arable land, may have fatal effects upon the original vegetation and lead often to accelerated succession. The natural changes involved in the formation of moors or the intrenchment of streams are often more rapid than silting up of ponds and lakes (*cf.* Godwin and Tansley, 1929).

By the lowering of a stream bed the vegetation of the lower flood plain gradually merges into that of the higher, *pari passu* with the lowering of the ground-water level, until the climax is reached.

Regular gage readings are necessary for the measurement of ground-water level. In various communities of a land-formation complex where the water does not lie exposed, perforated metal pipes (boiler pipes of 5 to 10 cm. diameter are adequate) are firmly sunk in the ground and made as invisible as possible. The readings should be made over a considerable length of time in order to obtain a picture of the seasonal fluctuations of the ground water (*cf.* Godwin, 1931).

3. SOIL TEMPERATURE

The physiological effect of water in the soil rises with increase of temperature. At soil temperatures below freezing, soil water is of no use to vegetation. Plant communities whose root layer lies many months in frozen ground develop late and show a floristic composition much different from that of the surrounding vegetation. In the "cold" moors of the temperate zone there are northern, subalpine, and even occasional alpine species in the midst of the region of beech forests. The subalpine moors of the foothills of the central European Alps, where in May and June at depths of 15 to 20 cm. frozen soil is common, are known as the refuges for relicts of former glacial epochs. Thanks to the local, low soil temperatures, these species have maintained their place in competition with the surrounding indigenous vegetation. In humus soil the process of thawing is slowest (Wollny, 1898).

Physiological investigations make it seem probable that the soil temperature acts upon the permeability of the plant tissues and thereby influences the absorption of the inorganic food materials. Cannon (1918) sought to determine experimentally the dependence of growth upon soil temperature of the habitat. He followed root growth of the desert shrub *Covillea tridentata* at different temperatures and obtained the following average value of hourly elongation:

Degrees Centigrade	Millimeters
15	0.1
20	0.2
25	0.4
30	0.5
32	1.6

The growth optimum of *Covillea* roots lies at 32°C. It is to be assumed that each species has its own optimum growth temperature.

The soil temperature is subject to considerable local and temporal fluctuations and is therefore important as a habitat factor. Measurements are of value for the comparison of different stations only when extreme temperatures are recorded or when records of long-continued observations are available.

Soil temperature is dependent upon the exposure and the physical nature of the habitat. Both dead and living ground cover are important. Radiation has a depressing effect on soil temperature. The greater the angle of incidence of sunlight and the longer its duration, the greater the intensity of insolation the higher the soil temperature. The contrasts are most marked in mountains, and this is one of the prime factors which cause the great differences in alpine vegetation in sunny and shady exposures. The scenery changes with surprising abruptness in passing from shady to sunny slopes. Maurer (1916) has made measurements of the relation between soil and air temperatures at different altitudes. They refer to soil temperatures at a depth of 120 cm., where the root layer is developed in good soil.

TABLE 24.—MEAN SOIL TEMPERATURES WITH INCREASING ALTITUDE IN THE SWISS ALPS
(After Maurer)

Altitude, meters	Soil temperature at depth of 120 cm., degrees centigrade	Excess of soil over air temperature, degrees centigrade
600	9.0	0.5
900	7.8	1.0
1,200	6.5	1.3
1,500	5.3	1.7
1,800	4.0	2.0
2,100	2.7	2.3
2,400	1.3	2.5
2,700	0.0	2.7
3,000	−1.3	2.9

The relative soil temperature thus shows a regular increase with an increase in altitude. While the annual average of the air temperature in the Central Alps reaches 0°C. at a little above 2,000 m., the soil temperature averages 0°C. only at 2,700 m.

An interesting treatise by Henne (1894) deals with the dependence of soil temperature upon the physical condition of the soil. He studied the temperature of the uppermost layers of differently colored soils. His observations extended over a period of seven months (April to October) and were carried out in the experimental forest garden of Adlisberg near Zurich, at depths of 3 to 5 cm.

TABLE 25.—SOIL TEMPERATURES (3 TO 5 CM. DEEP) IN WEATHERED RUBBLE WITHOUT HUMUS
(After Henne)

Kind of rock	Soil color	Mean, degrees centigrade	Mean maxima (1 p.m.), degrees centigrade
Slate	Black	16.8	20.4
Verrucano	Red	16.8	20.3
Gneiss	Yellowish gray	16.2	19.5
Jurassic limestone	Yellow	15.9	18.2
Cretaceous limestone	Gray	15.4	17.5
Clay soil	....	15.4	17.5

The mean temperature of the air at the same time was 14.2°C.; the mean maximum, 15.6°C. The soil temperature during the seven months of the experiment was considerably higher than the simultaneous air temperature; the temperature of black soils was considerably higher than that of soils of other colors. This circumstance makes thinly vegetated basalt, phonolite, serpentine, and dark-colored dry, porous soils in general especially well suited for thermophilous southern plant communities. Among such soils are the volcanic soils of the Hegau, of the Kaiserstuhl, of the Auvergne; the serpentine soils of the Mur valley in Styria and the basalt soils of southern France. The flora and vegetation of the basaltic soils of Roquehaute near Agde, France, are famous throughout Europe. There in a limited area are found a whole group of liverworts, mosses, and flowering plants, whose main distribution is in northern Africa. The peculiar *Isoetes setacea* association, with *Marsilia pubescens*, *Pilularia minuta*, and *Peplis erecta*, is nowhere else in all France so richly developed and so abundant as it is around the black pools of Roquehaute, which in the summer for weeks at a time are decidedly hot. Ramann (1911, p. 395) has emphatically stated the important influence of soil structure upon soil temperature. *In Wirkung treten die hohe Wasserkapazität, Wärmebindung infolge Verdunstung, Anderungen der Temperatur tieferer Schichten beim Eindringen von Wasser und der Einfluss von Oberflächenwasser auf die Bodentemperatur.* Thus the effect of water is very considerable. The so-called "cold soils"—humus and clay—are very retentive of water. G. Kraus (1911, pp. 120–123) has shown by numerous measurements the differences between the temperature of wet and dry soils. Unfortunately he did not attempt to discover any relation of this to the vegetation.

Figure 112 illustrates the annual cycle of temperature measured in the forenoon at various depths in the soil at Montpellier, France.

In multilayered communities—scrub and forest—the soil temperature is more equable and lower than in exposed soil. For this reason, according to Bühler (1918), tree seeds germinate more slowly in the shade of woods. In openings germination is best toward the center of the area. In this case probably light is a factor worthy of consideration.

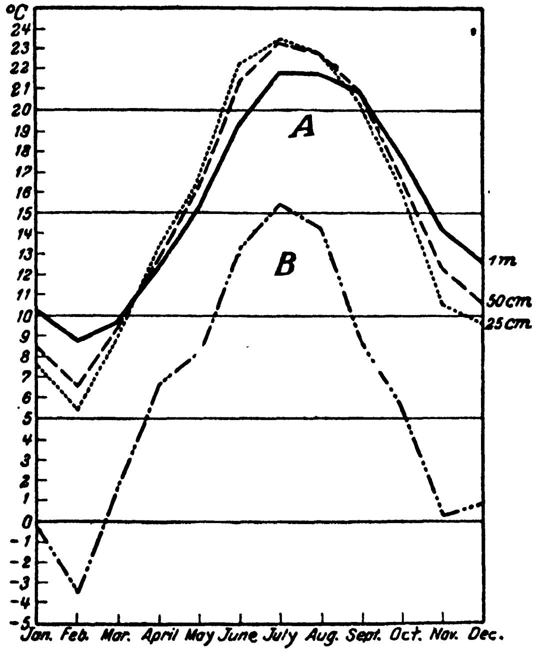

FIG. 112.—*A*, The yearly range of mean soil temperature at various depths; and *B*, the air temperature 20 cm. above the soil, at 9:00 A.M., near Montpellier, France.

Maximal Soil Temperatures.—The highest soil temperatures are attained in open, single-layered plant communities of the arid regions. While Kraus (1911, p. 109) gives the maximal temperature of the topmost soil layer (2 to 5 cm.) in natural sod communities (Bromion) near Würzburg as 38.5° to 44°C., and Allorge (1922) in the Paris basin as 49°C., the temperature in the steppe soils of Russia reaches 50° to 60°C. or more. In the desert region of Arizona, Sinclair found a temperature of 71.5°C. at 4 mm., and Buxton (1924, p. 132) observed near Jerusalem 63.4°C. on the surface of the soil in August.

Such extreme temperatures, especially when accompanied by extreme dryness, permit only a few plants to live for any length of time. Chamaephytes and nanophanerophytes endure them, while therophytes and geophytes avoid them by shifting their vegetative period. Tree seedlings die out. In the steppes of southern Russia on the Dnieper river, Ramann observed a large number of year-old oak seedlings with a layer of the stem 1 mm. thick killed at the soil surface. Extreme heat must have caused this damage.

Decrease of Temperature with Depth of Soil.—The decrease of temperature with increasing depth proceeds the more rapidly the more highly the upper soil layers are heated. Even at the highest surface temperatures (above 70°C.) the heat is barely noticeable at a depth of 15 cm. (Fig. 113). Deep roots are, therefore, never exposed to excessive heat. The excessive surface heat and the wide range of surface temperatures constitute a condition that results in the death of many young plants (Fig. 114).

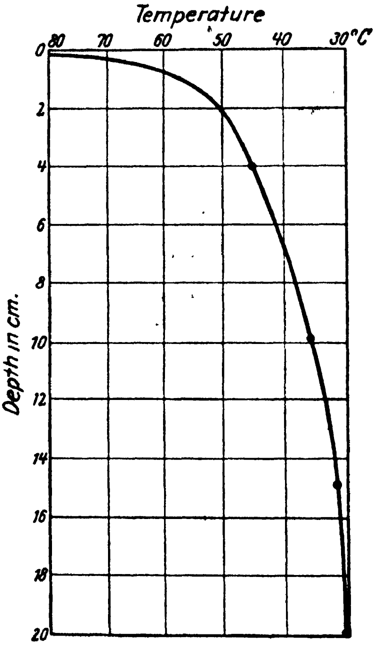

FIG. 113.—Decrease of soil temperature with depth in the semi-desert of Arizona. (*After Sinclair.*)

While the maxima in the uppermost soil layer by far exceed those of the lowest air layers, the minima fall only slightly below those of the lower layers of air. The denser the soil structure the more readily frost penetrates and the deeper it goes. For this reason loose humus soils are most resistant against frost injury.

In the colder regions of the earth the season with the lowest temperatures coincides with the months during which an insulating snow blanket covers the soil; hence, there is little frost damage to roots in the coldest climates. Mats of dead leaves and lichens and mosses are also excellent insulators.

Nothing is known about damage to roots of wild plants by spring and autumn frosts. In the case of cultivated plants (seedlings of rye, wheat, peas, maize), Zacharowa (1925) has determined that the difference in the cold resistance of the separate parts of the roots is influenced by the reaction of the cell sap. The more resistant cells show a more alkaline reaction than the more sensitive ones. The more alkaline the reaction of the cell sap the more resistant to cold injuries are the roots. This seems due to the fact that the proteins of the protoplasm coagulate at a lower temperature in an alkaline medium.

Measurement of Soil Temperature.—Numerous soil thermometers are in use for the measurement of soil temperature. However, they all have the disadvantage that they are introduced into the earth from above and therefore, at least in soils which are not very loose, call for some sort of excavation. This, of course, destroys the natural soil arrangement somewhat, and the reading may be erroneous. Toumey and Stickel (1925) propose an excavation from which the thermometer can be introduced horizontally at various depths. Superficial, individual measurements are usually made with the so-called punch thermometer in a brass case, but these readings can claim no great accuracy.

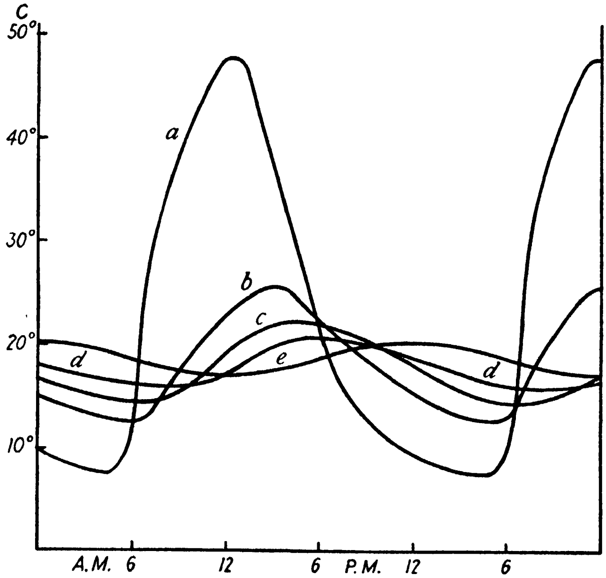

FIG. 114.—Diurnal variation of soil temperatures at Giza, Cairo: (*a*) at the soil surface; and at depths of (*b*) 5 cm.; (*c*) 10 cm.; (*d*) 15 cm.; and (*e*) 20 cm. (*After McKenzie-Taylor and Williams.*)

4. SOIL ATMOSPHERE

Carbonic acid is continuously released in the soil by the action of soil organisms and by the respiration of roots. Moreover, the living organs and organisms demand oxygen, which they can obtain only from the air by gaseous exchange. For the great majority of the higher plants an active exchange of gases in the soil is a necessity of life. Livingston and Free (1917) have shown that the labiate, *Coleus blumei*, ceases to absorb water through the roots within a few hours after the withdrawal of oxygen. Contrariwise, *Salix nigra* was not affected at all by this treatment. The effect of aeration upon the germination of seeds of *Impatiens* was studied by Hunter and Rich (1925), who show better germination for well-aerated soils (Fig. 115). They have also shown by experiment that the development of the root system is directly dependent upon soil structure and that thus the growth of the organs aboveground is indirectly affected.

Well-aerated soils always show a high oxygen and a low carbonic acid content. The slower the gas exchange proceeds the more the carbonic acid accumulates. Consequently, the oxygen content drops, and the floristic composition of the vegetation changes accordingly.

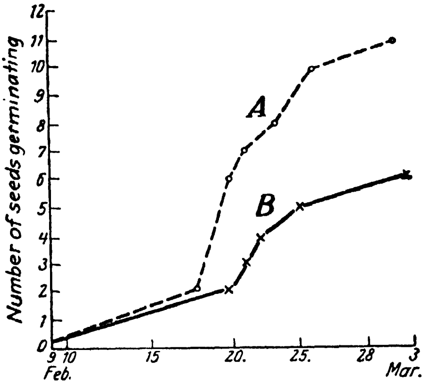

FIG. 115.—Germination of seeds of *Impatiens* in well-aerated (*A*) as compared with non-aerated (*B*) soils. (*After Hunter and Rich.*)

Oxygen Content of the Soil.—The oxygen content of the soil and its ecological effect have been examined by Hesselman (1910), Russell and Appleyard (1915), Cannon (1924), and still more critically by Romell (1922). Romell determined both the oxygen and the carbonic acid content, the analyses being made with Krogh's microanalytic apparatus.

Romell established beyond question the fact that soil aeration by diffusion occurs to a notable extent in natural soils and more particularly in forest soil. This is opposed to the prevailing view which follows Ramann and Mitscherlich. The oxygen deficit and the surplus of carbonic acid are at any given depth directly proportional to soil activity, other things being equal. With equal activity (CO_2 production) and uniform distribution of activity in the soil, these values are inversely proportional to the air content of the particular soil. In coarse soils the size of the grains is of secondary importance for aeration. Aeration is considerably decreased, however, in finely dispersed clay soil (down to about one-hundredth normal). Of course, soil water presents the greatest obstacle to aeration. When the pores are clogged with water, aeration falls to about one ten-thousandth normal value.

The activity and air content of the superficial soil layers determine the conditions of soil aeration. Moreover, there are such large fluctuations from time to time that individual tests made at random give little evidence of the actual conditions. Romell always found the highest deficit of oxygen together with the highest surplus of CO_2 in soils which were so wet that water dripped from the soil sample. An almost complete lack of oxygen was found in boggy raw humus soils. In the light of recent investigations, the claim, formerly made by Gräbner, that non-boggy raw humus soils and hardpan layers are lacking in oxygen can no longer be maintained, at least not in that general form. The poorest kind of raw humus of beech woods has been found to give perfectly normal O_2 and CO_2 values, even after periods of rain.

The oxygen content of air in the superficial root layers approaches that of the atmosphere and is usually around 18 to 20 per cent by volume.

Carbonic Acid Content of the Soil.—Since the oxygen and carbonic acid content of the soil bear a definite ratio to each other, and vary simultaneously, only one of the factors needs to be measured. Lundegårdh has decided in favor of the carbonic acid. The determination of the carbonic acid content of the soil air is carried out in the same manner as that of oxygen, with the aid of the portable gas-analysis apparatus. Romell (1922) and Lundegårdh (1925) give details on this subject. The reports of both of these investigators are indispensable to anyone who is engaged in studying the composition of soil air. It is possible here to state only a few of the results which are most important ecologically. While the oxygen content decreases with depth of soil, the CO_2 content, as a rule, rises. In deeper soil layers the percentage (by volume) of carbonic acid may reach that of oxygen or even exceed it.

Fodor (1875) measured, under a meadow sod, in Cluj, the CO_2 and O_2 quantities shown in Table 26 on page 226.

Fodor records 14.3 per cent as the maximal CO_2 value at a depth of 4 m., while Russell and Appleyard (1915) have found a maximal value of 9.1 per cent of CO_2 in a wet moor sod near Rothamsted, England, at a depth of only 15 cm.

Romell (1922) gives comparative data on the formation of carbonic acid at different depths under natural plant communities in Sweden. In a beech wood with *Vaccinium myrtillus* ground cover he found the following CO_2 content of the soil:

CO_2 at 15 cm. 0.2 per cent; at 30 cm. 0.4 per cent; at 60 cm. 0.4 per cent.

That is, the soil was well aerated. In a wet deciduous forest he obtained rather different results (Table 26, II).

TABLE 26.—INCREASE IN THE CARBONIC ACID CONTENT WITH DEPTH OF SOIL: I ACCORDING TO FODOR; II ACCORDING TO ROMELL

	Depth, millimeters	Volume percentage	
		H_2CO_3	O_2
I	1	1.9	19.2
	2	3.8	18.6
	3	10.8	8.6
II	15	0.2	21
	30	1.0	20
	45	2.0	16

At 45 cm. depth the accumulation of carbonic acid in the deciduous forest is so great that only a few willows and alders, *Alnus incana* and *A. glutinosa*, can withstand it. Carbonic acid concentrations of 1 to 2 per cent have toxic effects for many plants; at 4 per cent the seeds of *Brassica alba* (temperature 3°C.) fail to germinate (Kidd, 1914); at 25 per cent of CO_2 the root growth of *Covillea tridentata, Krameria canescens, Mesembryanthemum* sp. is completely stopped in a few hours (Cannon). The forester thus finds it necessary to determine the specific resistance of the trees against carbonic acid poisoning and the means to combat this danger. Nothing is known of the part which the individual wild plants play in the accumulation of CO_2. Parker's (1924) experiments with cultivated plants lead us to expect different effects from the different species. While buckwheat released very little CO_2, bean roots gave off considerable quantities.

How widely the carbonic acid content varies in closely adjacent areas is shown by the observations of Lundegårdh (1925). In the *Carex vesicaria* bog with *Peucedanum palustre* he measured 1.24 per cent; and only 2 m. away, at the same depth (15 cm.) in the alder thicket with *Oxalis, Maianthemum*, etc., he obtained a value of 0.24 to 0.50 per cent of CO_2.

Valuable data for the estimate of soil aeration are afforded by purely physical methods for the determination of pore volume and air capacity. At the same time, also, water content and water capacity of the soil may be determined (see p. 231).

Pore Volume.—Pore volume means volume of the air-filled hollow space of the dry soil. If a graduate cylinder of 1,000 cc. is filled with natural mature soil and dried, the volume of the measuring cylinder (1,000 cc.) minus the volume of the dried, solid soil particles gives directly the hollow space or pore volume of the soil in thousandths. Ramann (1911, p. 308), who examined the pore volume of a diluvial sand dune near Eberswalde, determined at different depths the following pore volumes:

Centimeters	Parts per 1,000
0 to 10	506
20 to 30	459
40 to 50	404
60 to 70	382
80 to 90	373

The pore volume decreases from top to bottom, rapidly at first then more slowly. The densest packing of soil is found under water (pore volume 200 to 300 parts per 1,000). In contrast to this, peat and moor soils are very loosely packed (pore volume 840 to 850 per 1,000).

More recent investigations by Burger (1922), using more delicate methods, confirm the general results of Ramann, both agreeing quite well on the investigations on the O_2 and CO_2 content of the soil.

TABLE 27.—PORE VOLUME OF THE SOIL OF TWO SEMINATURAL PLANT COMMUNITIES, PARTS PER 1,000
(After Burger)

Depth in soil, centimeters	Dry meadow (Bromion?)	*Quercus pedunculata* forest, 150 years old
0 to 10	487	592
20 to 30	443	463
50 to 60	. . .	397

In the dry meadow the topmost soil layer is rather densely packed, whereas in undisturbed soil of the oak woods with its blanket of dead leaves a loose upper layer favors the growth of rhizome geophytes. The dense packing of the open meadow soil is due to dense root systems and even more to the puddling effect of rainfall. After deforestation, the pore volume of the soil decreases considerably. From the curves plotted by Nitzsch (1925) for the elucidation of the relation between water capacity and pore volume it follows that with increasing looseness of the soil the water capacity is raised. Beyond a certain limit, fixed by habitat conditions, it then decreases rapidly.

Air Capacity.—Having determined the pore volume, including all hollow spaces not occupied by solid soil particles (earth, stones, roots), we are in a position to measure two additional features. By saturating a known volume of soil with water, the air and water capacities are determined. In the water-saturated soil we have the equation:

$$\text{Total volume of soil} = H_2O \text{ content} + \text{air content} + \text{volume of solid particles.}$$

The air content of the saturated soil (air capacity according to Kopecky, 1914) is that pore volume which, after saturation of the soil up to its absolute capillary capacity with water, still remains filled with air.

The air capacity thus indicates the air content still available even in the water-saturated soil. This is the air content which is available to plant roots under all circumstances. In short, these are hollow spaces, which due to their size have no capillary effect. In all regions with abundant, continued precipitation, as well as in swamps, the available air content is occasionally reduced to a minimum and then becomes decisive. Since, as we have seen, the lack of O_2 in poorly ventilated soils is less detrimental than the accumulation of CO_2, the determination of air capacity, which runs more or less parallel to the CO_2 measurement, is sufficient in most cases.

Burger (1922, p. 54), who examined air capacity from the forester's point of view, always found that the greater air capacity indicates a higher value in forestry. Siegrist (1930) also found that *Picea excelsa* thrived on a soil with an air capacity of 10 per cent producing needles 10 to 12 mm. long, while on a neighboring area with soil with an air capacity of 2 per cent it grew feebly with yellowish needles only 4 to 6 mm. long. When in spring with alternating rain and snow the soil almost reaches its saturation point, root respiration in soils of low air capacity is stopped or at least restricted. This is especially true of deep-rooting trees. As with pore volume, so air capacity decreases with depth, first rapidly, then more gradually. Burger found the highest air capacity (25.2 per cent) in the uppermost layer (0.10 cm.) of a mixed fir and spruce forest with scattered beeches. Dry meadow communities mostly show a low air capacity in the uppermost layer. The proportions of solid particles, soil water, and air at various depths in the soil of a mixed deciduous forest near Zofingen (beech-oak forest) and of a dry meadow (probably Mesobrometum) are clearly shown in Fig. 116.

Aichinger and Siegrist (1930) studied the air capacity of the soil in relation to the successions on the gravels of the Drava in Carinthia. They showed that the appearance of the assembly of plants of the mixed forest floor, including such species as *Convallaria majalis*, *Maianthemum bifolium, Paris quadrifolia*, and *Oxalis acetosella*, was accompanied by an increase of the air capacity of the soil from 8 to 23 per cent.

The studies of Braun-Blanquet and Pawlowski (1931) show that the air capacity of a given soil is a relatively constant factor. In soils where the annual variations of air content are very great (Deschampsietum mediae), the air capacity increases a little whenever the air content is at its annual maximum.

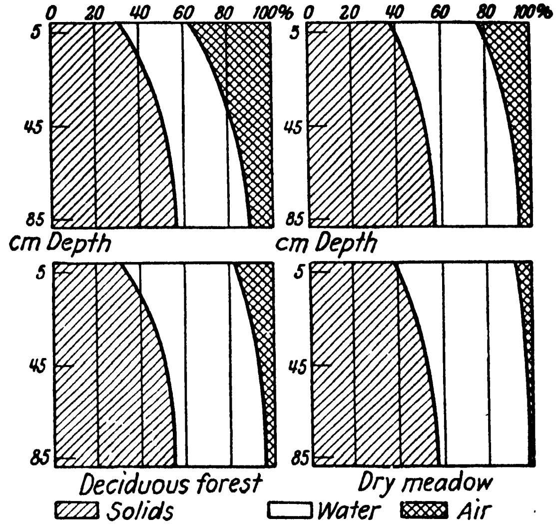

Fig. 116.—Solids, water, and air in the soils of Zofingen. The left-hand diagrams from 100-year-old deciduous upland forest, the right-hand from a permanent dry grassland. Upper diagrams from soil as taken in the field, the lower with maximum capillary water capacity. (*After Burger.*)

Moor vegetation requires only a low air capacity of the soil (see Kopecky, 1914). If, however, the air content falls below a certain minimum for a considerable length of time, numerous plants die. This phenomenon is most apparent in floods or in a long-continued high level of ground water.

Actual Air Content.—While the air capacity of the soil is rather constant, the actual air content at any given time may vary widely. After a rain, the air in the soil is always less than during a period of drought. A relatively impermeable soil shows an annual curve very different from that derived from a permeable soil. The seasonal variations of the air content of a soil often influence vegetation more than the air capacity itself. The first investigations of the seasonal fluctuations of associations were carried on by Braun-Blanquet and

Pawlowski. In the Deschampsia media association on marly soil near Montpellier an air content of 2 to 9 per cent by volume for three-fourths of the year rose to 35 to 40 per cent at the end of the summer after a dry period. The entire ecology of this association is dominated by this factor (Fig. 117).

Certain alluvial soils on the shores of the Mediterranean Sea, especially near the mouths of streams, are very densely packed, finely dispersed, and poor in air content. One may walk on these sparsely vegetated places without sinking into the soil very much, even after several days' rain. On investigation of the recently inundated soil (water 5 to 10 cm. deep), it is found to be almost dry at a depth of only 15 to 20 cm., crumbly, and entirely free from roots.

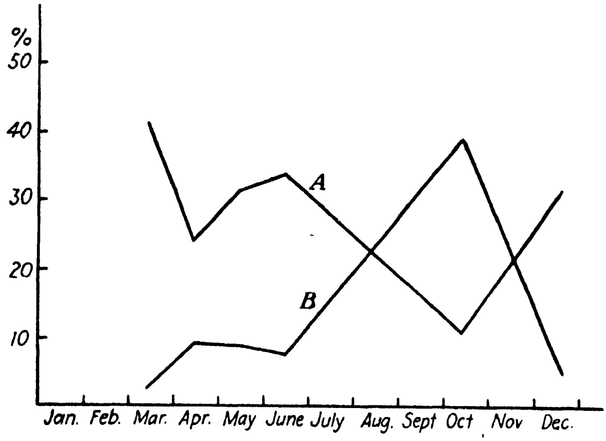

FIG. 117.—Seasonal range of water (*A*) and air (*B*) in the soil of a *Deschampsia media* association. (*After Braun-Blanquet and Pawlowski.*)

The Salicornietum macrostachyae (Fig. 118), a pronounced halophytic association, is characteristic of these soils. Besides the mostly dominant *Salicornia macrostachya* and the sparsely intermixed dwarfed specimens of *S. fruticosa* and *Atriplex portulacoides* (all nanophanerophytes) there are also a number of short-lived therophytes such as *Sphenopus gouani*, *Frankenia pulverulenta*, *Sagina maritima*, and *Hutchinsia procumbens*, which shoot forth after the spring rains and whose roots penetrate scarcely to a depth of a centimeter. Even the shrubs have very superficial roots. The luxuriant shrubs of *S. macrostachya*, often more than a meter wide, resembling giant turtles, can easily be lifted from the ground with their whole root system. It is surprising to find that the highly developed root mat extending in all directions and filling the upper layer of the soil in a dense network consists of strong main and tributary axes but only short, vertical feeding roots, rarely exceeding 15 cm. in length.

Determination of Air Capacity.—The pore volume of a soil does not give a reliable measure of its aeration. Burger (1922, p. 185) has shown that even a soil with a pore volume of 70 per cent may be poorly aerated in the saturated condition. It is for this reason that the determination of air capacity is recommended, not only because of its great practical significance (*e.g.*, as an important criterion for the estimation of the quality of a forest soil) but also because an approximate method, proposed by Wiegner, furnishes useful results without much trouble.

FIG. 118.—An association of *Salicornia macrostachya* on a saline soil of polygonal structure; aestival aspect. Etang de Vic, France. (*Photo by Braun-Blanquet and Keller.*)

Soil samples collected in undisturbed condition in steel cylinders of 1,000 cc. volume, which are closed at one end with a tightly fitting steel cover, are put into a basin of water and left there until completely saturated with water. After 24 hr. the cylinders are closed under water by putting on the second steel cover. The cylinders are taken out of the bath, wiped dry, and weighed. In order to separate the gravitational water from the capillary water both covers are removed and the cylinder containing the soil is placed on a fine sieve. The gravitational water will drip off within 2 hr. After putting on the covers, the weight is taken and the difference gives the air capacity. Drying at 110°C., and reweighing, permits the calculation of the water capacity.

A modification of this method has been introduced by Siegrist, who intensifies the air replacement by water by applying suction from a vacuum pump. He makes use of cylinders of 250 cc. capacity, as they are more easily manipulated. The cylinders containing the undisturbed soil are put under water in a vessel connected with a vacuum pump. By suction the air contained in the pores of the soil is driven out. The cylinders are closed as in the previous method, weighed, and the separation of capillary from gravitational water is carried out as directed above. Weighing, and drying at 110°C., permits the calculation of both air and water capacity.

Permeability.—The permeability of the soil is a very important factor in countries which like the Mediterranean region are subject to torrential rains. The denuded clay soil is often not able to retain the water which floods the lower areas of the river basins. These areas of impermeable soils should be kept with their plant cover intact or should be reforested, as a biological defense against erosion.

CHAPTER VIII

SOIL ORGANISMS

The number of lower plants and animals which are temporarily or permanently housed in the soil and draw nourishment from it is quite astonishing. Nine-tenths of all insects spend some time in the soil. Their harmful activities through devouring of roots (grubs), damage to seedlings, unfavorable physicochemical influences on the soil, etc., are exceeded by their profoundly beneficial activities.

Darwin was the first to call attention to the importance of earthworms in working over the soil. By their burrows, which penetrate to a maximum depth of 7 m., they open up the lower layers of the soil. They grind up large amounts of earth with their principal food, which is decomposing plant materials. The excreta of worms are deposited occasionally within their burrows but usually on the surface of the ground in little spiral heaps. This material, as D'Auchald has ascertained, is richer in nitric acid and calcium carbonate than the original earth. For this reason the soil reaction of the worm excreta shows a somewhat lower H ion concentration. Salisbury, too, found a higher carbonate content in worm excreta, and thus, as compared to the acid soil, a lower H ion concentration.

Earthworms in this manner not only further the loosening and crumbing of the soil, but they render the nutritive substances of the soil more easily available for plants and thereby increase the store of nutrients. They are most abundant in nearly neutral soil and are rarely found in soils with an acidity higher than pH 6. However, Wherry (1924, p. 309) has shown the presence of *Helodrilus lönnbergi* in peat soils of 4.7 pH.

Soil Fauna.—Compared with the activity of earthworms, the importance of insect larvae, ants, centipedes, mites, etc., in the soil is probably very small, but very little is definitely known on this subject. "Springtails" (Collembola), according to Handschin (1925), are permanent inhabitants of the surface soil, but they withdraw, under certain circumstances, to greater depths, in pursuit of more favorable life conditions. In cemeteries great aggregations of springtails are found upon corpses, at depths of 120 to 180 cm.

Shelford (1913) and Buckle (1923) have written about the ecology of soil insects. The original assumption that special communities of soil insects correspond to certain plant communities has been shown to be greatly overdrawn. The great majority of the species inhabit soils of the most diverse compositions.

According to the food habits of soil animals, Buckle (1923) distinguishes earth eaters, meat eaters (carnivores), and plant eaters (herbivores). The meadow and grazing soils of central England which he examined contained at least 50 per cent of herbivores, while carnivores were in the majority in tilled soils. This fact is probably related to the circumstance that, unlike meadow and grazing lands, the tilled vegetation does not cover the soil throughout the year.

In the mangrove swamps of the tropics small crabs grind up the organic remains.

An abundant microfauna, composed of infusoria, rhizopods, rotifers, and nematodes, inhabits the soil and especially the root layers down to a depth of 15 cm., and participates in the processes of soil formation, even at the extreme outposts of life.[1] The biology of the microorganisms of the soil has been well discussed by Waksman (1931). Heinis (1920) has investigated the development of the microfauna in the highest plant cushions of the Alps. He found at 3,500 m. and higher numerous rhizopods, rotifers, and nematodes inside the *Androsace* and *Saxifraga* cushions. He considers them of extreme importance in the formation of humus.

Examination of soil samples from Spitzbergen have shown that in the humus as well as in the mineral soils of the far north a rich protozoan fauna occurs, which is strikingly similar to that of the temperate zone. A high development of the protozoan fauna corresponds, as a rule, to an impoverished bacterial flora. The development of bacteria and their activity are affected unfavorably by the presence of large numbers of Protozoa.

Soil Flora.—The microflora of the soil plays a much more significant rôle than the animals in soil economy. This flora is composed of countless bacteria, fungi, and algae, which live preferably in the root layer of the soil and are exceedingly active there. Their significance is indicated by their function of nitrogen fixation, as well as by the fact

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[1] Useful papers may be cited: Cutler, D. W., and L. M. Crump, Daily periodicity in the numbers of active soil-flagellates, *Ann. Appl. Biol.* **7**: 11–24, 1920; France, R. H., "Das Edaphon," Stuttgart, 1921; Russell, E. J., Soil Protozoa and soil bacteria, *Proc. Roy. Soc.* Lond. **89**, 1915; Sandon, H., Protozoa from the soil and mosses of Spitzbergen, *Jour. Linnean Soc.* **34**, 1923; Shelford, V. E., "Laboratory and Field Ecology," 125–127, 1929.

that they make more available many substances already in the soil but difficult of assimilation by higher plants.

1. NITROGEN FIXATION

For the synthesis of proteins the plant requires nitrogenous compounds. To a small extent these are supplied in inorganic form from the atmosphere. During thunderstorms considerable quantities of oxygen combine with the nitrogen of the air. Thus by the aid of atmospheric moisture nitrous and nitric acids are formed, which reach the soil in rain. Nitrogen in the form of nitric acid, HNO_3, is easily assimilated by plants, while free nitrogen is absolutely useless to most plants. In addition to this inorganic source of nitrogen, vegetation has another, not less important, organic one in the subterranean associations of nitrogen-fixing bacteria, fungi, and algae.

The discovery of the anaerobic schizomycete, *Clostridium pastorianum*, by Winogradsky, has furnished us the key to the scientific explanation of the long-recognized fixation of atmospheric nitrogen by plants. With adequate aeration this schizomycete fixes 0.0025 to 0.003 g. of atmospheric nitrogen for each gram of glucose consumed. A great increase in the nitrogen content of the soil is followed by the cessation or retardation of the nitrogen-fixing activity of this bacterium.

The investigations by Truffaut and Bezssonoff (1925) make it seem probable that *Clostridium pastorianum*, which fixes atmospheric nitrogen abundantly in soil free from nitrogen and carbon, is able to draw its food from the root secretions of the higher plants (these experiments refer to *Zea mais*).

Two species of *Clostridium* (*C. americanum* and *C. aerobicum*) have been isolated by Pringsheim as nitrogen fixers. *C. aerobicum*, as the name indicates, functions in the presence of air. Equally aerobic are some of the later-discovered bacteria, especially of the genus *Azotobacter* (*A. choococcum*, *A. beijerinckii*, *A. vinelandii*, *A. agilis*, and *A. vitreum*). *A. choococcum*, a notable nitrogen collector, is distributed in most soils. Out of 562 soil samples from Bavaria it was found in 341 (61 per cent). It was absent in soils of high H ion concentration (below pH 5.6) (Niklas, 1925). It thrives best in lime soils at an optimum temperature of about 28°C., while sodium chloride and sulphates are destructive. The former acts toxically even in doses of 0.5 per cent; it can endure sodium sulphate up to 1.25 per cent (André, 1921).

Anaerobic and aerobic nitrogen fixers often occur associated together in the same soil, and with them certain fungi (*Aspergillus*, *Phoma, Gymnoascus, Alternaria,* etc.) and algae. All of these seem able to fix free nitrogen. Some such fungi and bacteria seem to stand in a symbiotic relation to each other.

The tubercle bacteria (*Bacterium radicicola, B. beijerinckii*) probably fix nitrogen only in symbiosis with higher plants (mostly Leguminosae but also *Podocarpus, Alnus, Elaeagnus,* and *Hippophaë*). The rôle they play in agriculture has been well known since the days of the classical investigations of Hellriegel and Wilfahrt. But we know nothing about their significance in the development of natural vegetation. It is probable that the tubercle bacteria make possible, or at least greatly favor, the usually luxuriant growth of numerous Leguminosae (*Lupinus, Lotus, Astragalus, Ornithopus,* etc.) upon the sandy soils of southern Europe and northern Africa.

The gain in nitrogen content of untilled, natural soils must be very considerable. Two fields in central England, which had been given no nitrogen fertilization for 22 and 24 years, showed, according to Russell (1927), a total increase in nitrogen content of 2,162 and 1,567 kg. per hectare. These gains of nitrogen were proportionate to the abundance of Leguminosae.

Microorganisms not only contribute to the increase of the food resources of the soil but also release inorganic food materials. Thus, by their mediation, the cycle which transforms dead organic waste into assimilable plant food is completed. A whole series of ecologically important microorganisms and groups of organisms (mostly bacteria) may be recognized. Physiologically, some have very definite, highly specialized activities; others are indifferent, adaptable to many different conditions of life. But their direct or indirect relation to plant sociology has received little investigation.

Ammonium Formation (Ammonification).—Nitrates are the most effective nitrogen compounds for the nourishment of plants. For all higher plants not living in symbiosis with the tubercle bacteria, nitric acid forms, if not the only,[1] at least by far the most important nitrogenous food substance. The nitrogen compounds present in the soil must generally be converted into nitric acid, HNO_3, or its salts in order to fulfill their physiological function. But this transformation can take place only with the cooperation of nitrifying bacteria. It proceeds step by step. The undecomposed organic matter first goes

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[1] *Cf.* Schreiner, A., The organic constituents of soil, *Science* **36**, 1912. According to the investigations by Ziegenspeck (1922), mycotrophic plants do not assimilate nitrogen in the form of nitrates but in that of ammonium compounds (or amino acids). Upon strongly acid soils where no nitric acid is formed, these plants, therefore, have the advantage over autotrophic plants.

through an ammonifying process wherein both bacteria and fungi participate (*Mucor, Aspergillus, Fusarium,* etc.). According to Marchal (1893), *Bacterium mycoides* plays a major rôle in ammonification, especially in cultivated soils. It is an intensively oxidizing organism, which, given a sufficient air supply, unites oxygen with the complex organic compounds and releases their nitrogen in the form of ammonia, NH_3. Numerous other representatives of the soil flora react similarly. The end product of this first transformation in the soil is ammonium carbonate, $(NH_4)_2CO_3$. Ammonium carbonate is also derived from the decomposition of urine and excreta under the influence of urine-fermenting bacteria (*B. coli, B. vulgare, B. fluorescens,* and species of *Micrococcus, Urococcus,* etc.). $(NH_4)_2CO_3$ is the initial substance in the formation of nitrates in the soil, that is, in nitrification.

Nitrate Formation (Nitrification).—Two specific groups of bacteria are involved in the process of oxidation which converts the amino radical into the nitrate radical. These two groups work hand in hand but cannot replace one another. First, the nitrite formers or nitrobacteria (*Nitrosomonas, Nitrosococcus*) begin the process, taking up the ammonia compounds and converting them by partial oxidation into nitrous acid or nitrite, HNO_2. The process is favored by the presence of alkaline substances, Ca, Mg, etc.

Then the nitrate bacteria (*Nitrobacter*) come into action. The process of oxidation goes on by their activity as far as nitrate, HNO_3. This is utilized readily by higher plants. *Nitrobacter,* which is morphologically different from *Nitrosomonas* and *Nitrosococcus,* cannot enter into the cycle earlier, since the ammonia compounds hinder its development. Ammonifying, nitrite, and nitrate bacteria are all three necessary for the completion of the cycle. Each group, but especially the nitrite and nitrate formers, has its distinctly limited sphere of action.

Nitrification is favored by light and by an increase of soil moisture, up to approximately the capillary saturation of the soil. Coarsely dispersed soils demand a smaller water content for favorable conditions of nitrate formation than in the case of finely dispersed soils; good aeration of the soil favors this process. In very acid soils nitrification is much decreased. Nevertheless, C. Olsen (1921) has shown that nitric acid formation does occur even in peat soil at pH 3.6.

Nitrification starts at a temperature of 5°, reaches its optimum at about 37°, and ceases at 57°C.

Nitrification Capacity.—The rate at which nitrification goes on seems to be independent of the quantity of organic nitrogen in the soil. But the nature of the humus nitrogen present probably affects the speed of ammonification very decidedly. In forests nitrification is most active in the horizon of decomposition, in this respect agreeing with the activity of mycorhizal fungi. It decreases with depth. Rather inert nitrogen compounds slow up nitrification (André, 1921, p. 179). Olsen (1925) has determined that soils of flat-moor communities with *Carices*, *Molinia*, and *Deschampsia caespitosa*, which did not show a trace of nitric acid at the first examination, showed 22 to 25 mg. per liter of soil after 25 days. From this it follows that the amount of nitrate present at any given time gives no indication of the nitrate supply of a plant community. Not only is nitric acid quickly assimilated by plants, but it is also leached out by rain and is often barely traceable. Thus the nitrate content of a soil is subject to considerable fluctuations from time to time.

These conclusions are of ecological importance because they lead us to consider not the nitric acid present, nor the quantity of total nitrogen, as a measure of the nitrate available to plants, but rather the capacity of the soil for nitrification. This is represented by the amount of nitrates formed during a certain period of time.

Investigations by C. Olsen and others show the dependence of many species upon the inherent capacity of the soil for nitrification. Thus a rich growth of *Urtica dioica* always coincides with an intensive capacity for nitrification in the soil, and it would seem that the rich growth depends directly upon nitrification. But the nitrifying *Urtica* soils contain also comparatively large quantities of phosphoric acid, PO_4, which possibly have a part in the luxuriant development.

Methods for the determination of nitrifying power are too complicated for general use. For further information on the whole question reference may be made to the investigations of C. Olsen (1927) and Nemec and Kvapil (1927).

✓**Nitrate Test with Diphenylamine.**—A simplified method which will permit the ecologist to estimate the nitrate factor in his researches has been introduced by Molisch and later used by Hesselman, Raunkiaer, and others in ecological studies. It is known as the diphenylamine method.

Hesselman (1917) and Raunkiaer (1926) started out with the assumption that the nitrate content of the plants themselves would give some information about the nitrifying power of a soil. No nitrate can be produced in the plant tissues, therefore the nitric acid present in the plant sap must have come from the soil. Negative results carry less weight than positive ones. Not all plants store nitrates. In some species young plants, capable of further development may under certain circumstances, contain large quantities of nitrates, while older specimens have none at all. The nitrate test is exceedingly simple. As Raunkiaer (1926, p. 9) showed, it is best to use plant sap which is pressed out of the plants.

To a fraction of a drop of plant sap in a watch glass a drop of sulphuric acid and a crystal of diphenylamine are added. A deep blue coloration takes place in the case of a high nitrate content. According to the intensity of the blue coloration, several degrees of nitrate content may be distinguished. This method is not applicable to woody plants, for in the presence of lignin the reaction does not occur.

Nitrophilous Plant Communities.—Although at present very few reliable investigations on nitrification in natural plant communities are on record, these are sufficient to indicate the range of influence of this factor. Intensive nitrification occurs in most meadow soils and in many forest soils with an herb layer. Individual communities such as *Alnus* woods with numerous herbs, and deciduous forests in Sweden, also the communities around springs are characterized by a high nitrate content. Snow-land communities composed of *Catabrosa algida, Poa alpina, Cerastium cerastioides, Saxifraga stellaris,* and other species were found rich in nitrates by Hesselman (1917, p. 40). Generally, flowing oxygenated water seems especially favorable to nitrification (see p. 172). Species of the halophilous shore vegetation, such as *Atriplex* and *Honkenya peploides,* also give a strong nitrate reaction. On the contrary, all plant communities which form raw humus are poor in nitrates. This has some connection with the lack of bases. Even though nitrate bacteria can endure strongly acid reactions, their activity is, nevertheless, greatly decreased in acid media. Soils of forests and heaths rich in *Calluna, Vaccinium,* and *Empetrum* all have a low nitrifying power. This seems to hold true also for high moors, while water-logged *Carex* flat moors and probably all communities of the Molinion nitrify abundantly.

In forest the best nitrification is shown after cutting when nitrification and decomposition of litter are favored by light. *Rubus, Galeopsis, Fragaria, Epilobium angustifolium,* and *Mercurialis perennis* form a group of nitrate indicators. According to Nemec and Kvapil (1927), mixed conifer and deciduous forests are more favorable for nitrification than pure stands of either sort. In the beech forest with *Rumex acetosella* nitrification is less than in that characterized by the presence of *Asperula, Mercurialis,* and *Paris.*

In the mild humus of deciduous forests the formation of nitrates proceeds normally. *Anemone nemorosa,* according to Raunkiaer, has its highest nitrate capacity in the beech woods. It is surpassed there, as in oak and alder woods, by *M. perennis.* Plants store more nitrates in the shade than in the sunlight.

In the mountains of central Europe the tall-herb association of the Adenostylion, which inhabits well-aerated, moist, weakly acid to basic soils, seems to be determined by the high nitrate content of the soil (Fig. 70). Nitrophilous communities are very widely distributed in dry, subtropical regions (Fig. 119). The most nitrophilous community of the Mediterranean region is the *Silybum-Urtica pilulifera* association of which all the species show a high nitrogen content when young.

FIG. 119.—Nitrophilous association with *Magydaris tomentosa* near Meknes, Morocco. (*Photo by Maire.*)

Notable among nitrophilous communities are the lichen associations (examined by Sernander (1912), Frey (1922), Gams (1924), Motyka (1924), etc.) of bird roosts and marmot rests, of stones and rocks wet with goat and sheep urine, and of similar, overmanured places.

If the supply of excreta is too great, only a few species can thrive, and even these are frequently dwarfed. According to their degree of nitrophily, the rock-lichen communities are often arranged in distinct beltlike order. Upon the bird roosts and marmot rests of the Alps and the Tatra the surfaces of the overmanured rocks are occupied by the extremely nitrophilous Ramalinetum strepsilis, with *Rinodina demissa*, *Xanthoria fallax*, and *Physcia tribacia* as characteristic species. On somewhat sloping surfaces, to which the nitrogen compounds are washed by rain water, grows the Alectorietum chalybeiformis, with *Gyrophora cirrhosa*, *Lecanora frustulosa*, and *L. melanophtalma*. The vertical surfaces are taken by the *G. cylindrica-Cetraria noermoerica* association (Fig. 120). Similar belt grouping, somewhat less pronounced, has been found upon the rabbit rests on basalt blocks in southern France.

The nitrophilous bark communities of lichens, mosses, and algae have been carefully examined by Ochsner and Frey (1925, 1928).

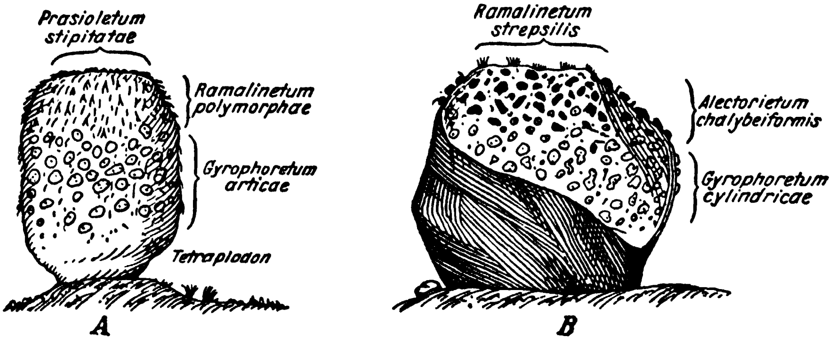

FIG. 120.—Belting of the lichen associations according to decreasing nitrate content of the habitat. *A*, Resting place of birds of prey in the high mountains of Central Scandinavia. (*After Gams.*) *B*, in High Tatra. (*After Motyka.*)

Ochsner distinguishes two markedly nitrophilous bark associations: the light-loving Physcietum and the Parmelietum acetabulae, comprising several sub-associations, which prefers older trees with furrowed bark.

Denitrification.—Over against the nitrate formers stand the denitrifying bacteria which destroy nitric acid (*Bacterium denitrificans*, *B. stutzeri*, etc.). Along with nitrogen-oxidizing processes we always find also nitrogen-reducing activities: nitrates are resolved into nitrites and these in turn reduced to free nitrogen by the destroyers of nitric acid. In case of direct denitrification, the free nitrogen escapes from the soil in gaseous form.

The living conditions for nitrifying and denitrifying bacteria must be somewhat similar, for the denitrifiers occur only where nitric acid is being formed. The soil conditions favoring one or other of these groups of bacteria determine whether construction or destruction of nitrates shall predominate. Very acid soils without herbaceous cover, in conifer forests, have a decided tendency toward denitrification.

2. ORGANISMS OF WEATHERING AND SOIL FORMATION

Microorganisms are directly concerned in the formation of soils by the disintegrating action which they exert upon inorganic mineral substances and by the separation of mineral particles. Their indirect action lies in the formation of humus.

Biogenic Weathering of Rocks.—The physical and chemical weathering of rocks is furthered not only by the higher plants but also by algae, lichens, and bacteria. The bacteria which cause weathering of silicates are probably the most important of all biological weathering factors. Bachmann (1915, 1916) has investigated algae and fungi which dissolve lime. He proved that algal filaments of *Trentepohlia* actually penetrate calcite crystals.

As early as 1890 Muntz called attention to the corrosion of rocks by nitrobacteria. In the bituminous schists whole rock layers are found permeated with and crumbled by nitrobacteria. From the decomposition of these calcareous slates an exceedingly fertile loam results which in high mountains is usually occupied by *Saxifraga biflora, Campanula cenisia, Leontodon montanus,* and in lower altitudes by such Leguminosae as *Hedysarum, Oxytropis montana,* and *Onobrychis,* long before any sign of humus formation is visible.

Kürsteiner (1923) found considerable quantities of *Bacterium mesentericus* and other schizomycetes in primary erosion layers free of humus and in fine rock crevices of high alpine summits even at heights of 4,000 to 4,200 m. These minute organisms probably hasten chemical erosion by production of carbonic acid, H_2CO_3. Carbonates dissolve in the presence of carbonic acid, especially the widely distributed carbonates of calcium, magnesium and iron. Silicates of the alkalies and alkaline earths are decomposed by carbonic acid (Ramann, 1911, p. 28). Very succinct data on the importance of microorganisms in weathering and soil formation are found in the work of Wollny (1898).

Humification.—Physicochemical weathering of rock furnishes the raw material for soil formation. Higher plants derive their elementary food materials from the residual soil and after death return them to the earth in complex compounds.

The dead plant material forms the starting point in the chemical transformations which are summed up in the term "humification"—the transformation of organic substances into humus. In this process the active forces are the communities of soil organisms, especially ically. These materials may be characterized by their common origin and by their similar state of dispersion.

All humus materials are colloid complexes; all of them have certain properties which are based upon their colloidal nature (see p. 161). Therefore from an ecological point of view one is justified in treating them collectively.

Humus substances absorb water with consequent swelling; they hold the water tenaciously. The absorbed water is removed only partially by evaporation. This notable ability to retain water and the loss of this ability with decrease of humus content in the soil are shown in Fig. 125.

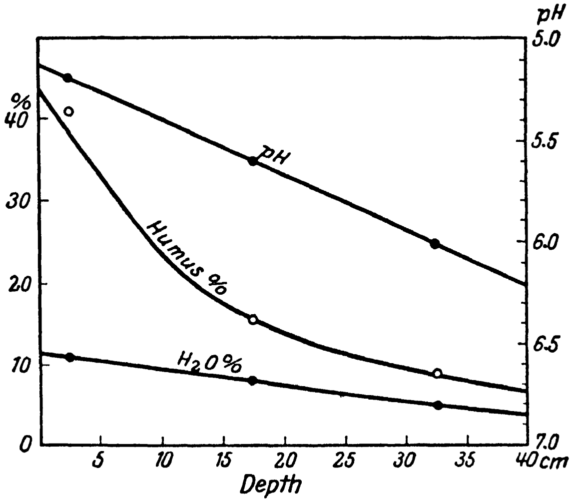

FIG. 125.—Parallelism between decreasing pH, humus content, and hygroscopic water (air dry) with soil depth in the climax Curvuletum at Schlern. (*After Braun-Blanquet and Jenny*, 1926.)

The chemical transformations in humus obey the laws of surface reactions and are considerably dependent upon the concentration of the solutions. Humus substances precipitate electrically charged colloids, such as ferric hydroxide, in a characteristic manner (Van Bemmelen, cited in Ramann, 1911). Humus samples, treated with hydrochloric acid and alkali, show a characteristic dark-brown coloration, due to certain compounds (humic acid, hymatomelanic acid, and sulphonic acids).

Adsorptively Saturated and Unsaturated Humus.—With respect to vegetation, humus substances are to be segregated into two qualitatively different groups: the neutral, mild, saturated; and the adsorptively unsaturated humus.

Adsorptively saturated humus is formed when aeration is good and in the presence of electrolytes, especially calcium ions, which neutralize the acid humus substances. The more lime in the soil the more humus is neutralized. The mild, saturated humus is relatively coarsely dispersed, crumbly, easily penetrated by plant roots, of dark brown to black color. It absorbs large amounts of water, without changing into a gelatinous form. Its favorable soil condition furthers the growth of minute living organisms and thereby the production of carbonic acid with its chain of consequences. This in turn leads, according to Wiegner (1926, p. 31), to a decrease in dispersity. Coagulated, saturated humus shows more or less neutral or weakly basic reaction. Its buffering capacity varies greatly; it may be low (mull forms of the Scandinavian forest soils) or very high (Caricetum firmae of the Alps). Adsorptively saturated humus soils support economically good, highly productive meadow and forest communities, such as the Caricetum ferruginei of the Alps with its many luxuriant herbs, the Seslerieto-Semperviretum, and notably the tall-herb communities of the Adenostylion.

Viewed simply as a soil type, as well as in respect to its effect upon vegetation, the adsorptively unsaturated acid humus is very different.

Unsaturated humus, as found characteristically in high moors and in the low-shrub heath, is poor in electrolytes, always gives an acid reaction, appears almost maximally dispersed, and, according to Wiegner, maintains the mineral dispersoids in a state of high dispersion. The interior surface is very great, involving a large water fixation; hence very acid humus soils are physiologically dry. An outstanding property of the highly dispersed sour humus is its marked ability to prevent the coagulation of ferric hydroxide, aluminum hydroxide, and silicic acid, in the presence of electrolytes (see p. 163). All communities with considerable quantities of *Nardus*, *Deschampsia flexuosa*, or *Vaccinium myrtillus*, such as the Caricion curvulae of the Alps, the Rhodoreto-Vaccinion, etc., are strictly confined to unsaturated humus soils.

For climatic reasons the adsorptively unsaturated, acid soils are limited to regions with low or moderate temperatures and moderate to abundant precipitation where decomposition of humus proceeds slowly (see p. 246).

Varieties of Adsorptively Unsaturated Humus.—Acid humus occurs in numerous forms, as yet not sharply defined. These forms are due to external conditions, especially to the plant communities, which initiated their formation. Only the more important of these forms are mentioned here.

Moor Peat.—Peat mosses (*Sphagnum* spp.) are especially responsible for the formation of this type of soil. Sphagnum peat, loose, of gray-brown, yellowish, or dark-brown color, contains 96 to 99 per cent of organic matter. Vaginatum peat, formed by *Eriophorum vaginatum*, is compact, of fibrous structure, and shiny brown. According to Zaidler, it contains about 98 per cent of organic matter.

The different kinds of peat have been described and investigated in detail by Waren (1924). He distinguishes three main groups: (*a*) vascular peat, (*b*) moss peat, and (*c*) lichen peat.

The vascular peat includes the following varieties: (1) reed peat, (2) *Equisetum* peat, (3) sedge peat formed mostly from species of *Carex*, (4) *Scheuchzeria* peat, (5) cotton-grass peat from *Eriophorum vaginatum*, (6) twig peat, and (7) wood or forest peat.

The lichen peat is poorly developed. Waren has also investigated the relations existing between the chemical composition of peat and the vegetation of the bogs and has found that here calcium is of great importance.

Raw Humus.—The widely distributed raw humus, shunned by foresters and alpine farmers, is a humus layer permeated with fungus hyphae and mycelia and thickly traversed by a network of roots of seed plants, especially of dwarf shrubs. It is sharply marked off from the underlying mineral loam and is in process of decay. Organic components predominate with mineral matter sparsely intermingled. Raw humus always gives a strongly acid reaction. The upper, slightly decomposed raw humus layer, which still permits at least a partial recognition of the individual plant fragments, is also called dry peat (leaf mold). Large quantities of dry peat are formed only when the forces of decomposition fail to keep up with the supply of dead leaves. In central Europe, therefore, the formation of dry peat does not occur in grassy places, and in southern Europe there is no formation of dry peat. Varieties of this dry peat may be designated *Loiseleuria* peat, *Vaccinium* peat, or fir peat, according to the principal plant providing the litter. It must not be confused with undecomposed litter. The formation of raw humus is a result of humid or perhumid climatic conditions with low temperatures.

Alpine Humus.—Ramann, Leiningen, and others call alpine humus the mild, adsorptively saturated humus of alpine and especially of subalpine calcareous soils. But Braun-Blanquet and Jenny would limit this term to the acid humus, which is to be considered the climax soil of the alpine zone of the Alps, of the summits of the high Cévennes and probably of other mountains with similar climatic conditions. It differs from the alpine humus of Ramann by its high dispersion and high concentration of hydrogen ions. The organic remains are thoroughly decomposed and frequently well mixed with mineral loam. The organic matter ranges around 30 per cent.

Mull and Duff.—Romell and Heiberg (1931) have discussed the formation of humus in the northeastern United States and have proposed a classification of the resulting forms. They distinguish two main classes, which are designated "mull" and "duff" and are in turn subdivided.

Mull is defined as a more or less friable humus layer of crumby or granular structure, with diffuse lower boundary, slightly or not at all matted. Some types of mull are inhabited by earthworms and possess a rich herbaceous vegetation in which spring geophytes such as *Dicentra*, *Dentaria*, and *Hydrophyllum* are a characteristic element.

Duff, in contrast, is a strongly matted layer of unincorporated humus, distinctly delimited from the mineral soil. It is quite lacking in plants typical of the mull soils.

Humus Determination.—For some time quantitative determinations of humus have been carried out, humus being understood to consist of organic matter in the process of decomposition. Soil samples from different root layers should always be examined separately. The simplest process for determination of humus is that used for soils with no lime and little clay. About 3 to 10 g. of air-dried soil are heated to white heat in a platinum crucible for 30 to 60 min., and the amount of loss determined. At the same time a sample is dried for 3 hr. at 110°C. The resulting loss of water is calculated for the ignited soil and deducted from the loss due to ignition.

The customary process in the case of soils which contain lime and carbonates is somewhat more complicated. The organic matter is ignited in an ignition tube, and the carbonic acid evolved is measured and multiplied by the factor 0.471, derived by the assumption that 1 g. of humus represents 0.58 g. of C.[1]

Degree of Humification.—The degree of humification of a soil is determined colorimetrically according to Melin and Oden (1917).

The humus soils are first leached out with HCl, in order to decompose the calcium compounds, then with alkali, to dissolve the humus acids. The more or less dark-brown coloration of the solution is compared with commercial Acidum huminicum and given a humification number according to the relation of its color to that of the com-

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[1] V. Anderson (1927, p. 84) has given the following method: 5 g. of soil, dried at 100°C., is treated with 5 per cent HCl, till all carbonates are removed, then washed and dried. The amount lost by ignition is then determined and reckoned as humus; the residue gives approximately the clay fraction (admixture of clay).

mercial product. Melin and Oden were thus able to prove that the humification of the high-moor peat is considerably hastened by drainage. Humification increases rapidly from the upper levels downward, as the following table illustrates:

TABLE 29.—HUMIFICATION OF A *Sphagnum fuscum* HIGH MOOR IN ANGERMANLAND, SWEDEN, DRAINED ABOUT 20 YEARS PREVIOUSLY
(Melin and Oden)

Depth, centimeters	Dominant peat former	Humification number	Remarks
5	*S. fuscum*	11.6	Brown; *Sphagnum* leaves well preserved
15	*S. fuscum*	12.4	
20	*S. fuscum*	18.4	
30	*S. fuscum*	26.0	
40	*S. fuscum*	23.7	
50	*S. fuscum*	28.0	About 50 per cent of leaves decomposed
60	*S. fuscum*	52.1	Dark brown to black; decomposition well advanced

Humification shows a different sequence in the high moor and in the flat moor. The flat-moor type has a humification number of 34 to 50 even in the uppermost soil layers; the high-moor type, of only 6 to 17.

To determine the degree of humification of acid forest soils, Nemec (1928) made use of a method introduced by Robinson and Jones (1925): the hydrogen peroxide method. The undecayed organic materials are not decomposed by H_2O_2, but the humified portions are separated out and decomposed by appropriate treatment by hydrogen peroxide.

One gram of air-dry humus is mixed with 60 to 100 cc. of hydrogen peroxide solution (180 cc. when the proportion of humus exceeds 75 per cent) and boiled for 10 to 15 min. Then the combustible material is determined. To determine the degree of humification the quantity of material decomposed by the H_2O_2 is compared with that obtained by the incineration method, and the result expressed as a percentage. Forest soils with *Calluna* and *Cladonia* show 43 per cent humification, soils with *Vaccinium myrtillus* give 52 per cent, while the forests with *Oxalis acetosella* prove most favorable for humification reaching 74 per cent.

Pallmann (1931) has given a simple method for separating the dispersed humus from the non-dispersed and for estimating the quantity of dispersed humus. It seems necessary to make this distinction, for Pallmann shows that the pH varies directly with the dispersed humus content.

CHAPTER IX

SOIL TYPES

Ever since the mutual dependence of soil formation and plant communities was first recognized and it was learned that soils as well as plant communities are to be regarded as biological units, efforts have been made to relate the units of vegetation with pedologically determinable units, the "soil types."

While the farmer considers only the superficial layers under the term "soil," in soil science all of the living part of the earth's crust is understood thereby as far as biological processes are demonstrable at all. Below this is the mineral layer, the solid crust of the earth, an inorganic dead mass.

The soil profile tells the character of the soil. Only on the basis of the profile can a scientifically accurate, natural classification of soil types be made. Each soil type has certain morphological and physicochemical properties which render it suitable for definite plant communities. The soil types distinguished to date, it must be admitted, are described only in roughest outline, and their derivatives have been studied only in part. Like ecological research, pedology has become an independent science only in most recent times.

Mineral Weathering.—In mineral weathering water initiates the process by hydrolysis. Simultaneously, or perhaps slightly later, oxidation joins in the process of weathering. The importance of temperature in this process is shown by the work of Ramann. He shows that the intensity of hydrolysis at 50° is about eight times that occurring at 0°C. For this reason solid rock will show considerable differences in the first stages of weathering in different climatic regions (Gschwind, 1931). Chemical changes proceed very quickly and thoroughly in the weathering of rocks rich in carbonate, while as Niggli (1926, p. 337) has shown, the weathering products of the silicates retain the chemical nature of the parent rock for a longer time. Under these conditions only acid humus seems to bring about a noticeable change of the chemical nature of the soil. Of course, acid humus appears invariably in humid, temperate, and cold climates, wherever there is adequate plant growth.

Soil Climax.—Since the weathering processes of rocks as well as the decomposition of humus go on at different rates under different climatic conditions, and since the vegetation of each climatic region reacts differently upon soil formation, the resulting mature soil must also bear the stamp of climatic influences. All soils, in fact, have a tendency under certain climatic conditions to develop into a certain type, the soil climax. The soil types of the earth are, in the main, climatically conditioned. The geological substrata influence soil development only to a small degree as compared to the effects of climatic factors. The soils of a climatically uniform region thus present either stages in development of the climax or the ultimate, climatically conditioned climax soil itself. This soil climax may develop from the most varying rock material, provided that the duration of development is not too short.

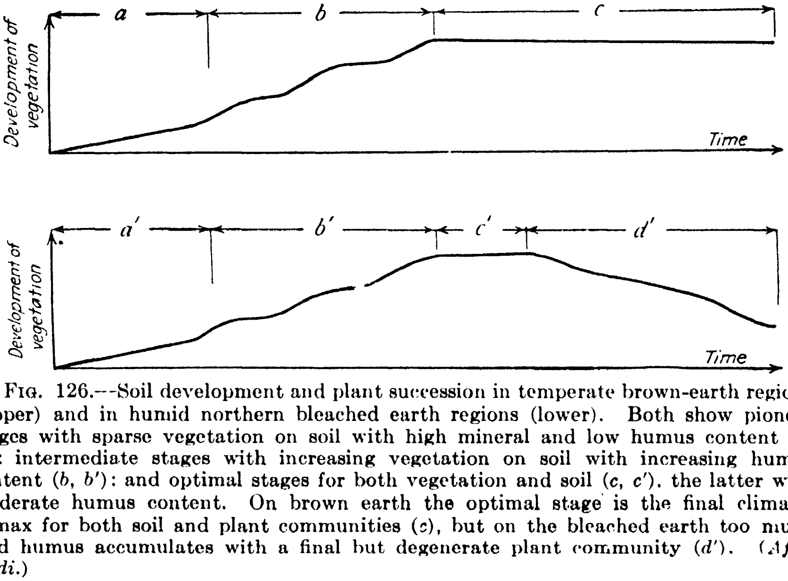

FIG. 126.—Soil development and plant succession in temperate brown-earth regions (upper) and in humid northern bleached earth regions (lower). Both show pioneer stages with sparse vegetation on soil with high mineral and low humus content (*a*, *a'*): intermediate stages with increasing vegetation on soil with increasing humus content (*b*, *b'*): and optimal stages for both vegetation and soil (*c*, *c'*), the latter with moderate humus content. On brown earth the optimal stage is the final climatic climax for both soil and plant communities (*c*), but on the bleached earth too much acid humus accumulates with a final but degenerate plant community (*d'*). (*After Lüdi.*)

Between the vegetational climax—the climatically conditioned climax plant community—and the soil climax there is an unmistakable analogy. Just as climatic regions and vegetational regions are distinguished, so must soil regions be recognized, and they correspond more or less closely to the vegetational regions of the earth (Fig. 126).

This viewpoint, which is slowly gaining ground, is destined to prepare the way for a classification of soil types primarily according to climatic control. Temperature, precipitation, distribution of rain, atmospheric moisture, and evaporation are the cardinal climatic factors in soil formation (see also Meyer, 1926).

These climatic factors affect:

1. The rate and kind of mineral weathering.
2. The rate and kind of decomposition of organic matter and the accumulation and distribution of humus in various layers.
3. The transfer of substances from one layer to another and the removal of substances from the soil.

Compared to the climatic factors, the nature of the organic substratum plays only a minor rôle in soil formation. The production of organic matter and the kind and intensity of its effects are, like the soil-forming processes themselves, subject to the climate.

Climatic Classification of Soils.—The climatic classification of soils had its origin in Russia, the land of boundless steppes, with uniform conditions of relief and vegetation.

Next to Dokutschajev and Sibirzev, Glinka has done most to advance the climatic classification of soils. Ramann, Stremme, and Lang have followed him in Germany; Treitz in Hungary; Wiegner and his collaborators in Switzerland; and Marbut (1928) and Shaw (1928) in America.

Glinka's division of soils upon a genetic basis forms the starting point of modern soil classification. According to him (1914), two genetically different primary soil forms are to be distinguished:

1. Ectodynamomorphic soil; in which soil formation is predominantly conditioned by the climate and the resulting vegetation.
2. Endodynamomorphic soils; in which soil formation is chiefly conditioned by the character of the underlying rock.

The ectodynamomorphic, climatically conditioned soils are, like the climax regions of vegetation, more or less geographically arranged. They are in an advanced stage of maturity and greatly predominate.

The endodynamomorphic soils are either limited to desert and mountain regions with sparse vegetation or they are to be considered merely as early stages of development of the ectodynamomorphic climax soils.

According to their moisture and humus content, which depends upon climate, these soils can be brought under three main groups.[1] The classification of the soil types of the earth thus broadly conceived is based therefore entirely upon the ectodynamomorphic soils:

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[1] Instead of three main types, Glinka (1914, 1927) distinguishes five: laterite, podsol, tschernosem, solonetz, and soils of swamps, which he divides into numerous subtypes.

1. Arid soils poor in humus:
   - a. Extremely arid desert soils.
   - b. Arid and semiarid saline soils (solonetz,[1] solontschak, white alkali, black alkali).
   - c. Semiarid steppe and loess soils (brown, gray, and reddish steppe soils).
2. Humid soils of warm regions poor in humus:
   - a. Soils with considerable moisture; tropics (laterite).
   - b. Soils with moderate to little moisture; subtropics (red soil; *terra rossa.* Probably also the little-known yellow soils).
3. Humid soils of temperate and cold regions, rich in humus:
   - a. Soils with moderate to little moisture (black soils (tschernosems), degraded black soils, chestnut soils).
   - b. Soils with medium moisture and leaching (brown and gray forest soils, brown soils proper).
   - c. Soils with medium to high moisture and severe leaching (pale earth, podsol; and podsol-like soils).
   - d. Soils with very high moisture (climatically conditioned peat and moor soils: tundra soils).
   - e. Soils with very high moisture and humus (alpine humus soils).

Besides these main soil types, probably a large number of subtypes of more local distribution are to be distinguished, whose definition must remain in the hands of the soil scientists.

In general, decreasing salt content of the top soil corresponds with increasing humus content in the above arrangement. In arid climates more water is evaporated than is received. Consequently, a rising stream of water exists, and soil salts accumulate in the upper horizons. The humus acids derived from decomposing plant matter are neutralized almost immediately in the Mediterranean climate, so that even upon silicate soil, on the surface, high pH values are found. Conversely, in humid climates the precipitation exceeds evaporation. The flow of water is downward; the top-soil layer is leached out more or less, and the soluble matter is carried away with the water or deposited in lower soil layers. Inasmuch as organic remains are decomposed only slowly at low temperature, the humus accumulates more and more, which leads to acidification of the soil and to low pH.

The relation between precipitation and evaporation and climatic soil formation has been investigated by Meyer (1926). On account of the paucity of evaporation data, he has considered the best expression of the relative moisture of a habitat to be the quotient of precipitation and saturation deficit, which has come to be known as the "N. S. quotient" (see p. 143).

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[1] The solonetz soil under special local conditions may appear extrazonally in adjoining climatic regions. This also applies to the other climatic soil types.

This N.S. quotient is:

1.	In deserts and desert steppes (arid soils poor in humus)	0 to 100
2.	In regions of the Mediterranean red soil	50 to 200
3.	In regions of chestnut and black soils	100 to 350
4.	In the brown-soil region	275 to 500
5.	In the podsol region	300 to 1,200
6.	In regions of moor and tundra soils	400 to 600
7.	In regions of alpine humus soils	1,000 to 4,000

Meyer constructed a N. S. quotient map of Europe (Fig. 127), and its outlines have been found to correspond fairly well to a map of the

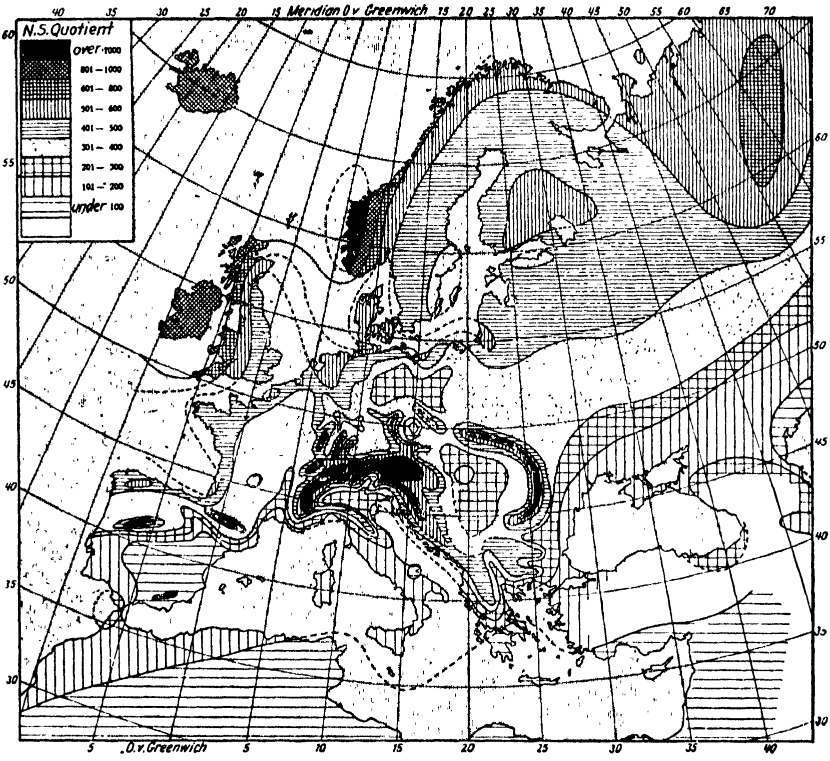

FIG. 127.—A humidity factor (N. S. quotient) map of Europe. (*After Meyer.*)

same continent showing the major soil types (Fig. 128). Using similar methods, Jenny (1930) has constructed a N. S. quotient map of the United States (Fig. 79) and also has mapped the major soil types of the same country (Fig. 129). These two sets of maps show the close correspondence between the climatic factors and the distribution of the climatic soil types.

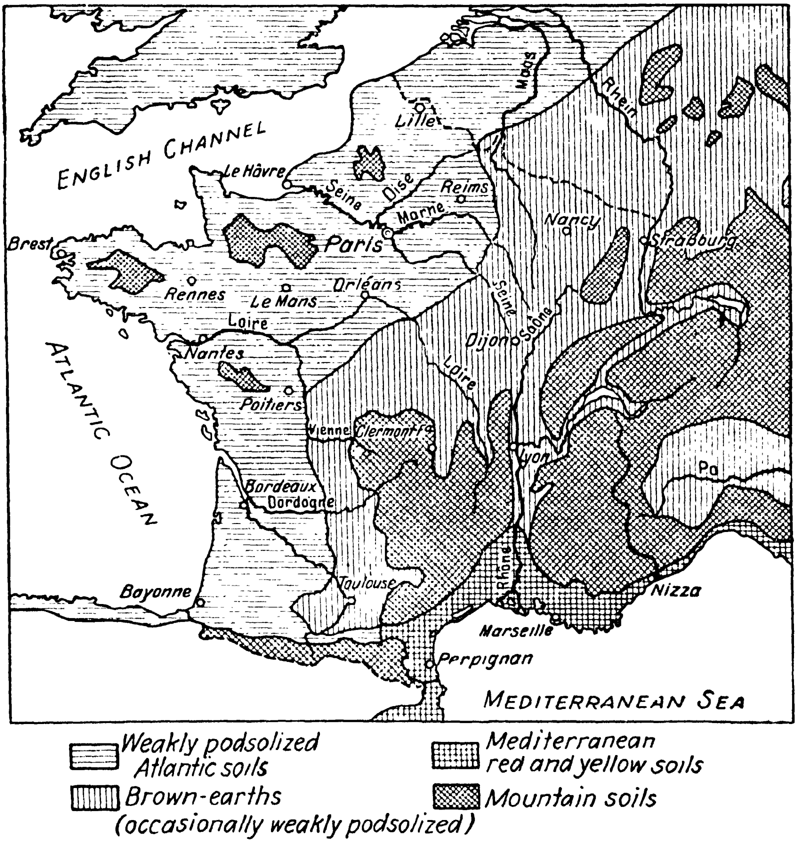

FIG. 128.—Map of soil types of a part of central and western Europe. (*Mostly after Agafonov.*)

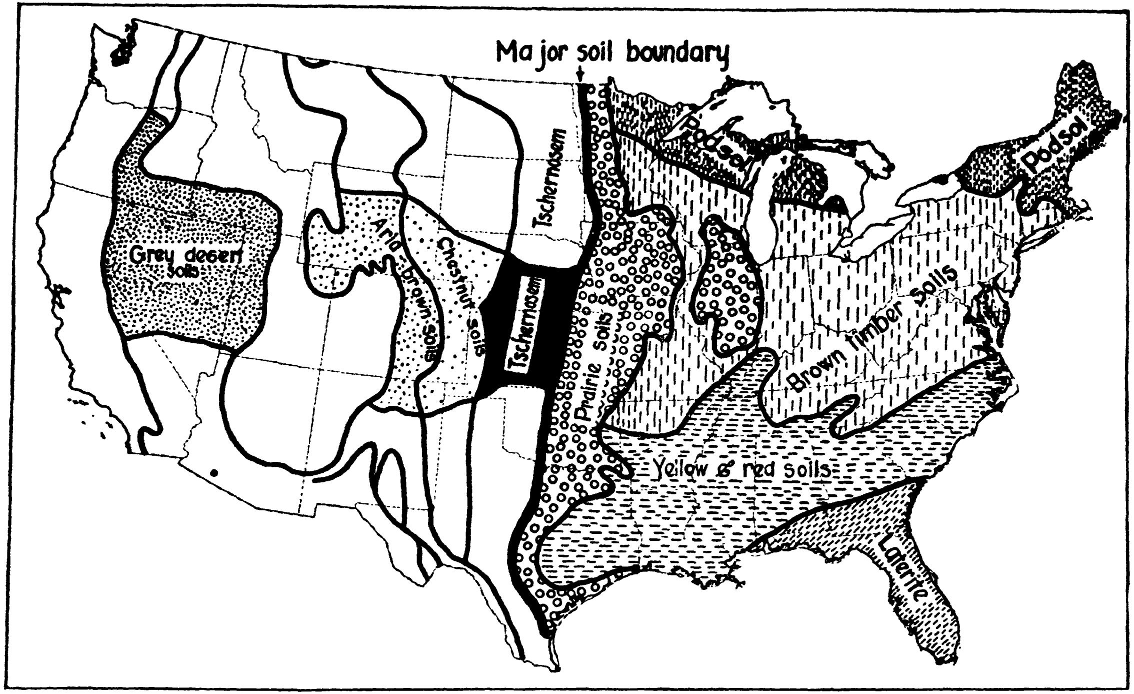

FIG. 129.—A map of the major soil types of the United States. (*After Jenny.*)

CHAPTER X

OROGRAPHIC FACTORS

Climatic and soil factors are variously affected by the contours of the land. Local or microclimate, in contrast to general climate, is largely controlled by orographic factors: mountains, plateaus, plains, exposure, and slope of the surface. Even the soil conditions and soil development are influenced by relief. The effectiveness of relief factors in the northern hemisphere seems to increase from south to north and from the foot of mountains to their summits.

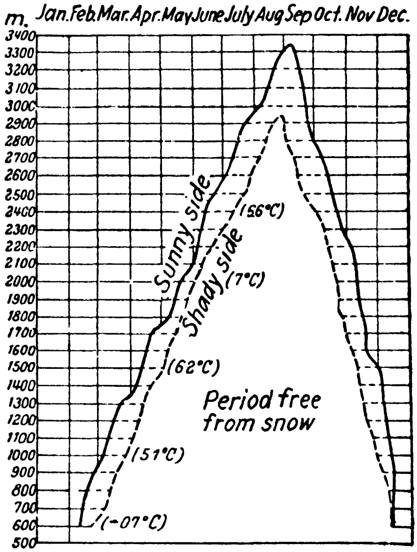

FIG. 130.—Duration of snow cover on the shady and sunny sides of Inn Valley. Mean of 16 years' record. Temperature of atmosphere at time of melting of snow. (*After Kerner.*)

Altitude.—In extra-tropical mountains, according to Hann, the mean temperature for the year decreases 0.55°C. per 100 m. elevation. This fall in temperature brings about a corresponding shortening of the vegetative season. Sixteen years of observation in the northern Alps showed that the average snowless vegetative period at an elevation of 1,000 m., on level ground, lasted 8 to 9 months; at 1,500 m., 7 to 8 months; at 1,800 m., 6 months; and at 2,400 m., about 3½ months. Figure 130 shows the progress of disappearance and appearance of snow at various altitudes on the shaded and exposed sides of the Tirolese Inn Valley. The shortening of the vegetative period often causes an acceleration of the life processes, especially of the flowering and fruiting of plants. In high mountains, on the border of eternal snow, we have the same phenomenon of hastened flowering and fruit as in the almost rainless deserts and steppes. In spite of the brief vegetative period, the seeds of the high-alpine plants of the Salicion herbaceae germinate very well; in *Veronica alpina* 80 per cent, *Gnaphalium supinum* 73 per cent, and in *Soldanella pusilla* 86 per cent.

Research on the dependence of the competitive power of plants (germinating capacity and growth of seedlings) upon altitude has been carried on by Hofmann (1921), in the United States with *Pseudotsuga taxifolia*. He found that the germinating capacity and growth of the seedlings decreased regularly with increasing altitude (Table 30).

TABLE 30.—INFLUENCE OF ALTITUDE OF THE PARENT TREES UPON GERMINATION IN *Pseudotsuga taxifolia*

Altitude of parent trees, feet	Germination of seed, per cent	Growth of one-year seedlings, inches
500	53.8	1.6
2,600	44.1	1.6
3,000	39.0	1.5
3,800	26.4	1 3

If the climate tends toward oceanic conditions, as in the case of isolated mountain summits, most (but not all) of the height limits are lowered. Plateaus which favor continentality, on the other hand, usually show a rise of height limits.

Plateaus.—The elevation of masses, that is, the mean rise of a very considerable region of the earth's surface, has a decided reaction upon all temperature conditions. On high plateaus, and in mountains which rise from plateaus, the isothermic lines are high. Thus the isothermic lines are higher on the Colorado Rocky Mountains which rise from plains with altitudes of 1,200 to 1,500 m. than they would be if the mountains rose from plains at sea level. This is due to increased irradiation and dynamic heating and to reduced cooling of the high surfaces. This favorable heat relation is the cause of the rise of any plant limits in the heart of mountains where the mean elevation of surrounding areas is great. Christ (1879) speaks therefore of the high surface of Grisons as the "Swiss Tibet" and calls attention to the high timber line in the Engadine and the Münster valleys. Next to the Engadine, in the Alps, the Monte Rosa region shows a considerable rise of the isothermic surfaces. Detailed maps of the isotherms and tree limits in Switzerland clearly show their correspondence to the distribution of mass elevation. The altitudinal distribution of the most important alpine plant communities also agrees with this scheme, as far as it is known. For example, while the maximal occurrence of the Curvuletum in the center of the Rhetic mountains is at 3,000 to 3,100 m. and in the central Valais at 3,100 to 3,200 m., it occurs in central Grisons between 2,800 to 2,900 m. and even between 2,600 to 2,700 m. in northern Grisons.

Exposure.—The course of the altitudinal limits of many plants and plant communities, with their irregular variations, is chiefly a function of inclination toward the sky. The graphic presentation of the melting of snow (Fig. 130) shows the advantage of south as compared with north exposure. A. P. de Candolle (1856) and Sendtner (1854) have recognized this. Sendtner devoted much time and patience to the determination of altitudinal limits in various exposures. In southern Bavaria he found the highest limits almost constantly on the southwest; the lowest, on north and northeast slopes, with a maximal difference of 213 m. for *Picea excelsa* and of 140 m. for *Alnus viridis*.

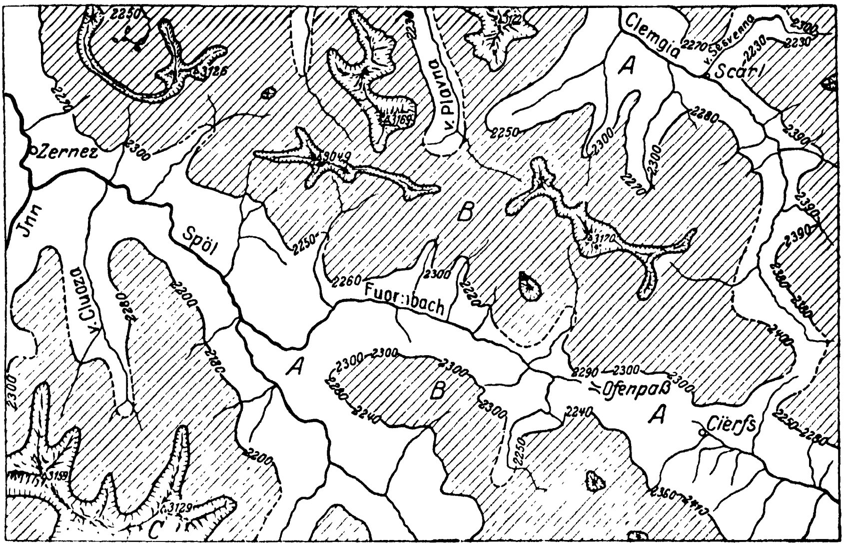

FIG. 131.—Timber lines on various exposures in the Lower Engadine Dolomites, Switzerland: showing the climax regions of the *Pinus-Larix* forests (*A*), of the Caricion curvulae (*B*), and of the crustose lichen communities (*C*).

The differences in the upward limits of the tree line in the east-central Swiss Alps are much smaller. In fact, as shown in Fig. 131, the upper boundary of the stone pine on a north exposure lies even higher than on any other exposure.

From this fact it follows that vegetation reacts variously to exposure, so that a correction of all altitude limits to a mean exposure cannot be made. Heliophytes and light-loving communities reach their highest limits on southern exposures, while shade plants such as *Pinus cembra* and shade-loving communities such as the Empetreto-Vaccinietum, Polytrichetum sexangularis reach higher limits on north, northeast, and northwest exposures.

It is well known that the differences in insolation and light absorption between south and north slopes in the mountains are very considerable, much greater than in the plains. The total light in a south exposure reaches 1.6 to 2.3 times higher values than in a north exposure (Rübel, 1908). The sharp distinction of the vegetation between the north and south slope is therefore not only due to temperature but due also to this distribution of light (Fig. 132).

In the higher chains of the Central Alps turfs of *Festuca varia, F. spadicea, F. alpestris* are restricted almost exclusively to hot, dry, or rocky south, southeast, and southwest slopes. On north exposures tall herbaceous communities of *Adenostyles tomentosa*, dwarf heaths, and clumps of *Luzula spadicea* take their place. The altitudinal distribution of these plant communities cannot profitably be compared, because they react so differently to the exposure of their habitats. The enormous advantages of south, southeast, and southwest slopes to organic life as a whole are very apparent. In the eastern Swiss Alps vascular plants ascend 400 to 500 m. higher on south than on north exposures.

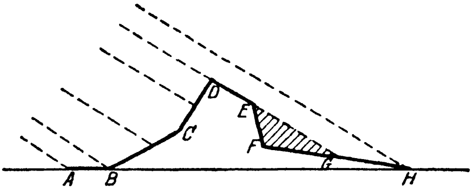

FIG. 132.—Differences in insolation; *C-D* receives the strongest radiation; *D-E* the least; *EFG* lies in the shade. (*After De Martonne.*)

The mean climatic boundary lines lie lower on south exposures and higher on north exposures than the theoretical orographic limits seem to require. Occasionally, some notable deviations are observed. Thus in the upper Engadine the orographic limit of alpine meadow on south exposures is above 2,900 m.; on north exposures it is at about 2,600 m. The *Carex curvula* association ascends to 3,050 m. on the south side of the Piz Sesvenna but stops at 2,650 m. on the north side. The summit flora of the highest elevations crowds together in the protected niches of the south side, in search of warmth.

Likewise the highest tilled lands, orchards and vineyards, lie on the south slopes with the highest winter retreats of civilization. Shaded slopes in the mountains are gladly left to the forests.

In dry regions, even in southern Europe, the shaded side affords better conditions for forest growth and regeneration, and it bears a rich, varied mesophytic flora, which in turn reacts upon humus formation and the acidity of the soil.

Gail (1921) determined upon the same geological substrata in arid Idaho a mean pH of 6.5 on a northeast exposure and of 6.8 on a southwest exposure.

The temperature, measured close to the soil surface, shows more pronounced differences than when measured 5 to 10 cm. above the ground, where the equalizing movements of the air become very noticeable. In rolling country the temperature differences between the tree layers of various exposures are more readily equalized than in the mountains, where the confining effect of steep slopes increases the contrasts even in the upper layers.

The changes in soil temperature at various exposures are of even more ecological importance than are those of the air. Such changes exert their influence upon root development even at considerable depths. Kerner's observations in the Tirolese Alps illustrate this point (Fig. 133).

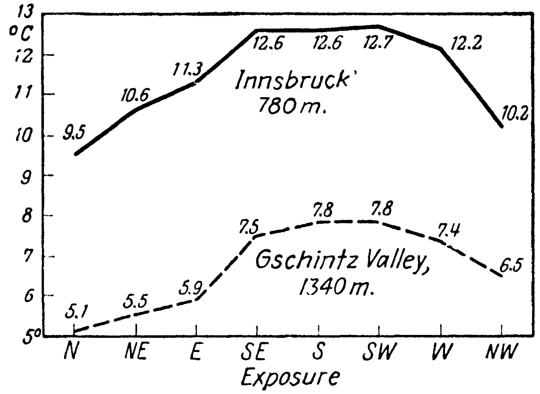

FIG. 133.—Influence of exposure upon the annual mean of soil temperature at a depth of 80 cm. (*From data by Kerner.*)

Foresters have also carried out similar investigations. Bühler (1918, p. 238) determined that in Zurich during the entire vegetative period the soil temperature at a depth of 5 cm. in all exposures except north is higher than the air temperature. The differences are greatest in the middle of the summer, especially around noon. For example, the soil temperature reached 38°C. at 1 p.m., Aug. 23, at a depth of 3 to 5 cm., with a simultaneous air temperature of 28.2° in the shade. Underneath the dense leaf cover of twenty-year-old beeches the differences in soil temperature in different exposures are practically equalized.

In North America Shreve, Bates, Gail, and others have investigated the problem of the influence of exposure on vegetation. Shreve set up self-recording thermometers in natural plant communities at a depth of 10 cm. and altitudes of 2,130, 2,440, and 2,740 m. in the Santa Catalina Mountains of Arizona. The results of these observations, extending from May to September, give quantitative proof of the fact that the difference in soil temperature between south and north sides increases with rising altitudes. In accord with this, there are sharp contrasts in vegetation between north and south slopes in the higher parts of the mountains.

A representative microclimatic cross section through a valley running east-west in the Rocky Mountains is given by Bates (1923) (Fig. 134). As a forester Bates was chiefly concerned with the changes of surface and soil temperatures and with evaporation. The inclination of the slopes was about 25 deg. The increase in temperature on the south sides corresponds, as might be expected, with the rise in evaporation and the decrease of soil moisture. However, the high maximum temperatures on the soil surface in south exposures must be held responsible for the composition of the tree layer, as also for the destruction of many seedlings. Seedlings of *Pinus ponderosa*, which germinate quickly and establish a rather deep root system, have been found the most resistant.

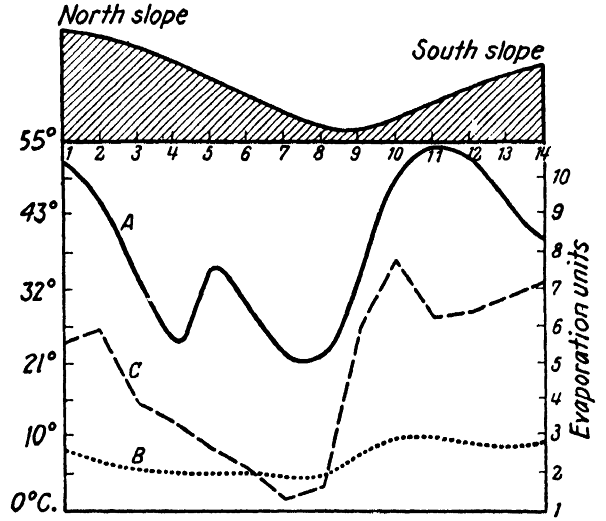

FIG. 134.—Section of the "micro-climate" of an east-west valley in the Rocky Mountains, Colorado: showing the effect of exposure on surface temperature (*A*); soil temperature at 1 ft. depth (*B*); and evaporation (*C*). July-August mean. (*After Bates.*)

When it happens that the side shielded from rain lies on the south slope of the mountains, the differences due to exposure are extreme, as seen on south slopes of the Bernese Alps in Switzerland, the Ötztal

Alps in the Tirol, and the south slope of the Great Atlas. Similar extreme conditions exist in the mountains of Idaho, according to Gail (1921). There in summer the mean relative humidity on northeast exposures is fully 22 per cent above that of the more windy southwest side. The curves of transpiration, evaporation, and soil moisture run similarly (Fig. 135).

The maximum of evaporation coincides with the minimum of soil moisture. For this reason at the beginning of August on southwest exposures all annuals are dried out. The dominant forest tree here is the drought-resisting *P. ponderosa*, while the northeast slope is occupied by the more mesophytic *Pseudotsuga* forests.

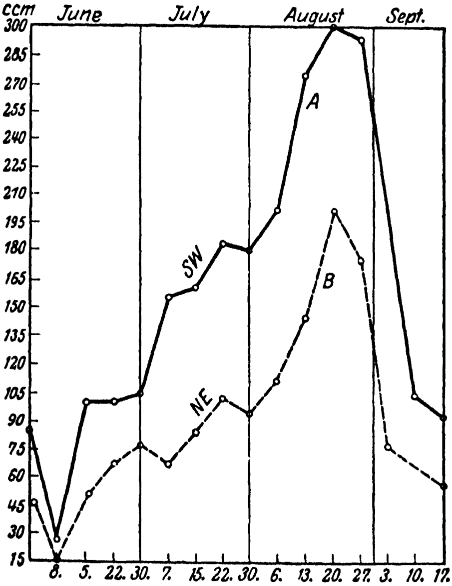

FIG. 135.—Evaporation in a southwest open exposure (*A*): and in a northeast exposure (*B*), under *Pinus ponderosa* and *Pseudotsuga taxifolia* (weekly mean). (*After Gail.*)

The map of vegetation by A. Luguet (1926) furnishes an excellent survey of the dependence of plant communities upon exposure in the Mont-Dore region. The rainy northwest side of the mountains is covered by gorse and ericaceous heaths, *Agrostis* meadows, and beech woods and extensive fir forests. On the southeast slope *Abies* is entirely absent, and in place of the Ericaceae and *Agrostis* there are fields of grain.

Differences due to exposure can everywhere be found, even in the smallest areas. Plant colonies which enjoy the warmth and dryness of the Mediterranean and Sarmatic climates are almost exclusively limited to the south, southeast, and southwest slopes of valleys, hills, and hummocks in west-central and northern Europe. Conversely, in southern Europe, even in southern France, the central European forest vegetation is strictly confined to shady north exposures. Classic examples of this are seen in the Montagne de Saint-Baume near Marseilles and on the Pic St. Loup, north of Montpellier.

The work of Pessin (1925) and of Ochsner (1928) illustrated the rôle played by exposure in the colonization of tree trunks by epiphytic communities. Pessin determined the differences in evaporation between northwest, northeast, and south exposures at various heights, on the trunk of *Quercus stellata* (Fig. 136). Ochsner examined the epiphytes at various points of the compass on the trunk of *Populus nigra* on the Swiss lowlands, with the resultant graphic view given in Fig. 137.

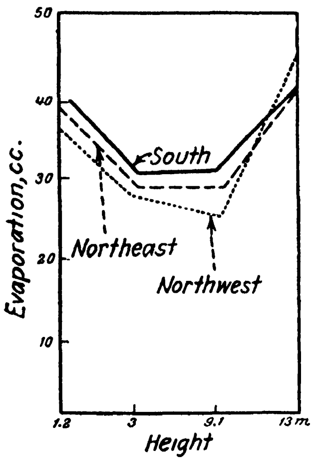

FIG. 136.—Differences in evaporation at various heights and in various exposures on the trunk of *Quercus stellata*. (*After Pessin.*)

The foliose lichens are localized almost entirely on the shady north side; the *Leucodon* type of mosses, on the sunny south side; while *Orthotrichum* and the liverwort *Radula* occupy the rainy west side.

Slopes of the Soil.—The slope of the soil surface affects vegetation directly as well as indirectly.

The indirect effect is due to the influence upon the water supply of the soil and the shifting of the angle of incidence of the sun's rays, modifying the intensity of insolation. With continued clear weather a horizontal plane in Davos at 1,500 m. would receive 141,992 gram calories, while one at right angles to the sun would receive 255,061 gram calories (Dorno).

Steepness of slope accelerates the circulation of soil water, which is an advantage to vegetation in humid climates but a disadvantage in arid ones. According to Piwowar (1903), the angle of inclination, however, is not conditioned by grain size but by the fracture and texture of the rock. The more massive, jagged, coarsely grained the steeper the rubble will lie. Thus granite slopes reach an angle of 43 deg.; slate, only 30 deg.

The steeper the slope the more speedily the superficial water is carried away and the more readily the rubble and the soil itself slide down.

Flow of soil, or solifluction, occurs mostly upon impermeable or frozen ground and is favored by repeated freezing and thawing of the superficial water-soaked "slide layer" (*Gleitschicht*) (Frödin, 1917; Nordhagen, 1928, p. 536).

The rubble flow in the limestone ranges of the Alps (Braun-Blanquet, 1926, p. 229) is also due to the steepness of the slopes but is not to be confused with solifluction. The more easily movable earth and rock particles are carried by rain and snow water along definite paths determined by the structure of the soil, forming tonguelike ridges of rubble as much as a meter high and slowly moving forward. They often considerably affect the minor topographic features. Tufts of *Dryas* and *Carex firma* take an outstanding part in the vegetation of these formations.

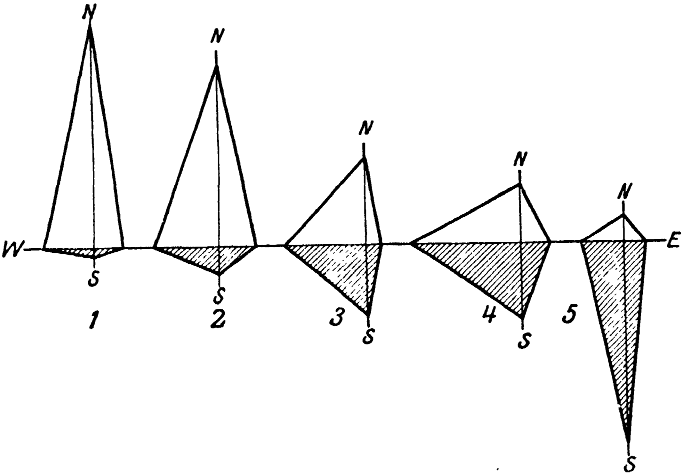

Fig. 137.—Manner of distribution of the various epiphyte forms according to exposure near the base (within 1 m.) of 100 poplars at Zurzach on the Rhine; showing the pattern for foliose lichens (1), crustose lichens (2), *Radula* form (3), *Orthotrichum* form (4), and for *Leucodon* form (5). (*After Ochsner.*)

In the subtropics, even in the southwest Alps and the Pyrenees and the southern Rocky Mountains, the vegetation on the steeper slopes is exposed to washouts and floods due to violent rainfall (see p. 115).

In the high mountains of central and southern Europe the steepness of the slopes is synonymous with a brief duration of the snow cover.

The vegetation on the slope awakens much earlier than that of the level places, not only because of the earlier melting of the snow but also because it often slides down the valley in avalanches. Avalanches also keep extended areas on steep slopes free from forest growth and the advance of alpine plant communities into the wooded region below is thereby favored (Fig. 138).

Finally the steepness of slopes and their surrounding conditions also affect the development of the climaxes of soil and vegetation. In the mountains of the temperate zones the climatic soil climax, and with it the climax vegetation, can mature upon calcareous rock only when a certain equilibrium in the slope is reached, and the angle falls below 10 to 15 deg. On steeper slopes than this, with basic soils, acidification is impossible because of continuous additions of calcareous rubble and water and also because of reduced humus formation. The climax vegetation of the alpine levels of the Central Alps, Caricion curvulae, is, therefore limited, in limestone mountains, to flat and moderately inclined slopes.

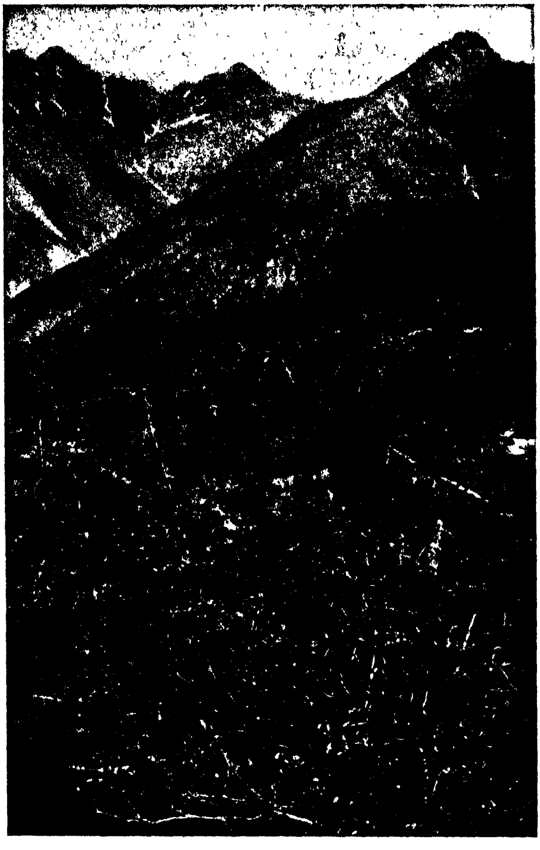

Fig. 138.—Path of an avalanche on Munt La Schera, 2,000 m. (Lower Engadine). In place of the destroyed larch climax forest a creeping scrub enters owing to repeated scouring by avalanches. (*Photo by Braun-Blanquet and Heller.*)

CHAPTER XI

BIOTIC FACTORS

The mutual effects of plants upon each other, or the phytobiological factors, have been discussed in the section on competition. A consideration of the influences of man and animals is also necessary for the complete understanding of vegetation. The present composition of vegetation over vast stretches of the earth's surface is more completely controlled by man and animals than is commonly supposed.

1. FAUNA

It will not be necessary here to return to the activity of soil organisms (see p. 233). Little attention has been given to the sociological importance of animals as agents of pollination and seed distribution. Active seed-distributing animals may be the deciding factor in the competition of plant communities pioneering on new land. The large ants of the garigue (*Messor barbarus*) carry quantities of the seeds of *Rosmarinus, Thymus vulgaris,* and other species more than 50 m. and thus hasten the spreading of these species over abandoned land. The *T. vulgaris* facies of the Brachypodietum ramosi in southern France may often be traced to seed distribution by ants. Similarly, birds and mammals may contribute to the success of certain communities by the distribution of their seeds.

Even in prehistoric times large game animals probably contributed to floristic equilibrium and to a modification of the vegetation of areas frequented by them. This is the only explanation we have for the wide and saltatory distribution of the *Lappula-Asperugo* association, which, characteristic of overhanging rocks in the Alps, is found in exactly identical habitats in the south German foothills.

Pasturing.—Farmers generally consider that moderate pasturing is beneficial to plant growth. The soil is fertilized; the distribution of seeds, as well as their germination, is favored. Swiss farmers assert that alpine pastures that are ungrazed for several years become rank with weeds.

Against this anthropocentric view it must be admitted that pasturing always prevents the development of natural vegetation. It retards, or prevents, the establishment and development of the climatic climax communities; it may cause profound disturbances and, in extreme cases, the destruction of vegetation. It is consequently of major importance to investigate the influence of this easily controllable factor in order to reconcile economic interests and exigencies with the duty incumbent upon citizens of maintaining intact the order of nature.

Causes of injury are:

1. The withdrawal of large quantities of plant matter.
2. Mechanical harm to plants by grazing, gnawing, brushing against, and trampling.
3. Selective destruction by pasturing animals. The desired plants are at a disadvantage, or entirely destroyed, while the undesirable ones increase abundantly.
4. Disappearance of dung-avoiding species from much frequented feeding places, and introduction of strongly nitrophilous communities (typical vegetation of cattle yards).
5. Direct effect upon soil formation by stirring of the fine earth and changing the microrelief (hummocks and paths).

The almost treeless plains of the Dark Continent are still inhabited by herds of wild game which number tens of thousands. One can hardly estimate the vast effect which such herds exert upon the original vegetation. Large quantities of dust are raised by hoofed animals so that the top soil is robbed of its finer particles. Before the advent of man the European steppes and grasslands must have been overrun from time to time by huge herds of game, for only thus can we interpret the great Tertiary fossil beds of Pikermi near Athens and of the Mont Luberon in Provence.

Nowadays the wild grazing quadrupeds are everywhere replaced by more or less domesticated herds of cattle. But the influence of the latter far exceeds that of the former, especially as it is continually augmented by man through the cutting of trees and bushes which interfere with pasture.

Intensive pasturing leads directly to a selective reduction in the number of species and also to the breaking of sod and the gradual erosion of the soil. Extended biotic grasslands due to excessive pasturing have sometimes arisen in the midst of a wooded region, and the bare, plantless soil appears where, within the memory of living men, trees have stood (Fig. 139).

Arid regions, subjected to excessive pasturing, have even assumed a desertlike character, as shown by vast expanses of north and south Africa, Australia, and western Asia.

The ancient centers of civilization on the shores of the Mediterranean Sea and in the Orient owe their most striking types of vegetation to excessive pasturing. The Spanish *tomillares*, the southern

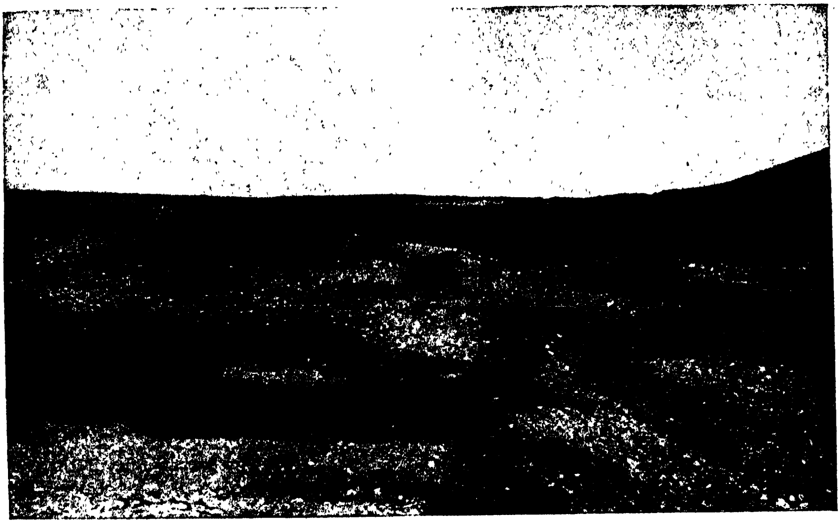

FIG. 139.—*Nardus* meadow destroyed by excessive sheep grazing and resulting erosion (rain) in the heart of the beech region of the Aigoual, 1,250 m., South Cévennes.

FIG. 140.—Thorn-bush garigue of *Astragalus poterium* with scraggly remains of the macchia of *Pistacia lentiscus* upon Majorca. (*Photo by Hoffmann-Grobéty.*)

French *garigues*, the Greek *phrygana* are convergent pasture types of the Mediterranean region. They are marked by their wealth of aromatic Labiatae, Cistaceae, Rutaceae, Artemisiae, Euphorbiaceae, thistle plants, and thorny bushes such as *Bupleurum spinosum*, *Poterium spinosum*, and *Astragalus*—all plants which are hardly touched by sheep or goats. The zoobiotically conditioned communities are, unfortunately, even today still prevailing against the struggling remnants of forest (Fig. 140).

While in the temperate and tropical zones the consequences of excessive pasturing are not so grossly apparent, owing to powerful regenerative forces of vegetation, they are not hidden from the trained observer.

There is an extensive literature on the influence of pasturing upon natural vegetation.

Clements and Goldsmith (1924) have carried out experimental investigations on the subject in the prairies of North America. For three years they weighed the production of grass on similar areas under examination.

This quantitative study of vegetation included plots under three conditions: (1) entirely ungrazed, (2) grazed by the rodent, prairie dog (*Cynomys gunnisoni zuniensis*), and (3) grazed by cattle and prairie dogs. The results are given in the following table:

TABLE 31.—INFLUENCE OF GRAZING UPON GRASS PRODUCTION
(In grams of forage per square meter)

Condition of area	*Agropyrum glaucum*			*Sporobolus cryptandrus*			Total forage		
	1919	1920	1921	1919	1920	1921	1919	1920	1921
Ungrazed	100	117	139	165	33	82	265	150	221
Rodent grazed	37	24	23	Trace	0	0	37	24	23
Cattle and rodent grazed	7	9	7	4	0	6	11	9	13

One of the dominant grasses, *Agropyrum*, bears pasturing fairly well, thanks to its underground rhizomes, while *Sporobolus* disappears almost entirely. The production of hay was reduced one-third to one-fourth by the prairie dog, but by the prairie dog and cattle to one-twentieth of the unpastured meadow.

The duration and intensity of grazing are of very great importance. According to the intensity of the pasturing process (for which unfortunately exact data are not available), in most pastured districts of the earth various degenerative stages appear, leading away from the climax. In the Mediterranean and north African countries characteristic degenerative phases of vegetation due to overgrazing include communities dominated by thistles and by such species as *Zizyphyus lotus*, *Ferula communis*, *Peganum harmala*, *Euphorbia characias*, *E. nicaeensis*. In southern France, with moderate overpasturing, upon compact limestone soil and red soil, the *Brachypodium ramosum-Phlomis lychnitis* association takes possession. In the mountains of central and southern Europe and in northern Europe, meadow communities with abundance of *Nardus* have become very widespread under the influence of severe pasturing (Fig. 141). A characteristic of heavily grazed land of central, western, and southern Europe is the prevalence of *Juniperus* bushes. *Juniperus communis* and, in the

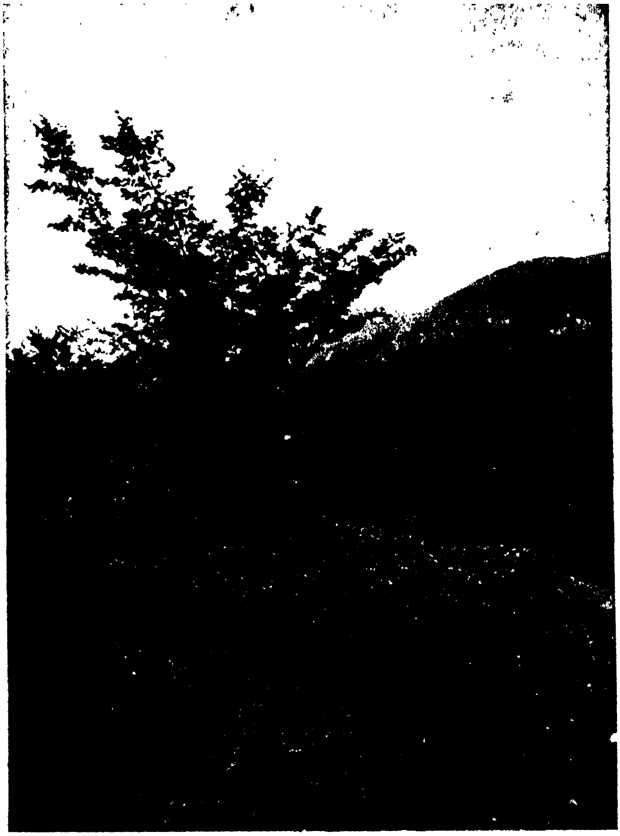

FIG. 141.—Effect of cattle grazing on *Fagus*. The Nardetum is conditioned and maintained by moderate grazing; in the beech climax of the Cantal mountains 1,200 m., Auvergne. (*Photo by Uehlinger and Rübel.*)

south, *J. oxycedrus* and *J. macrocarpa* are about the only trees which manage to attain their maturity in a pasture and to maintain themselves—thanks to their spines. They form either a parklike, open landscaping of the heath regions (Fig. 16) or a dense, low scrub. In Obervinschgau, between Schlanders and Mals (800 to 1,200 m.), intensive goat pasturing has transformed the forest of the south slopes for many miles into unsightly *Juniperus* thickets, which are quite as forbidding as the Mediterranean thorn scrub. Likewise, the southern stands of *J. oxycedrus* are due to grazing (Fig. 142).

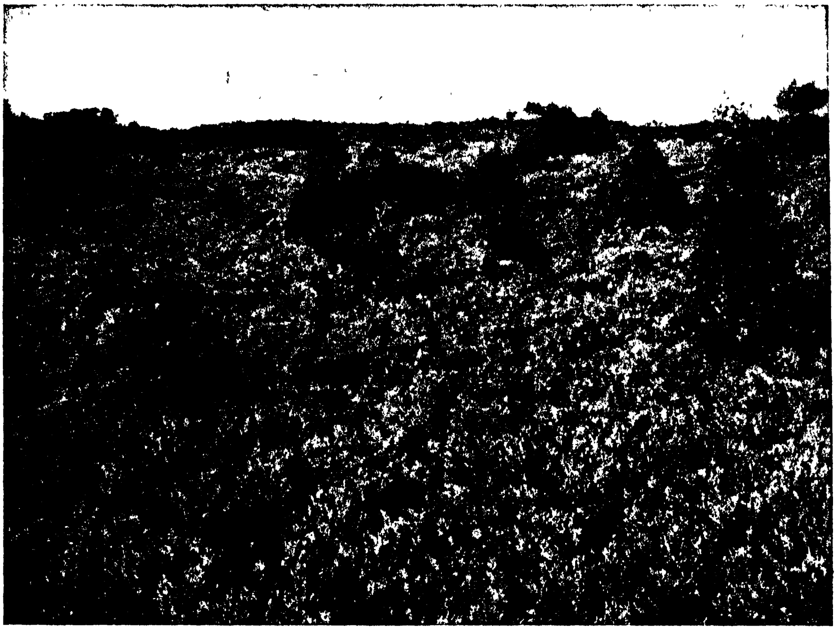

FIG. 142.—Sheep-trampled, deserted farm land near Montpellier. *Juniperus oxycedrus* enters the *Thymus vulgaris* facies. (*Photo by P. Keller and Braun-Blanquet.*)

Resting places of game and cattle are marked by a rank growth of tall, juicy ruderal herbs, characteristic of soils of mesic deciduous forests. In the mountains of Europe the genera *Rumex*, *Aconitum*, *Senecio*, *Cirsium* and in lower altitudes species of *Carduus*, *Onopordon*, *Cynoglossum*, *Urtica* rise in tall thickets on places frequented by cattle and game. The meadow communities of the high mountains are very different from this luxuriant dung vegetation.

With excessive amounts of manure the soil is stimulated to very great bacterial activity. This explains the rich development of nitrophilous dung plants which are able to store considerable quantities of nitrates in their tissues. According to the ability of the individual species to endure the active nitrogen compounds, various degrees of nitrophily may be distinguished, and a whole series of floristically related, more or less nitrophilous "animal resting-place communities" may be recognized. These nitrophilous communities might very well be taken as indicators of the capacity of the soil for nitrification. It must not be forgotten, however, that where therophytes are not numerous, communities once established have considerable endurance and often maintain themselves in changed conditions. Since the establishment of the Swiss National Park (1911), the cattle yards there are no longer in use as such. Nevertheless, the floristic composition of the vegetation upon them has not changed in the least. The *R. alpinus*, *Chenopodium bonus henricus*, and *Aconitum* stands have withstood outside competition very well, even where the soil today has a strongly acid reaction.

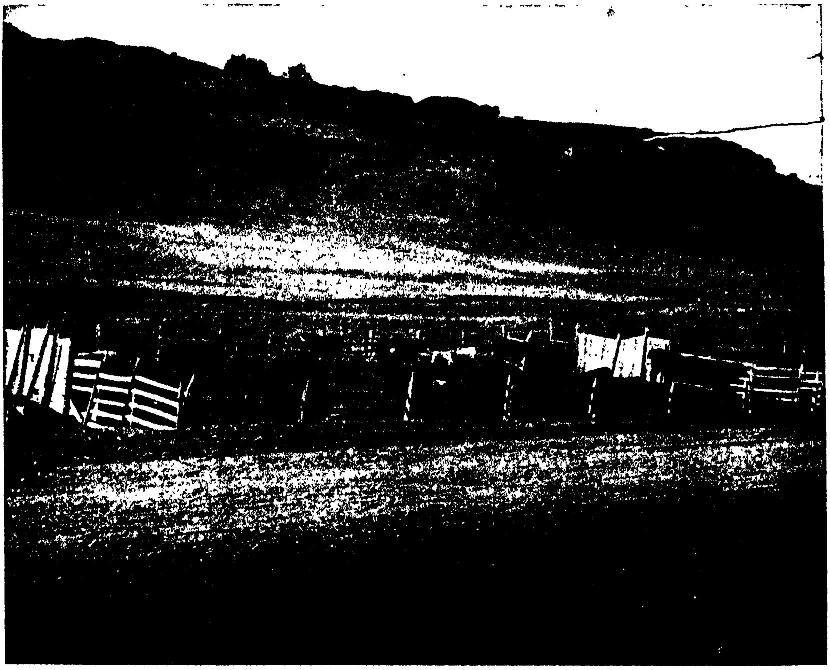

FIG. 143.—Yarding of grazing stock in the beech climax region of the Auvergne, 1,100 m. (*Photo by Bador.*)

Meadows are frequently fertilized for the improvement of the sod by means of pasturing. The yarding of cattle, that is, a brief maintenance of cattle upon an enclosed area, is especially effective for the improvement of the meadow with dung. The whole maintenance of meadow in the subalpine levels of the mountains of central France is based upon the yarding method. From the phytosociological viewpoint this process is a continuous battle against the extension of the *Genista pilosa-Calluna* association, leading to the climax, which takes possession of all dry pastures. In order to stop this climatically induced degradation of the pastures, every square foot of the ground is subjected to several weeks of cattle yarding at intervals of from fifteen to twenty years. The temporary enclosure in which the cattle spend the nights is moved from time to time (Fig. 143). As soon as pasturing is discontinued, everywhere the natural tendency toward the climax resumes its sway.

2. MAN

There is no sharp line of distinction between the influence of man and animals upon vegetation except in man's use of fire. Man's influence is often exerted through his domestic animals.

The effect of man's destructive hand upon vegetation is visible everywhere, from the tropics to the poles, and from the valley floors to the mountain tops. If we speak today of "untouched vegetation," we exaggerate greatly; Chevalier (1925) reminds us that even the concept of "virgin tropical forest" is a mere myth.

In all records of vegetation one should first attempt to account for the degree of human influence. Even our paleolithic ancestors of the early and middle Quaternary, with their primitive implements, knew fire, and they may have encouraged certain types of vegetation (meadow, steppe) at the expense of others (virgin forest). With the rise of commerce and transportation, agriculture, and stock farming in the neolithic period, the era of vegetational change begins. Great plant migrations which began under the influence of the "lords of creation" have not yet reached their conclusion (see particularly Thellung, 1915; Hauman, 1928).

No other factor of vegetation has been investigated and written upon so much as the influence of man. In fact, hundreds of volumes in agriculture and forestry have reference to it. We are obliged to limit ourselves to a few points and to refer, in general, to the texts on agriculture and forestry.

Fire.—The most remorseless associate of man in the destruction of native vegetation is fire. While prairie and forest fires may occasionally be caused by lightning, that is the exception rather than the rule. In 90 out of 100 cases they are caused by man, either willfully or accidentally. Contrary to the opinion of some American investigators, therefore, fire is to be classed among the anthropogenous factors.

Fire is particularly destructive upon very thin, sterile soils and especially in the transitional region between forest and prairie, where both types of vegetation are struggling for control. Wherever natural reforestation today is accomplished with difficulty, it is exceedingly difficult to reconstruct the original, natural appearance of the forest or to delimit exactly the forest and grassland climaxes (Fig. 144).

In humid regions, which present no special hindrances to regeneration, fire is a periodically repeated phenomenon, even a form of cultivation. True cultivation with the aid of fire is still employed on a large scale in Finland and in the Atlantic regions of Europe. Elsewhere fires are employed in the destruction of noxious shrubbery, for the improvement of pastures, for increased blossoming (bee pasture), for cattle or game feed, and probably also for the mere pleasure of burning and, finally, out of sheer carelessness.

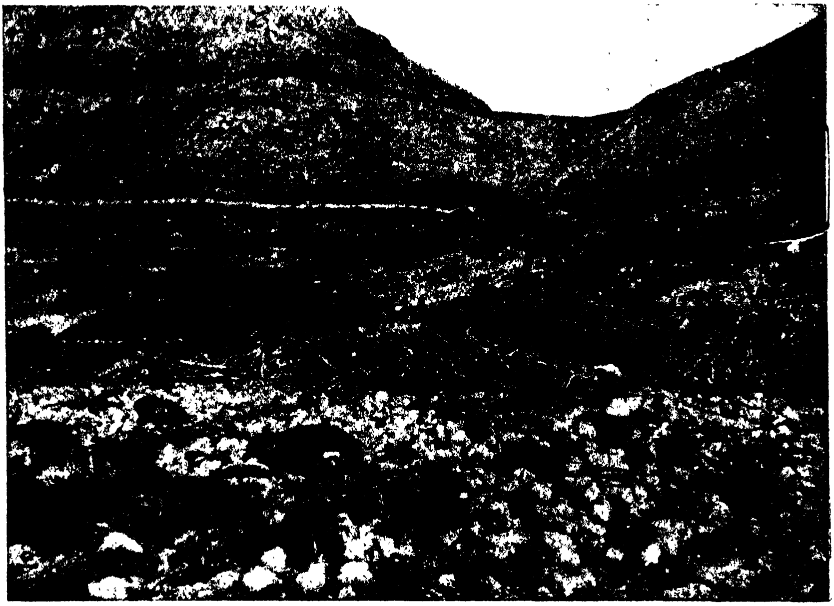

FIG. 144.—Example of the systematic destruction of the *Quercus ilex* climax forest in the Mediterranean region by charcoal burners; Majorca. (*Photo by Hoffmann-Grobéty.*)

Effect of Fire upon Succession.—Fires are always followed, whether the original vegetation is destroyed partially or entirely, by a secondary succession, which tends anew toward the climax. Careful examination of changes in the vegetation after fires has been made in England, Finland, southern France, North America, and probably elsewhere.

In the heath regions of the European-Atlantic province, where heath burning is carried out periodically for the renewal and refreshing of worn-out heaths, the natural revegetation, unaffected by man, has been studied in a careful fashion by Fritsch, Parker, and Salisbury (*New Phytologist*, 1913, 1915). *Calluna* reappears very quickly. A test quadrat of 25 sq. ft. showed 2 years 8 months after the fire, 4,641 *Calluna* seedlings in addition to 11,513 seedlings of *Erica cinerea.* The revegetation here passes through six stages: the first stage is characterized by algae (*Cystococcus humicola, Gloeocystis, Trochiscia, Dactylococcus*) together with the fungus *Ascobolus atrofuscus* and sparse shoots from surviving roots of *Ulex.* The mosses *Ceratodon* and *Funaria* appear in the second stage, together with a number of grasses and herbs, such as *Aira, Carex pilulifera,* and *Rumex acetosella.* The third stage comprises the algae of the first, along with *Mesotaenium violescens* and numerous lichens, such as the *Cladonias.* The flowering plants increase. The fourth and fifth stages are marked by the final predominance of the heath with *Calluna, Ulex,* and *Erica.* In the region investigated (Hindhead Common) a sixth and final stage follows, consisting of such trees as *Pinus, Betula,* and *Pirus,* a proof that here the heath cannot maintain itself without the aid of man. Aside from the conditions of competition, the changes in humus content and water supply of the upper soil horizon play a great rôle in the revegetation of a region. Parallel to the accumulation of humus runs the increase in the water content. Thus the bare soil of a burned surface after eight days of rain contained 11.19 per cent; the soil of the *Calluna* heath, 31.39 per cent, and the *Vaccinium myrtillus* heath, almost 70 per cent of water by weight.

The revegetation of a heath surface following the removal of the upper surface of the soil, in the northwest German heath region near Hanover, is shown in Fig. 145. The field represents a sheep pasture no longer used, sprinkled with *Juniperus* in which *Pinus silvestris* has naturally established itself and increased since cessation of pasturing.

In the Mediterranean region, in western North America, and in South Africa periodic bush fires are the regular method for the improvement of pastures. Continuous repetition of bush fires in southern Europe produces special communities rich in geophytes and therophytes which attain widest distribution in southern France and northern Spain. Species of *Cistus* are the first shrubby pioneers on the burnt places (Fig. 146). They soon collect in extensive clumps but die out after ten to fifteen years if not burned again and are succeeded by other shrubs: upon silicious soils by species of the *Lavandula stoechas-Erica scoparia* association; and upon soils with

FIG. 145.—*Calluna* heath in Hanover after plowing (foreground); self-sown seedlings of *Pinus silvestris* in old pasture in background. (*Photo by Tüxen.*)

FIG. 146.—*Cistus monspeliensis* fire facies of the *Lavandula stoechas-Erica scoparia* association near Montpellier, France. (*Photo by P. Keller and Braun-Blanquet.*)

high lime content, by the *Quercus coccifera* association. The latter is able to regenerate repeatedly after fires by sprouting from the roots.

Perrier de la Bathie (1921) and Humbert (1925) call attention to the tremendous influence of the bush fires in Madagascar. The Madagascar prairie, which today covers four-fifths of the total area of the island and is composed mostly of cosmopolitan tropical grasses, owes its origin exclusively to the periodic bush fires. It lacks almost entirely the old endemic species which do not survive the fire, while the original dry sod, untouched by fire, is composed exclusively of the old Mascarene Tertiary endemics.

Chevalier (1925, p. 1106) gives some interesting data on the influence of the steppe fires in the Sudan.

In California, according to Show and Kotok (1924), the hard-leaved chaparral has gained tremendously in extent through fires, while the forest has been reduced. The forest of Douglas fir in the Puget Sound district owes its predominance solely to fires and cannot be regarded as a climax forest.

Usually fire for the purpose of improving pastures is condemned and probably justly so. In contrast, however, four years' experiments by Hensel (1923) in the North American prairie region show that under certain circumstances fires may increase production. Hensel subjected quadrats to an annual shearing; pasturing was prevented. After four years, with regular burning down each spring, instead of the poor *Andropogon furcatus*, the better *A. scoparius* showed an increase of 48 per cent; upon the unburned square, however, it had decreased by 61 per cent. The number of shoots and dry weights of Gramineae and Cyperaceae showed the following changes in the course of the investigations:

TABLE 32.—INFLUENCE OF PRAIRIE FIRES UPON GROWTH OF GRASSES

Year	Burned surface		Unburned surface	
	Gramineae and Carices, number of shoots	Dry weight of hay, per cent	Gramineae and Carices, number of shoots	Dry weight of hay, per cent
1918	1,561	33.5	811	66.5
1919	2,303	47.5	1,680	52.5
1920	2,268	49.0	2,139	51.0
1921	2,237	53.0	1,934	47.0

The duration of the experiments probably was too brief for an ultimate pronouncement upon the effect of fires.

The influence of fires upon the forests of Finland has been studied in detail by Heikinheimo (1915) and Kujala (1926).

Cutting.—The utilization of the forest by cutting it down began when man of the later stone age gave up his caves to build huts. The natural forest landscape was subjected to a marked change only by the complete cutting down of large areas of forest. Not only does such cutting considerably change the lighting conditions, but wind and precipitation are given freer rein, and the soil structure itself is changed markedly. While the power for nitrification increases, air capacity and permeability of the soil are reduced. In this way complete clearing impoverishes the soil, even where floods and erosion are not to be feared. Burger's (1922) experiments on the influence of clearing upon forest soil are very instructive.

On a clearing near Zurich the air capacity of the top-soil layer was reduced by one-third. The permeability of good beech-wood soil near Bienne was thirty times that of soil which had lain waste for ten years and had been used part of that time as a logging camp.

The vegetational changes which take place upon cleared land have been dealt with by Sendtner (1854) and Kerner (1863) and by more recent authors. The changed light conditions bring about a regular series of changes in vegetation. Dziubaltowski (1918) gives exact data on the floristic phases of development upon cut-over *Quercus pedunculata-Carpinus betulus* woodlands in Poland. A phase with many "accidental" pioneers of a ruderal character is followed by a sod carpet of *Agrostis alba;* and *Salix caprea* and some shrubs such as *Genista germanica, G. tinctoria,* and *Cytisus nigricans* appear. From the eighth year onward, herbs and shrubs decrease continually because of the increasing shade of trees, until the equilibrium of the shady high forest is reached. However, we have few precise data on the simultaneous ecological changes, and the subject must be recommended for further study. As a preliminary, the studies of Salisbury (1924) on the regeneration of British low woods are to be mentioned.

The vegetational changes in the regular operation of selective cutting are less apparent than in bare cutting. The chosen trees are taken out at intervals, and no important changes of light and soil conditions are caused. In the composition of the forest, however, a change due to preference and protection of certain tree species may take place. Repeated cutting is followed by the dominance of the most vigorously growing timber varieties. In this way almost pure dwarf woods of *Q. pedunculata* and *Carpinus betulus* are formed in the beech region of central Switzerland. Long stretches of the famous Mediterranean *Macchia* are nothing but high forest which has been permitted to degenerate in this manner into dwarf or low woods, where formerly *Q. ilex* dominated (Fig. 147). In the excessively deforested Islamic lands the graves of saints (Marabouts) are refuges for the original vegetation, since trees in the immediate vicinity enjoy the protection of the faithful.

The secondary tropical "virgin" forest owes its origin to complete cutting followed by fires. If the surfaces are left to themselves, even for ten years, the secondary virgin forest appears with a 25-m.-high tree layer of soft woods and impenetrable undergrowth. The hard woods of the primary virgin forest, on the other hand, appear much later, and centuries may pass before the original tropical climax forest comes into its own once more (Chevalier, 1925; Perrier de la Bathie, 1921; Benoist, 1923).

FIG. 147.—*Quercus coccifera* scrub (left); sclerophyll macchia due to 20 years of cutting on right; center, large *Quercus ilex*, a remnant of the former climax forest, valley of the Vistre, southern France. (*Photo by P. Keller and Braun-Blanquet.*)

Mowing, Fertilization, Irrigation, Reclamation.—With the use of sickle and scythe in the bronze and iron ages we see the beginnings of the cultivation of food plants, the extension of cultivated and semicultivated land. Mowing has about the same effect upon the vegetation as moderate pasturing. Usually, however, mowed land is also fertilized and, often, irrigated and seeded. This brings about the anthropogenous rich meadows, which have such a surprisingly uniform floristic appearance over large areas. All over central and a large part of western Europe man has for a very long time controlled the grassland according to uniform and widely accepted practice. The result is a very uniform rich type of meadow with numerous species: the Arrhenatheretum elatioris.

The most extensive and richest hay meadows are not in the regions of climax grasslands but in the regions of forests. Cutting and clearing are usually followed by pasturing and only later by mowing for hay.

The natural development of vegetation is permanently retarded by regular mowing. The scythe exercises a rigid selection and kills off all species, sooner or later, which do not ripen their seeds before the first mowing or which have not enough regenerative power to shoot up anew.

The influence of manuring, irrigation, and reclamation upon natural and semi-natural plant communities is so fully discussed in agricultural literature that consideration of these topics here seems unnecessary.

Cultivated lands, such as vineyards, potato fields, grain fields, truck gardens, etc., often exhibit quite characteristic "weed" communities, with numerous characteristic species along with the cultivated plants. These communities reflect the specific ecology of the habitat. We cannot accept Alechin's (1926, p. 43) view that everything of this sort is accidental and artificial. These communities have a definite geographic distribution and often show pronounced stratification. They may exhibit very definite seasonal aspects; the composition of the autumn aspect, the fallow period for grain and potato fields, is very different in various associations but not less constant than it is in so-called semi-cultivated communities. Allorge, Gaume, Luquet, Kühnholtz-Lordat, Tüxen, Koch, and Braun-Blanquet have distinguished and described a number of ecologically interesting associations of southern and central Europe which have been conditioned by cultivation.

Chevalier gives a comprehensive classification of the cultural plant communities of the world, with the types of culture, in De Martonne's "Handbuch der Geographie" (1925) to which the reader is referred.

The ultimate aim of every reasonable attempt to control vegetation, aside from purely aesthetic aims, consists in influencing with the least possible effort the conditions of the habitat so as to give permanently the greatest possible returns. But this goal can be approached only when farmers and foresters alike acquaint themselves with and apply the teachings of soil science and plant sociology.

Sogar bei den künstlichen ephemeren Pflanzengesellschaften auf Kulturland kann die Berechnung der sozialen Lebensmomente nach den Methoden der Phytosoziologen durchaus positive Resultate ergeben. Das sind die wichtigsten Bahnen zur Anwendung sowohl der Methoden, als auch der Ergebnisse der Phytosoziologie in der Landwirtschaft.[1]

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[1] ABOLIN, *Bull. Inst. Pédologie Géogr. Botan. de l'Univ. de l'Asie Centrale* **1**: 104.

CHAPTER XII

LIFE FORMS AND SYNECOLOGICAL UNITS

The form which the vegetative body of the plant produces as the result of all the life processes which are affected by the environment has been designated the "vegetative form," "growth form," or "life form." Under the caption of life form are brought together those organisms that in their entirety show similar morphological adjustments to the environmental complex.

As far back as the work of Alexander von Humboldt ("Physiognomik der Gewächse," 1806) we find attempts at a grouping of the forms of vegetation. Although the basis of his nomenclature was physiognomy, a few of his plant forms, such as cactus form, banana form, casuarina form, express an ecological adjustment. Building upon Humboldt's ideas, Grisebach (1872) attempted to prove the dependence of plant forms upon climate. His summary of plants under 54 different "forms of vegetation" adhered much too closely to physiognomy, that is, to the leaf form, and became lost in its own complexity. Kerner (1863) divided the manifold forms of plant life into 11 purely morphological "basic forms." He emphatically stated that these basic units must be chosen independently of the systematic position of the plants. *Pflanzenphysiognomik und Systematik gehen ja ganz verschiedene Wege* (p. 281). He distinguished: trees, shrubs, undershrubs, mat plants, herbs, lianas, filamentous plants, reeds, grass forms, fungi, and crustose plants.

More recently Drude attempted to "cull out the ecologically uniform members of the major phylogenetic series of the plant world and to classify them from a morphologic-systematic viewpoint" (1913, p. 23). Warming (1908), like Kerner, threw aside purely systematic-morphological distinctions for the characterization of life forms. At the same time he was not unmindful of the almost insurmountable difficulties which stand in the way of any attempt to bring order out of the chaos of individual organic forms. For his classification he used various characteristics of the plant, such as structure of the shoot, sequence of shoots, bud and root formation, sequence of flowers and leaves, duration of life, overwintering, rejuvenation, and reproduction. Warming's own system of life forms, however, has found little acceptance, perhaps just because of its variety and its lack of a coordinating principle. Nevertheless, from the ideas of Warming has developed the system of life forms by Raunkiaer, which is today generally accepted in its most significant features.

Raunkiaer's System.—Based upon sound morphological and biological principles, Raunkiaer's system is marked by simplicity, clarity, and compactness. The principle of classification is simple. No attempt is made to take account of all the infinite variety of ecological adjustments. Instead, Raunkiaer chooses for his basis of classification a single very important feature, namely, the adjustment of plants to the unfavorable season. It is this which gives the system its clarity and completeness. Plants with similar adjustments are first classified in five main types (life-form classes). Within each class a number of subtypes or life-form groups are distinguished.

The position of a plant in this system is determined by the location and protection of the perennating organs during the unfavorable season, that is, during the cold winter or the dry, hot summer. On this basis Raunkiaer distinguished: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes, and therophytes. The cryptogams are not included in this system. Later, Raunkiaer raised the number of life-form classes by the segregation of stem succulents, epiphytes, helophytes, and hydrophytes. Allorge, Gams, E. Frey, Hayek, Jenny-Lips, Linkola, W. Koch, Ostenfeld, Vahl, Braun-Blanquet, and others have made changes in the designation and limitation of some of the types.[1]

The value of Raunkiaer's concept, however, seems to be a relative one. In investigations of the vegetation of the high Alps Braun-Blanquet (1913, p. 38) reached the conclusion that for many of the alpine species their success in life depends not on their adaptation to the rigorous season (winter) but rather to their adjustment to the very short, cool summer. He says:

> The better a species can adjust itself to the short vegetative season, the more rapidly it completes its life cycle the more completely is it suited to live and spread in the high Alps. Probably the determining factor for the northern extension of the range of many arctic plants is the preparation of new buds in the fall, or under the snow covering, and the consequent rapid resumption of vital activities in the spring with early fruit formation during the favorable season.

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[1] Du Rietz (1931) has given a careful analysis of all the literature relating to the various classifications of life forms. This includes an extensive bibliography and suggestions for a new classification with many new subdivisions.

The studies of Resvoll (1917) and of Nordhagen (1928) entirely confirm this conclusion.

In the following classification of life forms, built on the framework provided by Raunkiaer, and including cryptogams, eight main classes are distinguished. The first three, comprising cryptogams exclusively, are greatly in need of further elaboration. The other classes have received more attention. Thus Raunkiaer's system, as modified by Braun-Blanquet and others, takes the following form:

I. PHYTOPLANKTON (microscopic floating plants):

1. Areoplankton: microorganisms floating in air.
2. Hydroplankton: microorganisms floating in water.
3. Cryoplankton, protista inhabiting snow and ice, such as *Sphaerella nivalis*, *Scotiella nivalis*, *S. antarctica*, *and S. cryophila*, which cause "red snow"; and *Ankistrodesmus nivalis*, *A. tatrae*, and *Stichococcus nivalis*, which cause "green snow" (see Chodat, 1896; Huber-Pestalozzi, 1925).

II. PHYTOEDAPHON (microscopic soil flora):

1. Aerophytobionts: aerobic soil flora (bacteria, etc.).
2. Anaerophytobionts: anaerobic soil flora.

III. ENDOPHYTES:

1. Endolithophytes: lichens, algae, and fungi (*Pharcidia lichenum*) which penetrate rocks.
2. Endoxylophytes: parasites living in plants.
3. Endozoophytes: protista living in animal organisms, often pathogens.

IV. THEROPHYTES (annuals): plants which complete their life cycle, from germination to ripe seeds, within a single vegetative period. Their seeds or spores survive the unfavorable season under the substratum. Due to this habit and their mobility they are widely distributed, even in the unfavorable hot, dry regions of the earth. They include:

1. Thallotherophytes: slime molds (Myxomycetes) and molds with heterotrophic nutrition, also annual surface algae.
2. Bryotherophytes: annual liverworts and leafy mosses such as *Riccia*, *Phascum*, *Ephemerum*, and *Physcomitrium*.
3. Pteridotherophytes: annual vascular cryptogams with summer resting period like *Gymnogramme* and *Selaginella*.
4. Eutherophytes: annual seed plants including:
    - *a.* Creeping therophytes like *Tribulus terrestris* and species of *Amaranthus*.
    - *b.* Climbing therophytes like *Vicia*, *Lathyrus*, and *Convolvulus*.
    - *c.* Erect therophytes like *Linum* and *Aira*. In cool countries this last is almost the only group represented.

Biennials which develop a leaf rosette in the first year and flowers the second are to be classed with the hemicryptophytes. For the development of eutherophytes the desert and steppe regions of the warm-temperate zone are particularly favorable, *i.e* , where the competition of perennials is limited. In the cool-temperate and cold zones they are mostly restricted to cultivated areas. where steppe conditions are artificially produced by man.

V. HYDROPHYTES (water plants); all water plants other than plankton. Their perennating organs are submerged in water during the unfavorable season. The subgroups are:

1. Hydrophyta natantia: free-floating water plants such as *Lemna*, *Ceratophyllum*, *Utricularia*, *Riccia*, and filamentous algae like *Spirogyra.*
2. Hydrophyta adnata: water plants anchored to the substratum, including algae, mosses (*Rhynchostegium rusciforme*, *Fontinalis*), liverworts, mosses, and fungi.
3. Hydrophyta radicantia: aquatics with roots such as *Potamogeton*, *Zostera*, *Posidonia*, *Nymphaea*, and *Hippuris*. According to Koch, this group comprises:
   - *a.* Hydrogeophytes such as *Potamogeton lucens*, *Zostera*, etc.
   - *b.* Hydrohemicryptophytes such as *Lobelia dortmanna* and *Isoetes.*
   - *c.* Hydrotherophytes such as *Najas* and the *Potamogetons* of the *Pusillus* group.

VI. GEOPHYTES (earth plants): plants with the perennating organs (buds, mycelia) buried in the substratum and therefore but little exposed to the influence of the unfavorable season. The subgroups are:

1. Geophyta mycetosa (fungus geophytes): fungi with survival through mycelia in substratum; nourishment heterotrophic. Including:
   - *a.* Tuberous fungi: fruiting bodies subterranean as in *Tuber.*
   - *b.* Aerial fungi: fruiting bodies aboveground.
2. Geophyta parasitica (root parasites): plants with their perennial organs subterranean, sunken in the host such as *Conopholis*, *Rafflesia*, and *Orobanche.*
3. Eugeophytes: divided into several groups (Fig. 148*f* to *h*):
   - *a.* Geophyta bulbosa (bulb geophytes): plants with underground storage organs, such as root tubers (many Orchidaceae and Liliaceae); stem tubers (*Eranthis*, *Corydalis*, *Bunium*, *Cyclamen*) or true bulbs (many Liliaceae, Amaryllidaceae, and Iridaceae). At the beginning of the favorable season the formation of leaf and flowering shoots begins. As soon as the flowering stage is completed, the parts aboveground begin to wilt and disintegrate. The plant withdraws again below the surface and spends the unfavorable, usually dry and hot, season in a resting condition. From the energy stored, it is able again to resume its life activity in the fall or spring, to bloom and fruit. The bulbous geophytes therefore are most abundant in warm, dry regions with a short vegetative period. Their climatic requirements are similar to those of the therophytes.
   - *b.* Geophyta rhizomatosa (rhizome geophytes): plants with rhizomes that are able to travel underground. They do not thrive on stony compact soils but rather on loose humus, sand, and mud soils. Climatically they are not very sensitive. The rhizome geophytes have the property of maintaining their runners and renewal buds at a certain depth under the surface of the ground. Here belong many of the plants of our deciduous forests, such as *Polygonatum*, *Paris*, *Anemone nemorosa*, and many Carices and Gramineae; also ferns such as *Dryopteris* and *Pteridium.*
   - *c.* Geophyta radicigemmata (root-bud geophytes): a transition group between the eugeophytes and hemicryptophytes. These vascular plants have perennating buds at the base of the stem, below the surface of

the ground. Here belong such plants as *Cirsium arvense* and *Aconitum napellus* (Fig. 148*h*).

VII. HEMICRYPTOPHYTES (Fig. 148*b* to *e*): plants with perennial shoots and buds close to the earth's surface. They often have the protection of a covering of dead and living scales, leaves, or leaf sheaths. The class is marked by great variety in the development of the vegetative shoots. Numerous cryptogams are to be counted among the hemicryptophytes.

1. Hemicryptophyta thallosa (attached thalloid plants): spreading mats of algae or fungi, closely attached to the substratum. They are filamentous, sod-forming, crustose, clump forming, or jelly-like. They include:
   a. Attached algae: such as the epilithic forms appearing as ink lines on limestone rocks, the green coverings on bark (*Pleurococcus*, *Protococcus*), and gelatinous algae like *Nostoc*.[1]

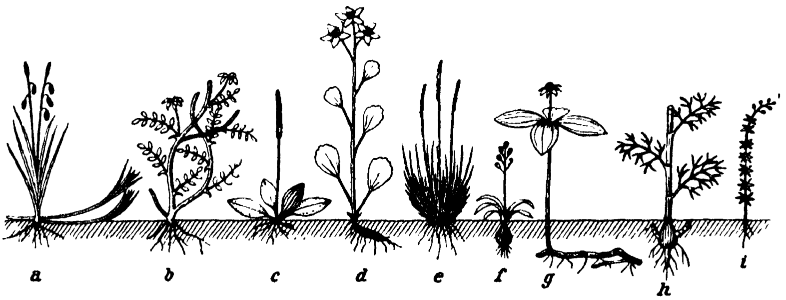

FIG. 148.—Types of life forms including chamaephytic creeping herbs (*a*) *Carex limosa;* hemicryptophytes (*b*-*e*); climbers (*b*) *Coronilla;* rosette plant (*c*); scapose plant (*d*); tufted plant (*e*); bulb geophyte (*f*); rhizome geophyte (*g*); tuber geophyte (*h*); and therophyte (*i*).

   b. Crustose lichens: such as *Acarospora* and *Opegrapha*.
   c. Thalloid bryophytes: liverworts, such as *Marchantia*, *Pellia*, *Clevea*, and *Grimaldia*.
2. Hemicryptophyta radicantia[2] (rooted hemicryptophytes).
   a. Hemicryptophyta caespitosa (tussock plants): with renewal buds surrounded and protected by a thick strawlike cover of old leaf sheaths. Tussock plants are common in moor regions and especially in the north and in mountains above the timber line, where tussock species of *Festuca*, *Sesleria*, *Carex*, and *Nardus* take an important part in the sod and soil formation of the alpine levels of mountains. *Carex elata*, with huge tussocks, up to one meter high and equally wide, is a main cause of land formation in our ponds and lakes. Giant tussocks are formed by *Poa foliosa* in New Zealand and by *P. flabellata* in South Georgia and upon the Falkland Islands.
   b. Hemicryptophyta rosulata (rosette plants): mostly low herbs with radical leaves arranged in a rosette and a leafless stalk, which bears the flowers. Species of *Fragaria*, *Viola*, *Primula*, *Gentiana*, and *Bellis* are found among

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[1] Algae whose ramifications enter the substratum (*Trentepohlia*, etc.) occupy a transitional stage.

[2] May be designated as Euhemicryptophytes.

these. Rosette plants are distributed over the temperate zones of the earth but also extend to the subtropics in considerable numbers.

c. Hemicryptophyta scaposa (scapose plants): mostly tall herbs, rarely grasses, usually with a solid taproot and with a more or less leafy stalk. The bottom rosette of leaves may be lacking as in *Thalictrum*, *Hypericum*, *Onobrychis*, *Epilobium*, and *Gentiana* or present as in *Ranunculus*, *Geranium*, *Campanula*, and *Phyteuma*. Many of the common meadow and woodland plants of Eurasia and North America are scapose plants.

d. Hemicryptophyta scandentia (climbing plants): hardy plants with annual climbing stems and renewal buds at the base. They are especially common in the warmer parts of the temperate zone and include species of *Convolvulus*, *Astragalus*, *Vicia*, and *Lathyrus*.

VIII. CHAMAEPHYTES (surface plants): with renewal buds above the surface of the earth; the plants enjoy only such protection as is afforded by the plant itself, either through protective mechanisms on the bud or by dense growth or by dead shoots. Important subgroups are:

1. Bryochamaephyta reptantia (carpet mosses): creeping carpet mosses such as *Hypnum*, *Hylocomium*, and *Leucodon*, which lie loosely upon the substratum and often form large beds.
2. Chamaephyta lichenosa (fruticose lichens): lichens, whose thalli often reach a height of 10 cm. and more, distributed as independent forms more especially in regions with cold winters, where they cover large areas either on forest soils or in open country. They are sensitive to changes in the moisture of the air, but in general they can bear low temperatures and severe wind without much harm. E. Frey (1922, p. 111) distinguishes three forms: (1) the Cetraria form (*C. islandica*, *C. nivalis*, *C. cucullata*, *Ramalina strepsilis*); (2) the Cladina form (*Cladonia rangiferina*, *C. alpestris*, *C. silvatica*, *Alectoria ochroleuca*); (3) the Usnea form (*Thamnolia vermicularis*). In humid regions Bryochamaephytes and Chamaephyta lichenosa frequently live epiphytically.
3. Chamaephyta reptantia (creeping herbs) (Fig. 148 *a*): herbaceous plants with creeping or ascending shoots, which survive the unfavorable season and bear the renewal buds. These actively creeping herbs such as *Trifolium repens*, *Thymus serpyllum*, *Veronica officinalis*, and *Linnaea borealis* often send out roots, a phenomenon which rarely occurs in the passively creeping, negatively geotrophic forms such as *Carex limosa*, *C. chordorrhiza*, *Cerastium latifolium*, *C. strictum*, *C. tomentosum*, and *Stellaria holostea*. Within a subform are to be classed the ascending creeping grasses of subtropic regions (*Brachypodium ramosum*, *Oryzopsis*) whose perennating shoots, 19 to 20 cm. high and sometimes higher, carry the plant through the unfavorable season. These sometimes develop into lianas.
4. Chamaephyta succulenta (leaf succulents): succulent-leaf perennials with water-storing tissues, which enable them to weather continued dryness. They are especially characteristic of arid climates, xeric habitats, rock, rubble, and sand substrata. The genera *Sedum*, *Umbilicus*, and *Sempervivum* offer numerous representatives of this group.
5. Chamaephyta pulvinata (cushion plants): with negatively geotrophic and densely crowded shoots so that typical cushions resemble a shield with upraised center. The center of the cushion (polsters) filled with

dead leaves and drifted dust, often traversed by tiny roots, holds water very well and thus reduces the danger of drying out. Cushion plants house a rich aggregate of minute animals and also serve as a rooting place for many hemicryptophytes. Cushion plants are xerophytes with numerous xeric adaptations (*cf.* especially Schröter, 1926; Hauri and Schröter, 1914). They can also withstand low temperatures and violent winds and are therefore adapted for the occupation of climatically unfavorable habitats in high mountains, in the arctic and antarctic regions, as well as in deserts. Typical examples are species of *Anabasis*, *Minuartia*, *Saxifraga*, and *Androsace* and flat cushions such as *Draba aizoides*, *M. sedoides*, and *Silene acaulis* (Fig. 149). The round, woody cushions (*Luftkugelkissen*), such as those of *Alyssum spinosum* and *Astragalus tragacantha*, are not to be classed with the cushion forms, because of the lignified shoots, but rather among the semishrubs and nanophanerophytes.

FIG. 149.—Desert-like steppe with globular cushions of *Anabasis aretioides* near Ain Chair, southern Algeria. (*Photo by Daguin.*)

A special group is presented by the mosses (*Grimmia* form), which appear as rock pioneers; and by the turf mosses, with their flat cushions (*Polytrichum* form). Numerous bog mosses must be classed with the Polytrichum form (*Philonotis*, *Pohlia*, *Bryum* species, and others). They are found in the cold and temperate zones.

6. Chamaephyta sphagnoidea (bog mosses): mostly oligotrophic species of *Sphagnum* with unlimited growth. They are dependent upon high humidity and precipitation and are therefore entirely lacking in arid regions. On the other hand, they advance far into the subarctic.

7. Chamaephyta graminidea (hard grasses): permanently assimilating, tall, tussock grasses and pseudo-grasses such as *Stipa tenacissima* and *Lygaeum spartum*.
8. Chamaephyta velantia (trailing shrubs, Fig. 150): creeping shrubs and semishrubs of the cold climates often carpeting the soil. The trailing shrubs (*Spalierstraücher*) utilize the soil warmth and defy the onslaught of wind by tightly clinging to the ground. In part they are evergreens like *Dryas*, *Loiseleuria*, *Teucrium montanum*, *Globularia cordifolia*, and *G. nana* and in part deciduous like *Salix retusa*, *S. reticulata*, and *Rhamnus pumila*.

FIG. 150.—Trailing shrubs. *Loiseleuria procumbens*, as pioneer in the Alps. (*Photo by Heller.*)

9. Chamaephyta suffrutescentia (semishrubs): especially common in the dry, warm regions of the subtropics. While the upper part of the shoots dries up, the lower parts remain alive and bear the renewal buds. The regions with Mediterranean climate especially rich in semishrubs are: southern Europe, northern Africa, western Asia, southwestern Australia, Cape Colony, and California.

IX. PHANEROPHYTES (aerial plants): especially trees and shrubs, bearing their renewal buds upon upright shoots at least 25 to 30 cm. high and therefore more exposed to unfavorable weather conditions than any of the previously mentioned life forms. Their center of distribution lies in the tropics and subtropics. The more northern phanerophytes are characterized by special bud protection, or they make use of the protection of snow by means of low growth. Their resistance to cold is to a large extent due to properties of their protoplasm.

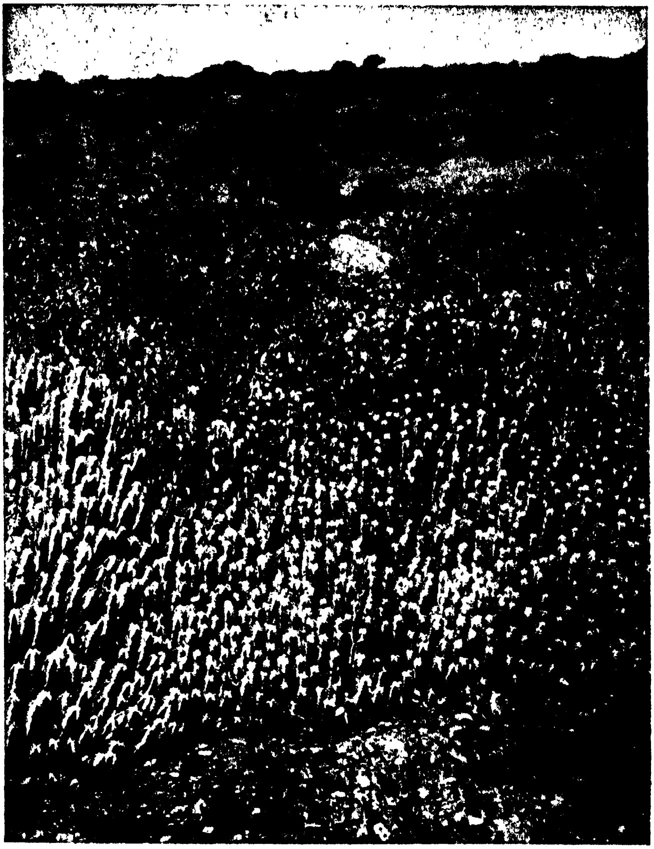

FIG. 151.—A cactoid euphorbia in the *Euphorbia resinifera-Acacia gumifera* scrub at the foot of the Great Atlas, Morocco, 800 m. (*Photo by Maire.*)

Among the numerous forms of phanerophytes Raunkiaer (1905) stresses 13 main groups, based upon height of plant, duration of foliage, and bud protection. To these are added the succulents and herbaceous epiphytes. For greater simplicity the 13 groups are reduced to the following 5:

1. Nanophanerophyta (shrubs): renewal buds about 0.25 to 2 m. aboveground; a most varied group with many subdivisions. Important structures that may be used as the bases of further classification are: foliage, evergreen or deciduous; leaf structure, sclerophyll, needle leaf or rolled leaf; leaf size,

leptophylls up to 25 sq. mm.; nanophylls up to 225 sq. mm.; microphylls up to 2,025 sq. mm.; mesophylls up to 18,225 sq. mm.; macrophylls up to 164,025 sq. mm.; and megaphylls larger than macrophylls (see Fuller and Bakke, 1918).

2. Macrophanerophyta (trees): renewal buds lie more than 2 m. aboveground. Raunkiaer (1918) distinguishes three size classes, but since the climatic difference between 30 cm. and 2 m. above the soil is much greater than between 6, 16, or 25 m., it seems justifiable to combine them. As in the case of the shrubs, a subclassification may be made.
3. Phanerophyta succulenta (stem succulents) (Fig. 151): characterized by the lack of leaves and fleshy, slightly lignified water-storage tissues. They are excellently adapted to steppe and desert conditions and actually inhabit chiefly the desert regions of the earth, reaching their culmination in the Cactaceae of North and South America. Europe has only a few representatives in the Mediterranean genus *Caralluma* and some introduced cacti. In north Africa there are a few succulent Euphorbias such as *E. resinifera*, *E. beaumierana*, *E. echinus*, and a few Compositae of the genus *Kleinia*. Winkler (1910) distinguishes:
   - *a.* Cactoid forms.
   - *b.* Barrel-shaped stems (Bombaceae, Sterculiaceae).
   - *c.* Fleshy stems (*Sarcocaulon*, *Pelargonium*).
   - *d.* Massive succulents (*Testudinaria*, *Adenia globosa*, etc.).
4. Phanerophyta herbaceae (herbaceous stems): characteristic of the moist, warm, equatorial regions; with the size of trees or shrubs they combine slightly lignified, herblike, and therefore tender aerial shoots, usually large leaves, and naked buds. They seem to thrive especially well under the protection of higher trees. This group includes species of *Begonia*, Euphorbiaceae, *Musa*, *Impatiens*, *Piper*, etc.
5. Phanerophyta scandentia (lianas): climbing plants whose renewal buds pass the unfavorable season high above the ground. The annual leaf and shoot climbers which die off every winter to the ground like *Bryonia* and *Humulus* belong to the hemicryptophytes and therophytes. The true lianas, woody plants which grow up to the light by the aid of various supports, are characteristic of the tropical virgin forest. They decrease in number with distance from the equator. Only a few of them reach the cold-temperate zone, such as *Clematis*, *Hedera* and *Lonicera*.

X. EPIPHYTA ARBORICOLA (tree epiphytes): highly specialized independent phanerophytes. They settle upon trunks and branches and live upon the food substances collected between the clefts and angles of the bark. Like the lianas, the higher epiphytes reach their fullest development in the humid tropical forest. In the tropical forest of Barro Colorado Island the epiphytes and lianas constitute respectively 10.4 and 15.7 per cent of all vascular plants, and hemiepiphytes are frequent (Kenoyer, 1929). In the temperate zone they are represented only by the woody hemiparasites (*Viscum*, *Loranthus*) and by the so called occasional epiphytes. A number of ecological subdivisions may be distinguished. Besides the semiparasitic epiphytes referred to above, there are: stem-tuber epiphytes (*Myrmecodia*, *Bolbophyllum*); humus-collecting plants with clustered roots (*Platycerium*, *Anthurium*); and plants with aerial roots (*Taeniophyllum zollingeri*, *Angraecum funale*, etc.).

Adaptability of Life Forms.—The leading idea of Raunkiaer's system of life forms—the adaptation of plants to the unfavorable season—requires the use of epharmonic adaptations for purposes of classification. The life forms must reflect, as truly as possible, the prevailing conditions of life. If this assumption is correct, then considerable changes in the conditions of life must entail also changes in the grouping of life forms.

As far back as Schloesing (1869), it was proved that tobacco plants grown in moist and in dry air showed very marked chemical differences.

TABLE 33.—PERCENTAGE COMPOSITION OF TOBACCO GROWN IN MOIST AND IN DRY AIR

Composition	In moist air	In dry air
Cellulose	5.4	8.7
Starch	19.3	1.0

This seems to show that moisture favors the production of starch. Dryness, on the other hand, increases the amount of woody supporting tissue. This agrees with common observation. A decreased water supply causes, according to MacDougal and Spohr (1918), a transformation of the polysaccharides into anhydride, that is, supporting tissue, and so a xeromorphic structure results. In succulents the conversion of the polysaccharides into mucous pentosans leads to succulence, which is also interpreted as an adaptation to dryness.

The influence of habitat conditions upon periodicity (duration of the development and function of the individual organs) as well as upon external and internal structure of plants is well known. We must here forego the opportunity to restate the anatomical morphological adaptive phenomena of plants, which are dealt with very thoroughly in all handbooks of plant geography (see also pp. 101, 125).

From the facts cited above it follows that the characteristics used in the delimitation of life forms are influenced by various external factors. They are predominantly phenotypical characteristics. This explains why one and the same species may belong to different classes of life forms under varying climatic conditions. Therophytes assume occasionally a hemicryptophytic form in cold climates (*Poa annua*, *Viola tricolor* and others). Chamaephytes may become nanophanerophytes (*Coronilla minima*, *Fumana*) when grown under subtropical conditions, while phanerophytes in the high mountains are often reduced to the chamaephyte form, and moist, warm regions favor the growth of lianas in various classes of life forms.

Since a single set of characteristics may be changeable or phenotypic in one systematic group, and unchanging or genotypic in another, it is impossible to separate the sets of characteristics absolutely. It is certain that numerous functionally important morphological characters which are used in Raunkiaer's classification of life forms are firmly fixed by heredity. These permanent genotypic adaptations may have arisen in the past by natural selection, under conditions wholly different from those of today. Their occurrence under definite climatic or edaphic conditions leads to the conclusion that they are in harmony with these conditions but not that they owe their origin to them.

Life forms cannot, accordingly, be considered as the unequivocal and direct answer of living things to dominant external conditions. Rather they represent a shaping of the more or less fixed phylogenetic basis in response to the particular habitat.

Life Forms in Plant Geography.—Raunkiaer originally intended his life forms to be used only in the ecological characterization of definite climatic regions, in the description of plant climates. For this purpose he determined the proportion of each life form in the flora of the world as a whole, and, arranging classes in a manner somewhat analogous to the arrangement of the colors of the spectrum, he designated the result a "normal biological spectrum."

Five of the classes are thought to be most significant and are designated by an appropriate letter here shown following the name. These classes are phanerophytes (F); chamaephytes (Ch); hemicryptophytes (H); geophytes (G) (or cryptophytes); and therophytes (Th). The biological spectra for the world as a whole (the normal spectrum) and for various typical areas are shown in the following table:

TABLE 34.—BIOLOGICAL SPECTRA ACCORDING TO RAUNKIAER

Region	F	Ch	H	G	Th
Normal spectrum	46	9	26	6	13
Central Switzerland	10	5	50	15	20
Paris basin	8	6.5	51.5	25	9
Switzerland, high Alps	0	24.5	68	4	3.5
Spitzbergen	1	22	60	15	2
Northern Africa	9	14	19	8	50
Death Valley, California	26	7	18	7	42
Seychelles	61	6	12	5	16
Connecticut	15	2	49	22	12

Central Europe lies in the midst of the hemicryptophyte region of the northern hemisphere; that is, hemicryptophytes exceed in number of species all other life forms. Central Switzerland, between lakes Geneva and Constance, with 1,700 seed plants, may be taken as typical of such a hemicryptophyte climate in Europe (Table 34); and with it may be compared Connecticut, in North America, with 1,400 species (Ennis, 1928). In both areas ruderal immigrants have increased the number of therophytes. The spectrum of the exclusively native species of the Paris basin also shows a hemicryptophyte climate, according to Allorge (1922).

In the north and in the high Alps along with the hemicryptophytes the chamaephytes come more and more into their own. Thus Spitzbergen has 22 per cent chamaephytes but only 2 per cent therophytes (*Koenigia islandica* and *Gentiana tenella*). The summer heat is not sufficient to ripen seed every year, and young seedlings are likely to be killed by frost. The spectrum of the life forms of the 260 flowering plants which make up the flora above the snow line (2,600 to 3,100 m.) in the Alps shows somewhat similar conditions (Table 34). At an altitude of 3,340 m. the percentage of chamaephytes has risen to 31.

The spectra of warm, dry regions are radically different from these, as shown by examples given by Raunkiaer. The flora of Cyrenaika in northern Africa, and of Death Valley, California, show comparable spectra. In contrast with the paucity of phanerophytes in these arid regions are the conditions in the rainy tropics, as exemplified by the spectrum from the Seychelles (Table 34).

Thus the spectra of life forms give a direct impression of the climatic peculiarities of the various phytogeographic regions of the earth. Regions with similar biological spectra may be joined by a line, the so-called "isobiochore."

Ecological Significance of Life Forms.—Raunkiaer's life forms in their present arrangement are of use also in the broad ecological characterization of plant communities. Without going as far as Vahl (1913), Gams (1918, 1927), and other writers, who base the classification and nomenclature of plant communities upon life forms,[1] it is at least desirable to give them a definite place along with the floristic differentiation and delimitation of communities. This use is particularly desirable in distant parts of the earth where the flora is little known. On a journey of investigation many species cannot be identified immediately, but they may be classified according to life forms, and thus a preliminary picture of the ecological character of the plant communities may be obtained. Life forms should not be neglected in a

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[1] Vahl (1913) speaks of Chamaephytae, Cryptophytae, etc.

thorough monographic presentation of individual plant communities. The biological spectrum of an association sometimes reveals interesting and unsuspected ecological relations. In the warm regions of the earth it may become necessary to make subdivisions of the life-form groups. In doing this, care should be taken to make the subdivisions in harmony with Raunkiaer's general outline.

Each plant community consists of a definite group of life forms. Each habitat favors certain groups of life forms and almost excludes others. The more extreme the habitat conditions the sharper the selection and the more pronounced are the ecological characteristics of the life forms. For this reason biological spectra for decidedly pioneer associations best reflect the ecological relations of the habitat.

The Loiseleurietum cetrariosum, an exceedingly wind-resistant dwarf-shrub community of snowless ridges in the Alps, is composed of about two-thirds chamaephytes, mostly fruticose lichens, and one-third hemicryptophytes. The rock-cleft association of the Androsacetum helveticae is similarly resistant to wind and frost with 50 per cent chamaephytes (45 per cent Ch. pulvinata, 5 per cent Ch. velantia), 45 per cent hemicryptophytes (30 per cent H. rosulata, 15 per cent H. caespitosa), and 5 per cent rhizome geophytes. The adjoining snow-protected Curvuletum, on the other hand, contains 64 per cent hemicryptophytes, 30 per cent chamaephytes, 4.5 per cent geophytes, and 1.5 per cent therophytes.

If the biological spectra of two or more regions are closely similar, one may assume that growth conditions are similar. A comparison of the spectra of the Agrostidetum tenuis of the south Cévennes (44° N.) and of the Trisetetum flavescentis of the Schanfigg (47° N.) proves that these two rich meadow communities are nearly ecologically equivalent, as shown by the similarity of their biological spectra (Table 35), in spite of their very considerable floristic differences.

TABLE 35.—BIOLOGICAL SPECTRA OF TWO RICH MEADOW ASSOCIATIONS OF THE ARRHENATHERION ELATIORIS AND OF THE FAGETUM OF THE SOUTH CÉVENNES

Association	F	Ch	H	G	Th
Agrostidetum of the south Cévennes	0	3	81	8	8
Trisetetum of the Schanfigg	0	4.5	89	4.5	2
Fagetum of the south Cévennes	2	4	51.5	40.5	2

The above percentage of types in the biological spectra can give only a very vague idea of the total physiognomy of a community, unless accompanied by records of mass and cover of the species. In the biological spectrum of the primitive beech wood of the south Cévennes (Table 35) *Fagus* plays only a most insignificant rôle (2 per cent), although it is pronouncedly dominant over all other species; in fact, it directly determines the entire association, which is strikingly characterized by the large number of geophytes. The loose, fertile upper-soil horizon favors the development of the rhizome geophytes, while considerable shading hinders the growth of therophytes. The significance of the phanerophytes appears in its proper light only when, along with life forms, the structural details of the community, such as number, mass, and layering, are duly considered (see Chap. III).

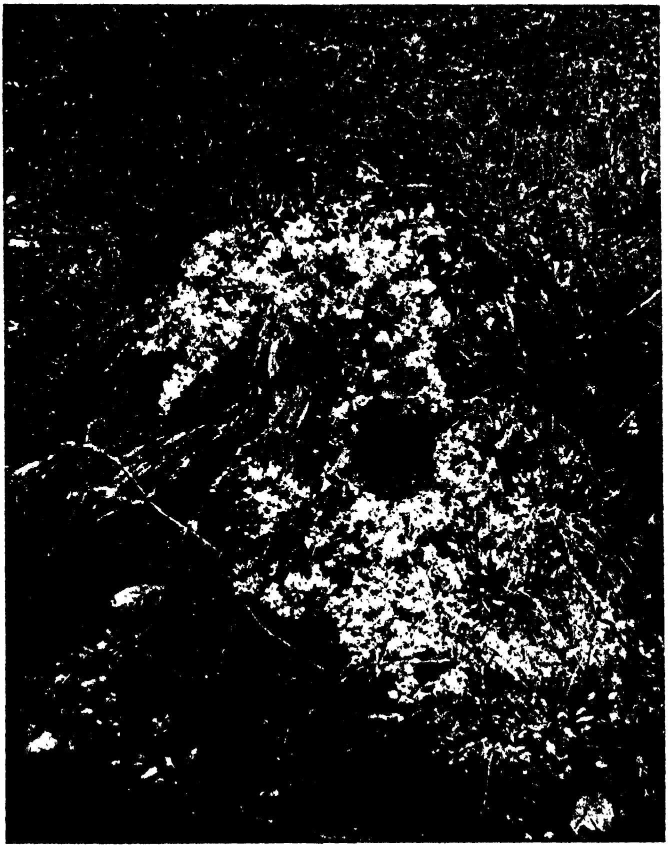

FIG. 152.—Fruticose lichen association on a tree stump in fir woods (*Cladonia alpestris, C. silvatica, Cetraria islandica*). (*Photo by Heller.*)

Synecological Units.—The general physiognomy of communities, based upon life forms, leads to the recognition of more or less uniform, larger and smaller physiognomic units of vegetation (formations, synusiae) which are entirely independent of floristic composition.

Synusia.—By "synusia" is meant a natural community of species belonging to the same life-form groups and with uniform ecological requirements. A cover of crustose lichens, a pure carpet of moss or of dwarf shrubs, the tree layer of a fir stand are ecological synusiae.

In the simplest case the association may coincide with a synusia (fruticose lichen carpet, algal cover) (Fig. 152).

As a rule, however, an association includes several, and in the case of a forest association many, ecological synusiae. With advances in the organization of the community the number of snyusiae increases. On one and the same locality several synusiae may follow one another in the course of a season. These synusiae then correspond closely to the seasonal aspects of the association. The *Juncus capitatus-Isoetes duriaei* association of southern France includes a winter synusia of liverworts and a geophyte-therophyte synusia in the vernal aspect.

Formation.—The combination of two or more synusiae with uniform physiognomy and more or less uniform habitat requirements constitutes a "formation." The formation is entirely independent of floristic composition and may, therefore, occur anywhere under similar external conditions. It depends upon geographic factors only as far as they directly affect the climate. Externally closely corresponding formation in widely separated parts of the earth, with similar physiognomy and in similar climates, are called homologous. To illustrate, the Californian chaparral and the Mediterranean sclerophyll scrub are homologous formations; so also are the north African *Artemisia herba-alba,* the Aralo-Caspian *A. maritima* and *A. pauciflora,* and the *A. tridentata* steppe of the United States. Formations with similar physiognomy compose "groups of formations." These are arranged in classes, and the latter finally in "types of vegetation." The vegetational types of the earth have been used ever since Grisebach's time in the rough characterization of the various parts of the world. They cannot, however, be used as permanent bases in the nomenclature and taxonomy of plant communities, and it will be wise to use the terms "formation," "groups of formations," "vegetational types," etc., with caution in the field of plant sociology.

PART IV

SYNGENETICS

CHAPTER XIII

THE DEVELOPMENT OF COMMUNITIES

Syngenetics is concerned with the rise and decline of plant communities and seeks to discover the laws which regulate their succession. It endeavors to solve the problems of the origin, development, and transformation of plant communities. What has been the origin of a given community? What potentialities for development lie within it? What are the external factors which have influenced it? Whither do natural processes lead in the development of the vegetation of a climatically uniform region?

Whereas formerly the vegetational changes of a given "topographical locality" was the central point of the investigation (Rübel, 1913, p. 903; Du Rietz, 1921), today the leading emphasis is being more and more directed to the evolution of the community itself. The principle of development is coming to replace the purely formal study of succession.

Historical.—Kerner was the real founder of the doctrine of the development of communities. "What a thrill there is in the study of the developmental processes of each society and in following its origin, maturity, and decline," he writes enthusiastically in his "Pflanzenleben der Donauländer" (1863, p. 12). Warming (1895) first called attention to the universality of vegetational change. The honor of grasping the full meaning of the dynamics of vegetation belongs to the North American scholars Cowles and Clements. The former in 1899 laid the foundation of the dynamic concept of vegetation which still prevails in the British and American schools of plant ecology. Clements sought to discover the great principles common to vegetational development throughout the world and to arrange them systematically (1916). He worked out methods for investigating the dynamic processes and sought to place the classification of communities on a dynamogenetic foundation. He has been criticized (Gams, 1918; Lüdi, 1921) for neglecting the static features of vegetation. His dynamics are often hypothetical, and the static social units are indispensable as a foundation for any study of vegetation.

The recent textbook of Weaver and Clements (1929) has devoted several pages to the elucidation of a purely deductive classification based entirely on the concept of the "climax formation," a concept which has been much emphasized by the two authors. It must not be forgotten, however, that the areas today occupied by climax stages have become greatly reduced and sometimes have become almost completely obliterated. The developmental stages, on the contrary, still occupy immense areas. It seems therefore unfortunate to burden terminology with the introduction of special terminations to distinguish stages which appear to be climax (-ation in association) and stages which are developmental (-ies in associes).

The principal criticism, however, to be directed against the Clements-Weaver system is that it makes no adequate provision for a graduated scale for designating vegetational units of different degrees. The climax formation embraces several climax communities (in our sense) to which are applied the term "association." This term thus acquires a meaning quite different from that given it by the Brussels Congress (1910) and from that in which it is used by the Montpellier school. It is, moreover, very poorly circumscribed, a fact which may perhaps explain why no American botanist has given a detailed tabular analysis of a single association. This unit is large and difficult to grasp, and the subordinate units are separated from it by a veritable hiatus. Any unit corresponding to our association is lacking. The "consociations" and "societies" of Clements and Weaver are based entirely upon the dominance of certain species; they are thus quite incapable of replacing our association in any system of classification. The "aspect societies," "families," and "colonies" of Clements and Weaver play very minor parts as systematic units. They are either concepts of periodicity or expressions of sociability.

It is therefore not surprising that no investigator has yet tried a detailed sociological description of any group of plant communities of a definite region or of an "association" delimited according to Clements' system. In an excellent paper, which may be considered a model of the Clements-Weaver school, Steiger (1930) has given a careful quantitative floristic and ecological study of a portion of the prairies. These valuable ecological data cannot, however, serve to individualize the sociological units.

This seems to furnish the best proof that the most exact ecological data remain sterile for sociological evaluations when assembled according to the system of Clements and Weaver.

From our present state of knowledge a few general laws may be deduced.

Early Colonization.—The first step in the development of vegetation is "migration." Next comes the establishment of the invading

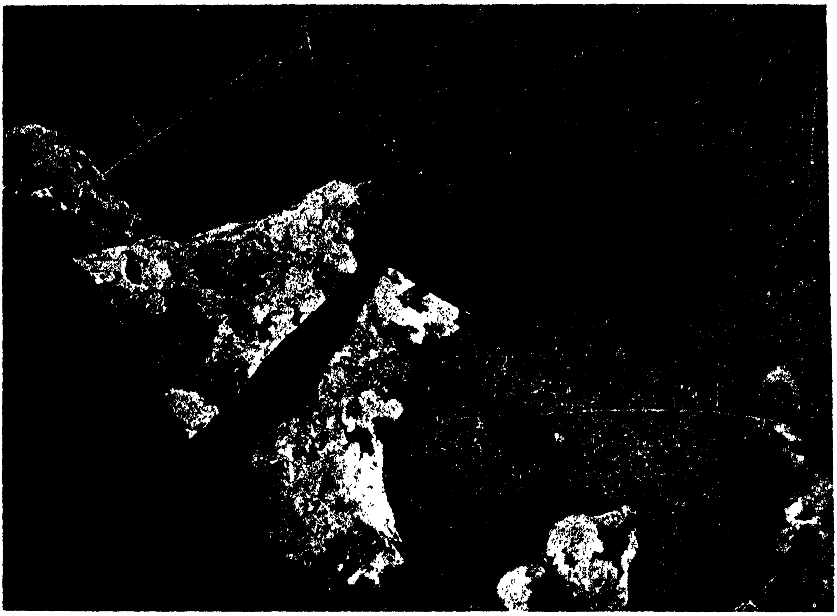

FIG. 153.—Lateral advance of the *Rhacomitrium lanuginosum* association upon basalt rubble near Dienne, Auvergne, 1,100 m. (*Photo by Uehlinger and Braun-Blanquet.*)

FIG. 154.—Centrifugal spreading and coalescence of plant cushions, *Astragalus tragacantha* on limestone rubble, Bonifacio, Corsica. (*Photo by Hoffmann-Grobéty.*)

species—"ecesis"—their arrangement in the new habitat, and finally their "competition."

The colonization of new unoccupied land by plant disseminules may be either by centrifugal or by marginal invasion. In the latter instance there is a closing in of surrounding vegetation, such as may be seen in mountains and elsewhere, where the first stage is determined by the neighboring vegetation (Figs. 153, 154). In case of centrifugal invasion where the distribution is by wind, water, or animals there appears at first a motley, but by no means accidental, mixture (Fig. 155).

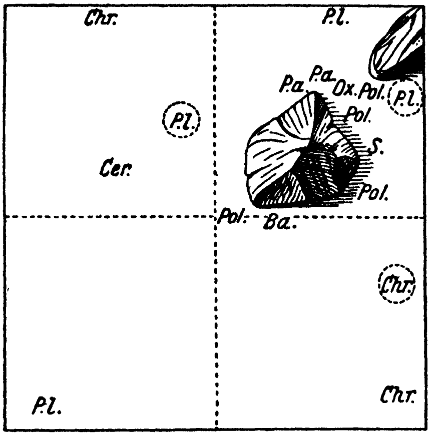

FIG. 155.—Initial phase of the Oxyrietum caused by scattering of seeds upon morainic soil on the Sesvenna Glacier at 2,700 m., 40 m. from the edge of the ice (1 sq. m.). *P. l.*, *Poa laxa*; *P. a.*, *Poa alpina*; *Ox.*, *Oxyria digyna*; *Pol.*, *Pohlia commutata*; *Cer.*, *Cerastium cerastoides*; *S.*, *Sesleria disticha* (sterile); *Chr.*, *Chrysanthemum alpinum*; *Ba.*, *Bartramia ityphylla*.

Assuming equal ecological fitness, the most favored plant colonists are the first arrivals, that is, species from neighboring areas and those with special facilities for distribution.

The conditions of the habitat determine whether or not there shall be at first a definite selection of species that are allowed to become established in the first stages of the community. The more extreme the habitat conditions the more relentlessly will seeds and early seedlings be weeded out. On exposed rocks and talus slopes of the Alps, on the tin soils of Germany, on strongly saline bottoms of lagoons only a limited number of species that are highly specialized can germinate and grow. They often form extensive, pure populations such as those of *Spartina*, *Salicornia*, and *Suaeda* on salt-marsh soil. On good soil in regions with numerous species the selection of species comes much later. Hence the motley communities of recent clearings, freshly exposed soil, abandoned fields, etc.

Usually the succession begins with the lowest organisms. But it is hazardous to attempt broad generalizations. Even trees may appear as first settlers, if the soil is good, and especially if some protection for the seedlings is available. *Salix caprea* and *Betula verrucosa* in central Europe follow directly after a forest fire. *Pinus mugho* establishes itself in the Alps directly upon naked, wholly plantless talus. The physicochemical factors of the habitats are selective in these first stages.

Soil bacteria and algae usually appear as the first plant community. *Microcoleus chthonoplastes* and *Lyngbya aestuarii*, as first invaders of dry salt marshes about the Mediterranean, form an algal crust before any seed plants gain a foothold. Similarly, *Zygogonium ericetorum* forms a thick, fibrous cover on the acid soil of fresh-water swamps. According to Treub, blue-green algae were the first plants to cover the naked slopes of pumice and ash on the island of Krakatao with a dark-green gelatinous coating.

Upon stumps there soon appears a luxuriant multiform saprophytic vegetation of low fungi and bacteria. On stumps of deciduous trees in southern Finland this initial stage includes species of *Endomyces*, *Saccharomycodes*, *Fusarium*, *Mucor*, and *Oidium* forming a distinct association. Later, algae such as *Nostoc* and *Chlorococcus* appear and are soon followed by scattered mosses and algae, forming the *Cladonia botrytis-Parmelia furfuracea* association (Krohn, 1924).

According to Van Oye (1924), the succession of epiphytes on the Javanese forest trees comprises three stages. There is first a pioneer association of Myxophyceae and *Trentepohlia*. This is followed by mosses, *Drymoglossum* and various Polypodiaceae, leading to the climax epiphytic association of ferns and orchids.

Lichens often come in first on resistant substrata, such as the bark of trees, wood, rock, gravel, and sand. Therophytes are pioneers on warm, porous soils of arid and semiarid regions. On the coarse morainal gravels of the high mountains of Central Europe hemicryptophytes and chamaephytes come first (Braun-Blanquet, 1926, p. 207). On finer moist gravel cushion mosses such as *Pohlia*, *Polytrichum*, and *Rhacomitrium canescens* precede. On the great basaltic blocks of the volcanic peaks of Auvergne and in the upper Rhone region, the carpet moss, *Rhacomitrium lanuginosum*, first spreads its silvery green tapestry (*cf.* Fig. 153). On the hard, wet clay of middle European swamps the rhizome geophyte *Tussilago farfara* plays an important rôle as pioneer colonizer. The erosion furrows and washouts in the Tertiary marls between the Rhone and the Aude are colonized by hemicryptophytes and shrubs, in spite of the enormously superior seed development of the abundant neighboring therophytes.

Birger (1906) had the opportunity to observe for many years the development of vegetation on a new island in Hjälmar lake (Sweden) caused by a fall in the water level. Four years after the change of level had occurred, 2 mosses and 113 phanerogams had become established. These included 40 individual trees belonging to five different species. Six years later there were 12 lichens, 18 mosses, and 184 phanerogams, of which 10 were trees. Twenty-two years after the change of level there were 32 lichens, 43 mosses, and 202 phanerogams, of which 14 were trees. The accompanying diagram (Fig. 156) gives the development of pioneer vegetation on newly exposed glacial soil in the Alps.

Development of Vegetation and Soil Formation.—There is an ultimate and intimate causal relation between the processes of soil formation and the development of vegetation. The forces operative in the early stages of soil formation causing the disintegration of the solid rock and the removal and deposition of the fine material by gravitation, wind, and water produce virgin soil. On this substratum is enacted the struggle of the plant communities.

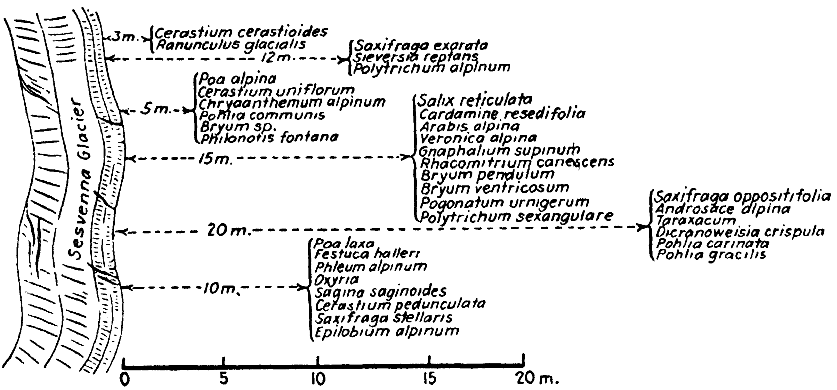

FIG. 156.—Appearance of pioneer species upon soil newly exposed by the Sesvenna Glacier, 2,700 m., Lower Engadine. (*After Braun-Blanquet and Jenny.*)

Living organisms then begin to play their parts, and the soil development is directed into definite channels. Penetrating roots and holdfasts disintegrate rock and earth; animals, too, cooperate in reducing the soil particles. Soil bacteria, fungi, and algae enter at an early period and by their activity assist the other vegetation in the formation of humus, effecting both chemical and physical changes in the soil.

Climatic factors influence the chemical composition of the soil more and more as it approaches maturity. Mineral salts are removed from certain layers and deposited in others (*cf.* p. 164). Since climatic processes proceed according to law, both soil formation and development of vegetation must ultimately be due to the prevailing climate.

The general climate of a region determines whether an accumulation of organic matter and nitrogen is possible and whether the upper layer of soil (root layer) is subject to increasing acidification or to an accumulation of salts. On this depends the whole course of the development of vegetation.

At the extremes, two principal developmental series may be distinguished: an acidophilous, with increasing acidity; and a basic, with the accumulation of soil salts.

In arid climates with scant precipitation and high evaporation the latter influence predominates and leads invariably to alkaline soils at maturity wherever the rain water cannot readily drain off. The high evaporation causes concentration of the soil solution in the upper parts of the soil. This concentration causes a speedy weeding out of the acidophilous species which are found in the first stages on raw silicious soils and sand. With increasing concentration of the soil salts all neutrophilous species give way, and even those basophiles which cannot endure high concentration of salts. The final stage is usually a halophytic shrub steppe or, less frequently, a scrub of deciduous small-leaved, broomlike, often spiny shrubs, such as *Acacia* and *Zizyphus* in north and central Africa, South America, and Australia; or succulents in South Africa and North America.

The opposite extreme of the developmental process is seen in the podsol regions of western and northern Europe, in the mountains of central Europe, and in northeastern North America. The heavy precipitation, coupled with high humidity (high N.S. quotient), greatly favors the accumulation of humus and the leaching of mineral salts in the upper layers of the soil (*cf.* p. 164 and Fig. 94).

In the first stages of rock weathering the soil solution is richer in OH ions and therefore less acid than in the later stages. This is true even in the case of non-calcareous silicate rocks such as granites, gneisses, and amphiboles. Basic raw soils in the podsol region can remain basic only where there is some interruption in the natural course of soil formation such as that due to soil movement through natural causes or human intervention or the addition or removal of soil particles by erosion. In the absence of such hindrances the development of vegetation, following in a general way the soil formation, proceeds in a manner to be described.

Alpine Regions.—The humus-forming power of the plant covering increases quite rapidly with decreasing temperature and increasing humidity. At alpine altitudes accumulation exceeds decay. Although we do not know the chemical composition of the decaying plant materials, we know that they are rich in organic acids and usually give an acid reaction. On calcareous substrata wind-blown dust and residual soil suffice at first to neutralize the acids. The result is a mild humus of deep-black color, of soft, sticky, and somewhat greasy consistency, with basic or neutral reaction. The *Carex firma* association or *C. mucronata* or *Sesleria coerulea* turf takes possession of such calcareous soils rich in humus. It withstands the wear of much rain and snow water. The abundant carbon dioxide of the adsorptively saturated humus leads to the formation of bicarbonates. Calcium and magnesium go into solution and are the more completely leached out as the humus is increased by additions of acid-forming litter from such tufted plants as *Elyna myosuroides* and *Agrostis alpina.* There results a deep, highly acid rendzina soil (pH 6.5 to 5.5).

The corresponding association in the Central Alps is the Elynetum on places briefly covered by snow or the *Festuca violacea-Trifolium thalii* association on areas with prolonged snow cover.

A decisive turning point is marked by the appearance of the decidedly acidophilous tufted *C. curvula,* which may occur at pH 6 but is sure to be present at pH 5.5 to 5.2. The humus-forming activity of this aggressive sedge increases the preponderance of hydrogen ions. Important changes of soil follow. The exchange of ions restricts the nutrient salts. The effect of humus upon dispersion and its action as a protective colloid become more prominent with increasing acidity. The sesquioxides and silicic acid, SiO_2, become soluble and sink to greater depths. With this begins the transformation of the rendzina into podsol. The acidophilous species now have a decided advantage over the neutrophiles and acidophiles. Their expansion can be followed step by step with the fall of the pH (p. 315). Whether the podsol is permanent or the soil development goes a step farther to a climax alpine humus, the development of vegetation always ends with

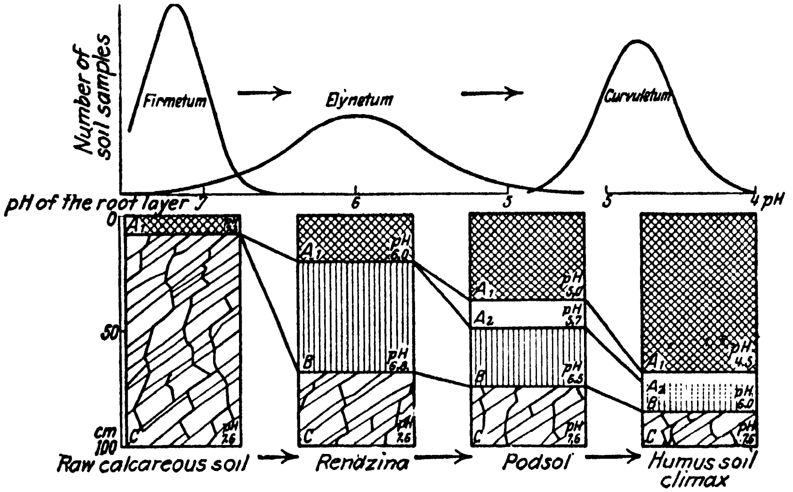

FIG. 157.—Soil formation and development of the vegetation upon limestone in high mountains (schematic). (*After Braun-Blanquet and Jenny.*)

the Caricion curvulae, the climax community of the alpine areas of the Central Alps (*cf.* Braun-Blanquet and Jenny., 1926, pp. 226–240).

The simplest form of this succession due to soil formation and the development of vegetation is graphically shown in Fig. 157.[1] The whole course of development, including soil formation, is to be regarded as irreversible.

The evolution of the soil and the development of vegetation follow a similar course in other mountain regions such as the Pyrenees, the Tatras, and the Colorado Rockies. It may be noted that the layer of humus accumulated in the climatic climax association of the Tatras and of the Alps is thicker than that of similar associations of the eastern Pyrenees or of the Colorado Rockies. In the Pyrenees the alpine climax is an association of *Festuca supina* and *C. membranacea,* which is less acid than the Curvuletum of the Alps or the Trifidi-Distichetum of the Tatras. In the Colorado Rockies the climax alpine stage is occupied by the Elynetum bellardii which appears to hold a position more comparable to the climax of the Pyrenees than to those of the Alps and the Tatras. The reason for these differences appears to be the greater evaporation and higher summer temperature (smaller N.S. quotient) in the Pyrenees and in the Rockies.

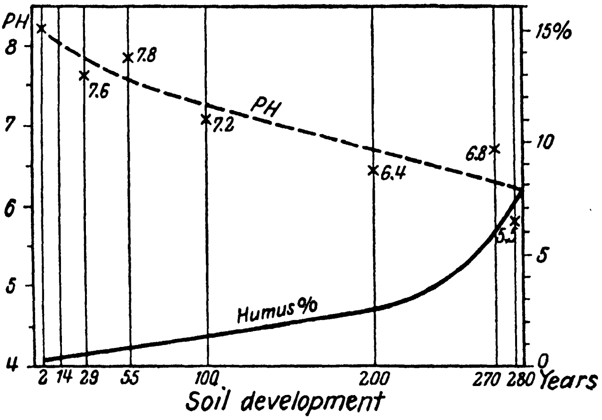

FIG. 158.—Humus accumulation and acidification of old dune soil at Southport, England, in the course of 300 years. (*After Salisbury.*)

Humid Regions of Europe.—It may be inferred that the laws of development of vegetation and soil established in the humid alpine region apply also to the humid regions of central, western, and northern Europe. In Sylene National Park (Norway) Christopherson (1925)

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[1] A somewhat different series, also leading to the Caricion curvulae, is shown in Table 36.

found the highest pH values on young soils with calciphilous plant societies. On the English coasts Salisbury (1925) has shown clearly the gradual acidifying of old dune soils and has expressed the belief that natural undisturbed soils "in this latitude tend to become more and more acid" (Fig. 158).

In the first stages of these dunes we find in abundance basophilous species such as *Carlina vulgaris, Euphorbia paralias, Senecio jacobaea, Gentiana campestris, G. amarella, Chlora perfoliata,* etc. In the later stages the basophiles disappear and *Calluna* becomes dominant. Similar changes occur on the dunes of Lake Michigan. The young dunes give a neutral or alkaline reaction; the older ones become somewhat acid with an abundance of *Vaccinium.*

Tüxen (1930) studied the climatic tendency toward podsolization in northwestern Germany and its relation to the development of vegetation. He concludes that, assuming the climate to remain constant, all the forest associations will become transformed into the Querceto-Betuletum, a decidedly acidophilous association. The forest succession proceeds as follows: Fagetum-hercynicum, calcicolous; Querceto-Carpinetum (two stages), basophilous; the climax Querceto-Betuletum.

In cool, humid climates the development of vegetation becomes essentially a struggle of the acidophilous against the neutrophilous and basophilous species, so that on originally similar substrata the acidophilous communities always indicate a more advanced maturity of soil than the basophilous. The distribution of the associations on the glacial gravel terraces of the Alpine foothills is similar: on the younger, lower terraces (Würm glaciation) basophilous and neutrophilous associations prevail; on the older, decalcified, high terraces (Riss glaciation) the acidophilous are found.

Deep-rooted trees are less dependent upon the changes due to soil formation than are other plants. In the struggle for supremacy among trees in the climax forest the decisive factors are climatic: temperature, precipitation, humidity, light.[1]

It is interesting to notice how rapidly the basophilous species are crowded out by the acidophilous under certain conditions on raw calcareous soils in the high Alps. In the initial phase of the snow-slide association of the Arabidetum coeruleae acidophiles are lacking and basophiles predominate over neutrophiles. In the terminal phase of the association the two groups of species are about balanced, or the

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[1] The seedlings of trees, however, are dependent upon the upper layer of soil. This layer is therefore a determining factor in the development of natural vegetation under all conditions.

acidophilous predominate. The curves in Fig. 159, based on 10 different stands in Grisons and Tirol, show clearly the continual decrease of basophilous and corresponding increase of acidophilous species. The curves cross in the terminal phase.

In the course of a succession the individual species of the association play very different rôles. *Salix herbacea*, a species of high dynamogenetic importance, is prominent as a maker and collector of humus.

1. Causative (Dynamogenetic) Value of Species (Constructiveness).—The earlier students of succession—Kerner, Gremblich, Fliche—long ago recognized the supreme importance of certain plants in initiating and promoting vegetational changes but did not draw any far-reaching conclusions therefrom. Clements has held that the plant community is an organic, closely organized, collectively reacting unit. If this idea is to be followed, the consideration of the differing specific constructiveness of each species has no value. Indeed, Clements in a flight of imagination compares the climax community to an organism which has birth, growth, maturity, and death. Du Rietz also remarks (1921, p. 202):

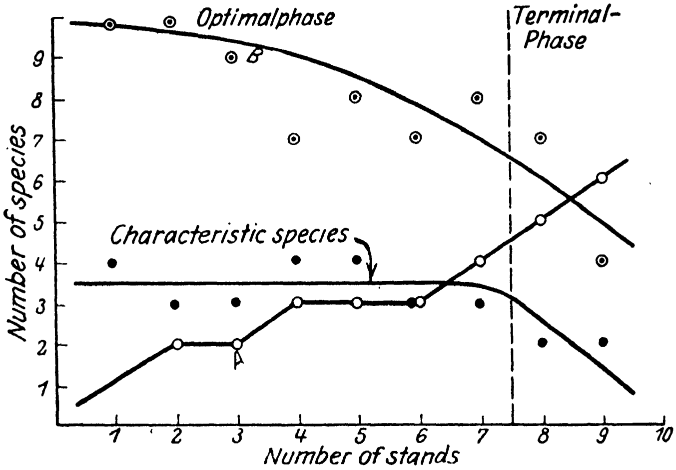


FIG. 159.—Increase of the acidophilous (*A*) and decrease of the basophilous (*B*) species; also characteristic species curve in the course of development of the Arabidetum coeruleae. Each dot or circle represents an individual stand. (*After Braun-Blanquet and Jenny.*)

> . . . dass eine ganze Artengruppe aus irgendwelchem Anlass eine im wesentlichen übereinstimmende Konkurrenzfähigkeit erhalten hat, mit anderen Worten, dass die Arten auf die Veränderungen der ökologischen Faktoren nicht einzeln, sondern gemeinsam reagieren.

The facts show these opinions to be wholly incorrect. The ecological factors within one and the same association may often vary, and the individual species react individually to these changes within the association. If this were not the case, one association would be immediately and completely replaced by another. Experimental studies of succession in the Swiss National Park and elsewhere show, however, that the replacement takes place gradually. A sudden and pronounced overturn of species occurs only when through external influences or by means of certain species of great dynamogenetic vigor the life conditions, and thereby the competitive relations, of the habitat are fundamentally changed. If this happens, all species with slight ecological plasticity succumb to the change in the habitat; at the same time, many others remain as before. Thus a similar degree of aggressiveness of the species has been assumed, when in reality we have a profound ecological revolution in the conditions of the habitat. This revolution is often due directly or indirectly to human agencies, but it may be due to natural causes, such as changes in the level of ground water, splashing or overflowing with salt water, influx of calcareous water, etc.

Species which greatly influence the habitat, or in other words species of high constructiveness, are mostly determinative also for the existence of numerous satellites. Their appearance or disappearance has as a necessary consequence the exchange of many companion species.

Expression of Constructiveness.—Pavillard (1919, 1920) first energetically urged the examination of the causative value of species. He distinguished in plant communities constructive, conserving, indifferent, and destructive species. These most important dynamogenetic phenomena may be expressed by the following signs:

↑ = constructive
◨ = conserving
⊡ = consolidating
□ = neutral
↓ = destructive

■ = conserving and consolidating

$\overset{\uparrow}{\blacksquare}$ = constructive, conserving, and consolidating

Great constructive or destructive activity is expressed by underscoring the appropriate sign.

Constructiveness is a character which expresses itself sociologically, as distinguished from aggressiveness, which, being more autecological, helps the plant in carrying on and winning in the struggle for existence. Very persistent species often are not of genetic value in the beginnings of the association to which they belong. Examples are seen in many annual dry grassland communities as *Carex tomentosa* in the Molinietum caricetosum tomentosae, and *Pinus halepensis* in the *Erica multiflora* facies of the *Rosmarinus-Lithspermum fruticosum* association. The tenacious *Genista scorpius* and *Juniperus oxycedrus* hold their ground with unyielding persistence against fire, pasturing, and erosion, and yet neither shrub is ever important in building up the community.

Trees are often destructive to a preceding community by changing the light, the aeration of soil, or the moisture conditions. On the other hand, they have great constructive value wherever, in their shade, special communities develop and persist. The primeval beech woods of the Cévennes, the Auvergne, the Pyrenees, and Corsica present combinations of companion species whose existence is wholly conditioned by the beech-tree layer (Braun-Blanquet, 1915). The same is true of the *Picea excelsa* forests of the Alps and the Tatra (Beger, 1922; Szafer *et al.*, 1923; Dutoit, 1923).

Many turf societies are dynamically independent of the dominant forest trees in such communities as the subalpine larch woods, the northern birch woods, and the Mediterranean *Pinus halepensis* forest, where the trees cast little shade and form little raw humus. Thus there are all transitions from direct causality to complete independence of ground vegetation in the forest. The relation of *Pinus halepensis* to the association of *Rosmarinus* and *Lithospermum fruticosum* (*Erica multiflora* facies) west of the Rhone is noteworthy. This association is identical both under a tree layer of *Pinus* and in the open but is continually threatened, especially on steep slopes, with being completely washed away by torrents of rain (*cf.* Fig. 65). A roof of pine branches benefits the shrub association by affording partial shelter from torrents of rain and by modifying the wind and the temperature. The normal shrub society is therefore better protected in the forest than in the open, as long as the light is not too much reduced by the trees. This could happen only under very special conditions in the *P. halepensis* forest. Thus the pine, while certainly not constructive, and only rarely destructive, is decidedly conserving and consolidating for the *Rosmarinus-L. fruticosum* association.

Further, the constructiveness of a species may change in the course of the development of an association. Certain species which are important constructive members of the early stages are rare or absent in the optimum phase. An example may be seen in *Dryas* and *Festuca* in the Seslerieto-Semperviretum. Other species appear only in the optimum phase. The appearance and disappearance of important socially constructive species may be used profitably for delimiting the individual stages of a succession. For fixing the time limits of successive associations, however, the exchange in the characteristic combination of species is conclusive.

The naming of the individual stages of a succession should be according to species of high constructiveness. We speak therefore of a

Prunus, an *Agrostis alba*, a *Brachypodium pinnatum* stage, designated by dominance of the species named. One and the same species may take part and form stages in various (not homologous) developmental series. Thus, *B. pinnatum* is constructive in the growing Xerobrometum of the limestone hills of the upper Rhine (Issler), while Tansley (1925) considers it destructive for the *Bromus erectus-Festuca ovina* association of southern England, and Scherrer (1922) and Koch (1926) point out its decidedly destructive activity in the Molinietum of northern Switzerland. The arctic-alpine creeping shrub *Dryas octopetala* is of great constructive importance not only in the north but also in countless alpine turf communities in the Carpathian, Pyrenees, and Rocky Mountains. In Alaska it is replaced by the related *D. drummondii*, a pioneer of the porous morainal soils in the neighborhood

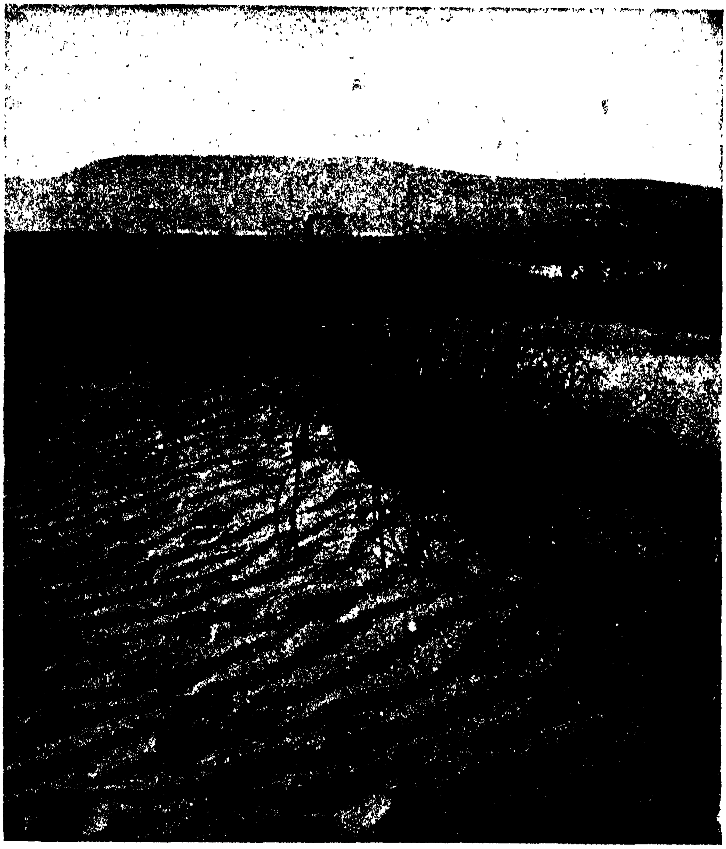


FIG. 160.—*Cyperus capitatus*, initial stage stabilizing a dune near Agadir. (*Photo by Maire.*)

of Glacier Bay (Cooper, 1923). *Rhacomitrium canescens* takes the same important place in the successional series on the fine-grained glacial and alluvial gravels of Alaska as in the Swiss and French Alps; *Cyperus capitatus* functions in the dune sands of Agadir exactly as it does on the Mediterranean shores of France (Fig. 160). In general, there are many parallel (homologous) developmental series in regions of similar climate, whose similarity is to be ascribed to similar changes in the habitat.

Constructiveness of Species in the Alpine Gravel Associations.—Scarcely anywhere is the constructiveness of species so unmistakably clear as in the gravels and the dune associations. The moving limestone talus of the eastern Alps is colonized by the "open" Thlaspeetum rotundifolii. Although the distance between individual plants is usually more than one meter, root competition is present. In the Thlaspeetum there appear constructive tufted plants such as *Festuca pumila* and *Sesleria coerulea* or creeping shrubs such as *D. octopetala*. The spreading *Dryas* carpets become destructive to the Thlaspeetum, but at the same time they are constructive for the following association: the Seslerieto-Semperviretum or the Firmetum. Humus accumulates in the dense mat of twigs of *Dryas* and is kept from washing or blowing away by the covering of the leaves. This forms a favorable seed bed for grasses. Thus the deeply anchored *Dryas* carpets become the centers of tuft formation on the talus. With the advent of the tuft-forming grasses and sedges, however, the creeping shrub is more and more overgrown and finally suppressed.

The dynamogenetic relations of the species of the Stipion calamagrostidis and the Thlaspeion rotundifolii of the alpine gravel slides are admirably treated by Jenny-Lips (1930); those of the Ammophilion of the Mediterranean strand dunes have been studied by Braun-Blanquet (1921), by Kühnholtz-Lordat (1923), and by Burollet (1922). Kolumbe (1925) and Christiansen (1927) give much information about the constructiveness of the various species of the north German dunes.

In strand regions and in high mountains it is especially evident that not every plant that functions in the geomorphic cycle as gravel holder or sand binder is also of sociological importance. Thus to none of the species of the Thlaspeetum cited above can be ascribed a constructive value for the association, although some species which hold the gravel may be called "consolidating."

The high moor furnishes a clear example of species of different constructiveness. The splendid monographs of moors recently published by Melin, Osvald, Hueck, Booberg, and others have not sufficiently emphasized this viewpoint.

Determination of the Constructiveness of Species.—For the determination of the constructiveness of species permanent quadrats (or areas) are used. Changes in the quantitative relations, the sociability and vitality of the species must be followed for years and decades before a conclusive judgment can be reached. Number of seedlings and their increase in size must be very accurately recorded. The factors of the habitat and their reaction upon the interrelations of the species must be investigated.

Jenny-Lips marked off a quadrat of 15 sq. m. on a fresh gravel slide in Switzerland, in 1922, and followed from year to year the introduction and establishment of plants upon the area. *Stipa calamagrostis* proved a species of great dynamogenetic value. Starting with one small plant in 1922, it had in 1928 surpassed all other species, with 59 individuals. This was in spite of the fact that in 1924 *Dactylis glomerata* and *Kernera saxatilis* dominated the heterogeneous new community with 30 and 44 individuals respectively against one individual of *Stipa*. *Gypsophila repens*, the characteristic species of the order, did not put in an appearance until 1925 but had increased to 54 individuals in 1928. The sociability of *Gypsophila* and *Stipa* has steadily and significantly increased. The former covers about 1 sq. m. in one place, while *Stipa* has developed a stand 70 cm. in diameter. In the intervening spaces there are various combinations of characteristic species ever on the increase.

2. Syngenetic Units.—Succession of vegetation consists, in last analysis, of the exchange (appearance and disappearance) of species or of changes in the quantitative relations of the species continuously present. Not every exchange of species is to be regarded as a stage of succession. Only when the existing equilibrium is obviously disturbed, the uniformity of the prevailing vegetation visibly altered, are we justified in speaking of a substitution of one dynamogenetic unit by another.

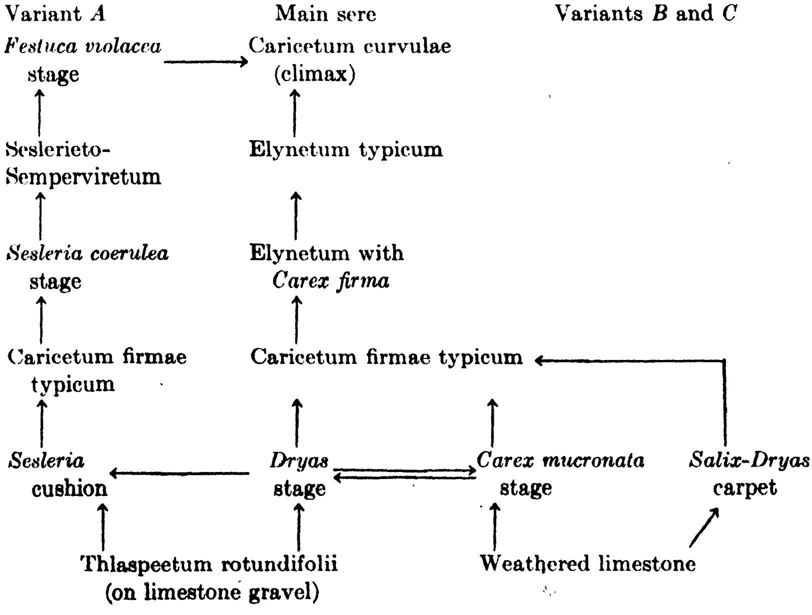
Stage.—A single clearly marked step in succession is called a stage—the lowest, indivisible concrete unit of development. According to the time of its appearance in the developmental series, it is designated as a pioneer, transitional, or terminal stage. Pioneer stages, the initial colonies of new land, are mostly sociologically simple, one layered, and composed often of cryptogams: algae, fungi, lichens, and mosses. In arctic and snowy climates and in deserts this pioneer stage is also the climatically limited final stage. The *Gyrophora cylindrica* lichen association of the snowy siliceous peaks of the Bernese Alps (Frey, 1922) is the beginning and the end of plant immigration.

The number of transition stages depends upon the prevailing climate and soil conditions, as well as upon the presence of dynamically important species which take part in the process of development. Even in temperate climates the transition stages are vastly more numerous than the pioneer stages. On the other hand, in each climatically uniform region there is only one climatically limited terminal stage, only one climax.

Phase.—Within the limits of an association, stages of development can be distinguished and can be floristically and ecologically defined. Speaking of developmental phases of the association, initial, optimal, and retrogressional or terminal phases may be distinguished. The static consideration of vegetation is generally based upon the optimal phases of the associations studied. For dynamogenetic considerations the initial and terminal phases are certainly equally important. The terminal phase of one association (A) is often identical with the initial phase of the succeeding association (B).

Sere.—The series of genetically related, sequential stages which follow one another regularly is called a "sere." A sere includes at least one pioneer stage, usually several transition stages, and a terminal stage. Whereas several or many seres may lead to the same end stage, or one end stage may be common to several seres, the pioneer stages are mostly different. Furthermore, each sere has a greater or smaller number of transition stages peculiar to itself. The independence of the sere is measured by the number, the structure, and the duration

TABLE 36.—CARICETUM FIRMAE-CURVULETUM MEADOW SUCCESSION



of the stages. If the course of succession shows small fluctuations which do not justify the recognition of a distinct sere, we may speak with Furrer (1922) of variant seres. Besides the variations due to climatic, edaphic, and phytobiotic causes, there are geographic variations due to local differences of floristic composition, and cultural variations due to cultural influences.

The Caricetum firmae-Curvuletum meadow sere of the east-central Alps furnishes an example of a relatively simple sere with three variants (Table 36).

This example, giving the development of vegetation on calcareous gravel and talus of the alpine levels, shows that one sere may start from several pioneer stages. Pioneer stages which are but little differentiated floristically are often genetically related, as shown in the table by horizontal arrows.

Complete Seres. Partial Seres.—New land arises by upheaval, falling of water level, deposition of sand or gravel by wind or water or by violent catastrophes such as landslides, volcanic eruptions, tidal waves, or through human agencies. The existing vegetation is completely destroyed. Regeneration begins with primitive pioneer stages and runs through the entire developmental series ("complete sere"). Complete seres are possible on new land of any kind.

Many natural phenomena, like earthquakes, avalanches, brief flooding, and many human activities, like clearing and fire, do not completely destroy the existing vegetation. They cause retrogressions, reversions, and delays. Regeneration in such cases begins not with a pioneer stage as of new land but with a suitable stage of the original sere. This results in a partial sere, which sooner or later runs into the original complete sere, provided its development is not stopped by man.

Every complete sere leads to the climatic terminal stage, the climax.

Climax.—We have seen (p. 255) that development of vegetation and formation of soil tend toward a definite end point determined and limited by the local climate. The smaller the periodic variations of climate and the longer a uniform undisturbed climate prevails the more completely and extensively will this end point be realized. This relatively permanent final condition we have called a soil and vegetative climax. But the climax itself, it must be expressly stated, is only a resting point, a breathing space in the ceaseless change of the composition of vegetation.

Permanent Communities.—Plant communities which have not yet reached the end point, the climax, and yet from whatsoever cause remain unchanged for a long time and maintain their social individuality may be called permanent communities.

The coating of blue-green algae on a limestone-rock surface, the carpet of creeping willows of alpine snow land, the grassy woods near the ground water along large rivers all are permanent communities. They are distinguished from climax communities in not being limited by climate and by possessing the potentiality of further development when certain limiting factors are removed. Climax communities can change only when there has been a change of climate.

Climax Complex. Climax Area (Gebiet).—All seres in a natural climatically uniform area must in the course of time, as the soil matures, lead to the climatic terminal community. Obviously, this terminal community will not be reached at the same time over the entire area; and erosion and orogenic agencies will constantly make new rifts in the mature plant covering. All long-cultivated regions, whose vegetation has been transformed according to human needs, show the terminal community only in fragmentary remnants. Reconstruction of the natural terminal community and its territorial delimitation are thus made very difficult. For this reason not one climax community in Europe has been exactly delimited. The principal climax communities in French northern Africa have been mapped by Maire (1926), and the great climax communities of the United States are given on Shantz's vegetation map in the "Atlas of American Agriculture." While rather too general, Shantz's map is valuable as a preliminary sketch of the natural vegetation of a large territory.

The culmination of all the seres that lead to one definite climatic terminal community is called the climax complex. The territory covered by a climax complex is the climax area. It covers the surface on which the climax community is theoretically possible. The boundaries of the climax area are, however, rarely well defined. In mountainous regions their course is irregular and follows the folds of the valley walls. Outliers of foreign climax regions push deeply into neighboring climax areas. The number of climax areas in central Europe is small. They are most clearly distinguished and most undisturbed in the Alps.

Lüdi (1921) distinguished in the Lauterbrunnen valley (Bernese Alps) six climax areas, corresponding to as many altitudinal belts:

1. The Fagetum silvaticae, up to 1,200 m.
2. The Piceetum excelsae, 1,200 to 1,900 m.
3. The Rhodoretum ferruginei, 1,900 to 2,100 m.
4. The Nardetum, 2,100 to 2,300 m.

5. The Caricetum curvulae, 2,300 to 2,700 m.
6. The Gyrophoretum, above 2,700 m.

In the mountains of central France (Auvergne) we find crowded together in narrow limits the climax areas of the Quercion roboris sessiliflorae up to 800 to 900 m., the Fagion, 900 to 1,500 m.; and the Genisteto-Vaccinion, 1,500 to 1,880 m.; in the southern Cévennes there are climax areas of the Quercion ilicis, Quercion pubescentis, and Fagion silvaticae (Fig. 161).

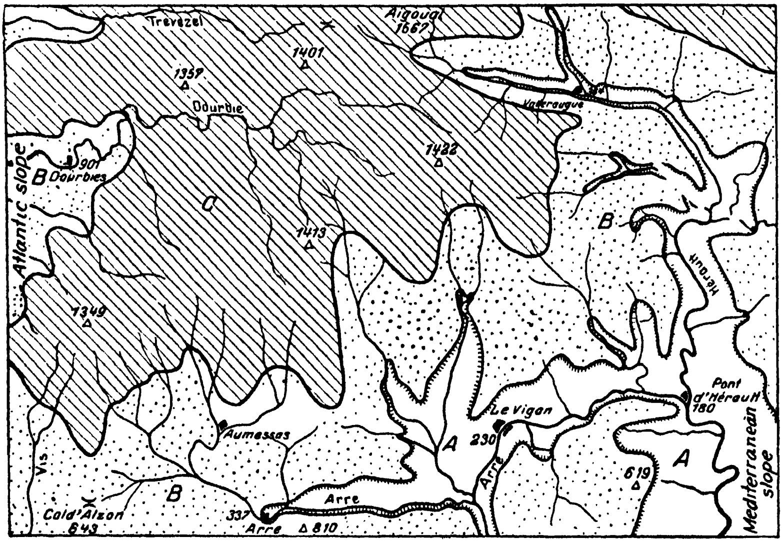


FIG. 161.—The South Cévennes, showing climax regions of *Quercus ilex* forests up to 600 m. (*A*); of *Quercus pubescens* up to 1,000 m. (*B*); and of *Fagus silvatica* up to 1,567 m. (*C*).

It would be most desirable to have the climax areas of central and western Europe described and bounded before forestry has transformed the last remnants of the ancient forests.

In naming the climax areas it is best to use the terminal climatic community in wider or narrower sense, as alliance or association. The climax area of the alpine turf of the eastern Rhetic Central Alps consists of two floristically related associations, the Curvuletum and the Festucetum halleri. The latter lies in narrow strips between the former and the timber line. In naming this region we have chosen not an association name but the name of the alliance; we speak of the climax area of the Caricion curvulae. The manner of bounding this climax area and distinguishing it from the adjacent pine-larch climax area is explained on page 263 (Fig. 131).

Progressive and Retrogressive, Primary and Secondary Successions.—All seres which lead toward the climax are progressive. Retrogressive successions, which recede from the climax, are often caused by man or animals (Fig. 145). The spread of moors following a rise of the water table is also a retrogressive succession (*cf.* p. 327).

The Anglo-American school distinguishes between primary successions or sequences of communities which originate independently of man and secondary successions (Clements, 1905, 1916) caused by human intervention. The most important causes of secondary succession are the complete or partial disturbance of original vegetation by fire, clearing, pasturing, or cultivation and consequent human utilization. Freed from the hand of man the vegetation again moves toward the climax (Fig. 147). Secondary successions are abundant in all civilized countries on abandoned arable land. In the "deflected succession" (Godwin and Tansley, 1929) normal development is prevented by anthropogenic influences but is not completely checked. For example, by grazing, the normal succession toward forest may be directed toward a grassland community.

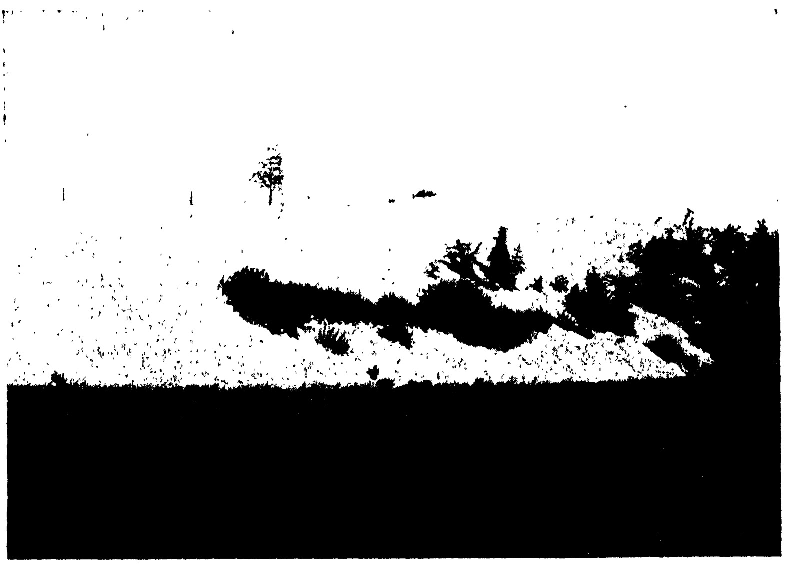
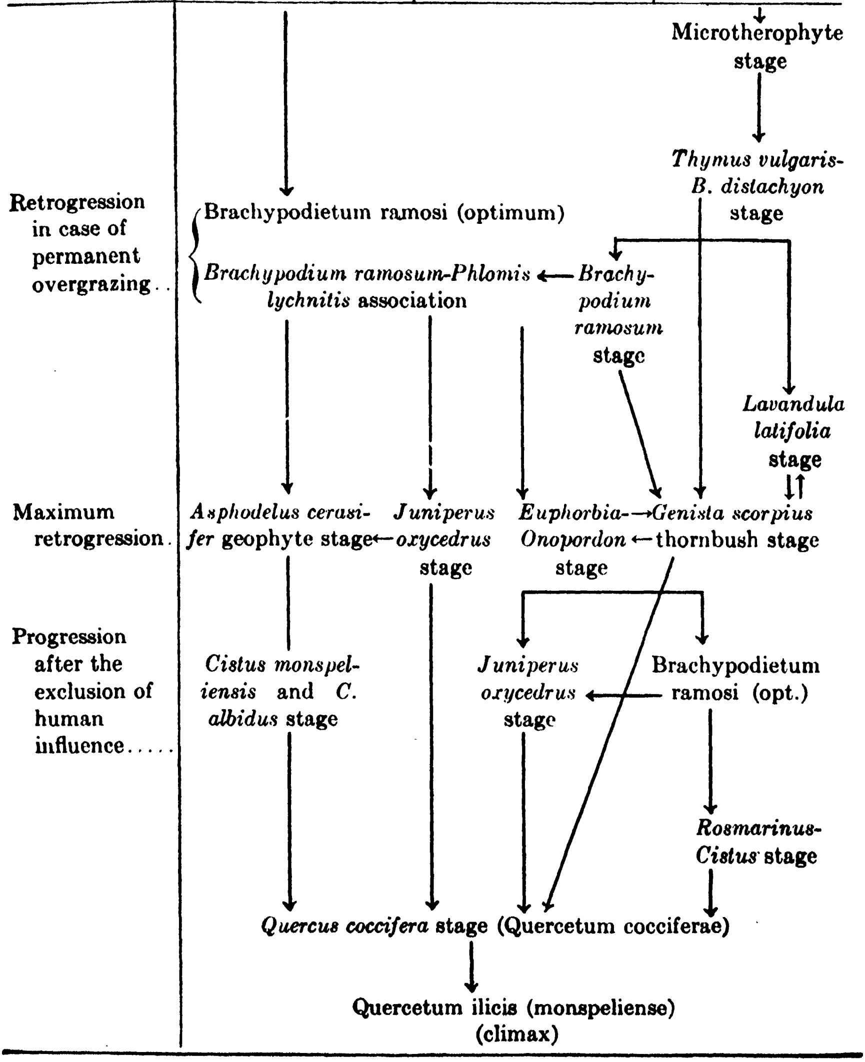


FIG. 162.—High dune advancing over swamp and forest. The willows surmount the advancing sand but many of the trees are killed. Dune Park, Indiana. (*Photo by Meyers.*)

Climax Fluctuations.—The mature climax of vegetation may suffer injuries through human or natural agencies, such as wind, snow, flooding or the advance of sand dunes (Fig. 162), which may

TABLE 37.—RETROGRESSION AND SECONDARY SUCCESSION IN THE MEDITERRANEAN GARIGUE
(After Braun-Blanquet, 1925)

Soil and vegetation.......	Red earth on compact limestone (*Quercus coccifera* scrub)		Disturbed stony limestone soils (cultivated)
Human interference..	Burning and pasturing	Clearing and pasturing	Cessation of cultivation and pasturing



be followed, by notable displacements of the species. These may best be classed as climax fluctuations (Furrer, 1922). Very marked changes in the appearance of the climax occur where two climax communities meet and compete for the supremacy. In such cases it is often difficult to decide whether a new climax community has taken possession of the habitat or there is simply a climax fluctuation.

Many cases where forest is converted into moor may be considered as climax fluctuations. A typical example of this is the Flahult moor near Jönköping, Sweden. According to Anderson and Hesselman (1910, p. 153), there is a 3-m. layer of Sphagnum peat covering a mineral soil which was originally forested. After the forest was burned off, the drying effect of the tree layer (transpiration, interception of rain) ceased. Immediately physicochemical changes took place in the soil. Favored by these conditions *Sphagnum* became very actively constructive and pushed a high moor with low shrubs and isolated distorted pines directly over the burned ground.

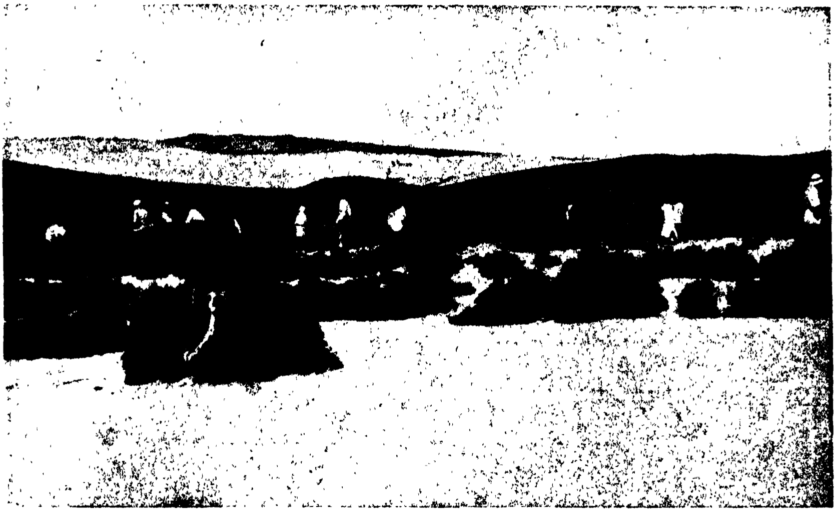


FIG. 163.—Artificial creation of the Ononidetum angustissimae by sowing; first step in fixing sand. (*Photo by Maire.*)

Practical Significance of Syngenetics.—The universal application of syngenetics to forestry and agriculture has long been recognized but has never been urged with sufficient emphasis, and these subjects have never been treated connectedly. The immense agricultural value of studies of the development of vegetation is shown by the history of the advance of moor in cool, humid climates, by the combat with the *savoka* and the dreaded fire steppes of Madagascar, by stabilization of moving dunes, and by draining of lagoons.

Among the stupendous syngenetical experiments that are now going on is the stabilization and forestation of the forbidding stretch of wandering dunes southward of Cape Sim on the Moroccan coast (see p. 153) the outcome of which will decide the fate of the flourishing commercial city of Mogador (Fig. 163). An equally gigantic syngenetical experiment of a very different sort is the successional study of the area exposed by the drying up and utilization for agriculture of the Zuider Zee, a scheme that is being carried forward by a special commission under the direction of the Dutch ecologist De Leeuw.

3. Methods of Syngenetic Research.—Since Clements (1905) first demonstrated the use of permanent quadrats, students everywhere have been following the actual course of succession by means of permanent areas of which from time to time minute records are made (Figs. 5, 6, 164, 165). Such studies are much enriched if, in addition to recording the periodic exchange in the floristic composition of the vegetation of these permanent areas, measurements of the principal ecological factors are frequently made. The syngenetic effect of a definite factor can be studied if one keeps all the factors constant except the one which is subjected to measured modifications.

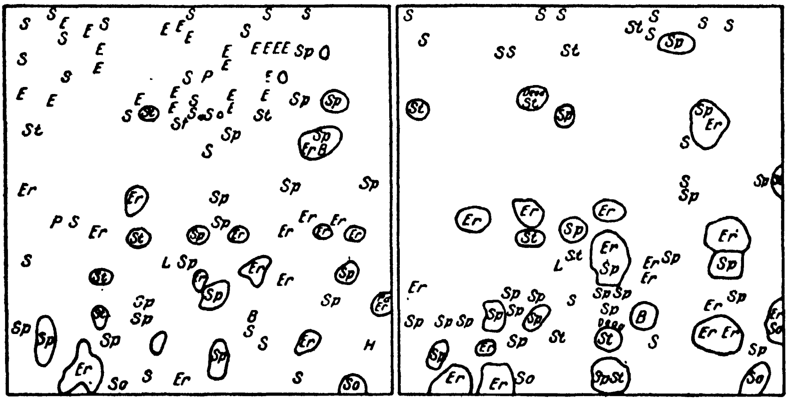


FIG. 164.—Permanent quadrat (1 sq. m.); examined in open prairie in 1916 (left) and 1918 (right) *B.*, *Bouteloua oligostachya; E.*, *Euphorbia serpens; Er.*, *Eragrostis pectinacea; H.*, *Helianthus subrhomboideus; L.*, *Laciniaria punctata; O.*, *Onagra biennis; P.*, *Physalis heterophylla; Pa.*, *Panicum capillare; S.*, *Solidago missouriensis; So.*, *Sorghastrum avenaceum; Sp.*, *Sporobolus longifolius; St.*, *Stipa spartea.* (*After Weaver.*)

The boundaries of small, permanent areas should be marked by an iron wire pegged to the ground. For larger areas colored boundary marks on trees and rocks are used. A general map should always be made, and when possible the area should be photographed from a fixed point. Cooper (1924) has constructed a stand for photographing permanent areas from above (Fig. 166).

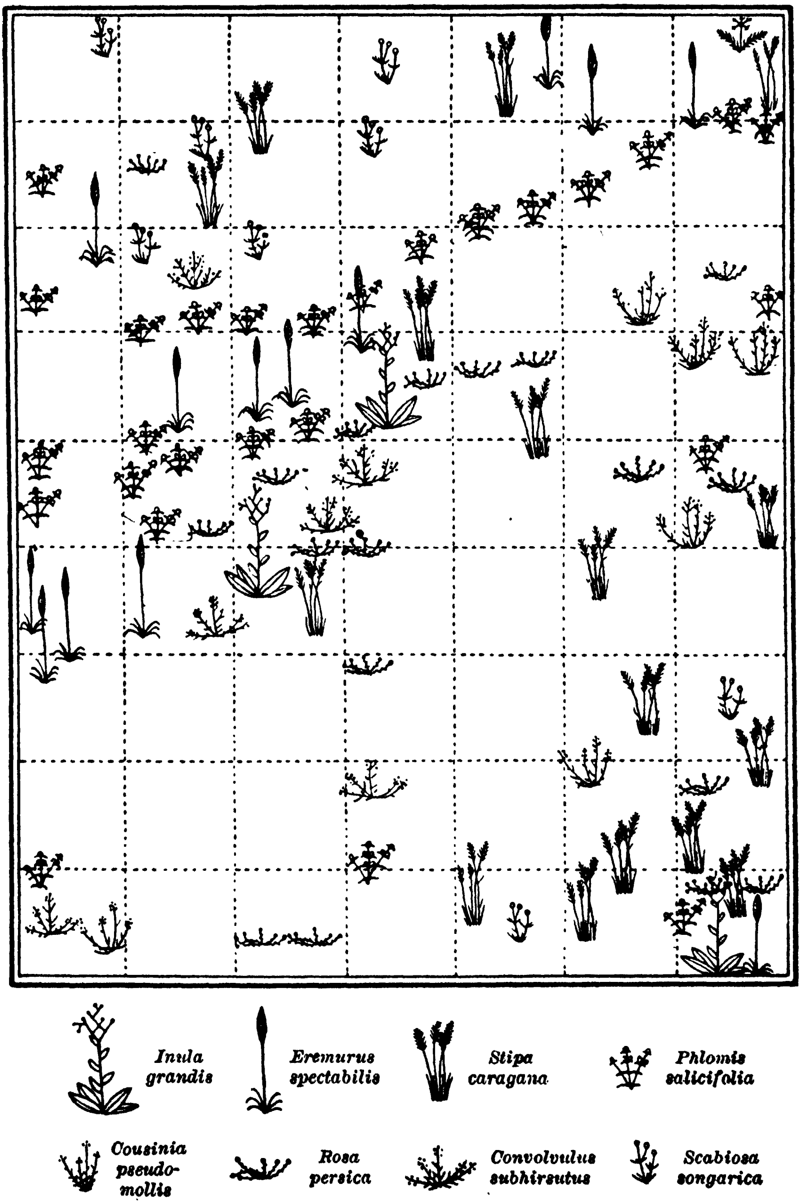


FIG. 165.—Quadrat in the central Asiatic steppe (30 sq. m.). (*After Kultiassoff.*)

The establishment of permanent areas for investigation is neither always possible nor universally desirable. In very many cases the comparison of existing bits of vegetation of different ages or the presence of relict societies or pioneers gives convincing evidence of past or prospective changes of vegetation.

If, for example, we find in a pine wood on an old sandy bank dying and dead *Salix incana* and tussocks of *Hippophaë*, and at the same time find that in neighboring vigorous stands of *Hippophaë* a young growth of pines is established, it does not require a permanent quadrat to make plausible the succession from the *Hippophaë-Salix incana* association to *Pinus silvestris* forest.

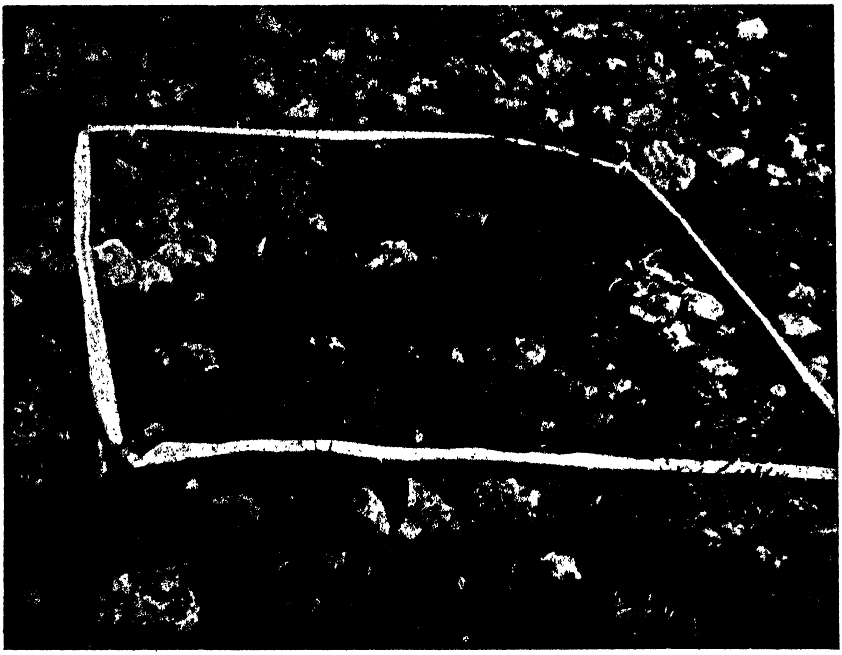


FIG. 166.—Permanent quadrat (1 sq. m.) in the *Brachypodium ramosum-Phlomis lychnitis* association at Villeneuve-les Maguelonne in January. Surface covered by vegetation, 80 per cent. (*Photo by Braun-Blanquet* and *Keller.*)

Another important example illustrating the significance of pioneer trees as syngenetic indicators is found in the *Pinus montana* forest in the Ofen Pass region. The limestone talus is prepared for the coming of trees by the stabilizing effect of such low shrubs, as *Arctostaphylos uva-ursi* and *Dryas*. Protected by these, in the absence of disturbance, there may come into the undergrowth an *Erica carnea-Juniperus* community with few mosses, to be followed in turn by a more mesic and more mossy type with *Erica carnea, Rhododendron hirsutum, Vaccinium uliginosum,* and *V. vitis idaea.* In this mossy community *P. cembra* is first able to come in and its seedlings may abound on the moist forest floor, whereas seedlings of *P. montana* rarely occur in this facies. Not less than 32 flourishing seedlings of *P. cembra* from 10 cm. to 5 m. high have been found under the shelter of one old tree of *P. montana* (Fig. 167).[1]

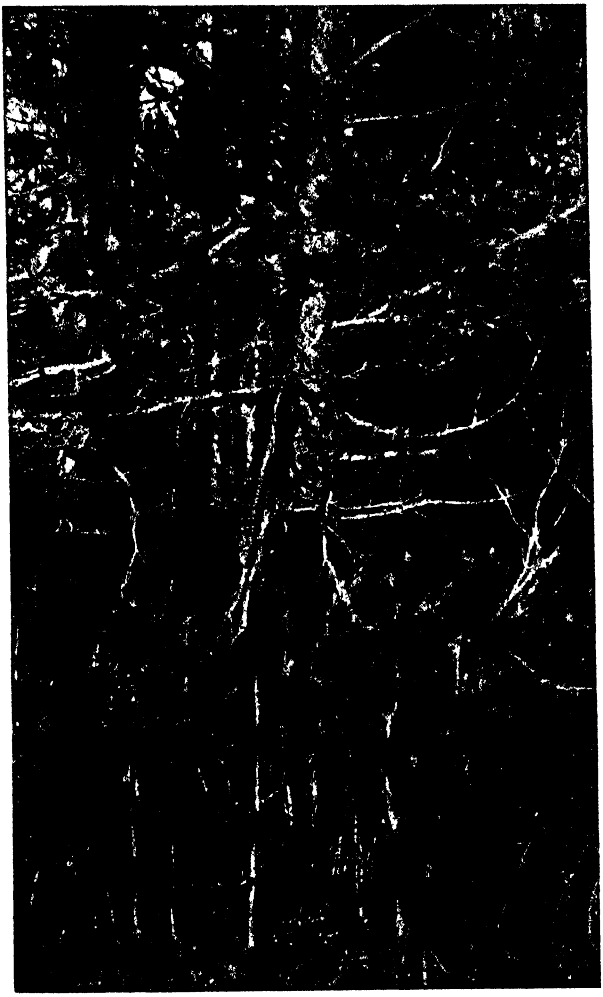


FIG. 167.—Dense growth of young *Pinus cembra*, in a pure stone pine forest at 1,800 m., Swiss National Park. (*Photo by Heller and Braun-Blanquet.*)

These results, significant for forestry and proving conclusively that the climax community of the region is not the present *P. montana*

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[1] In such studies it is important to determine accurately the number and size of the tree seedlings.

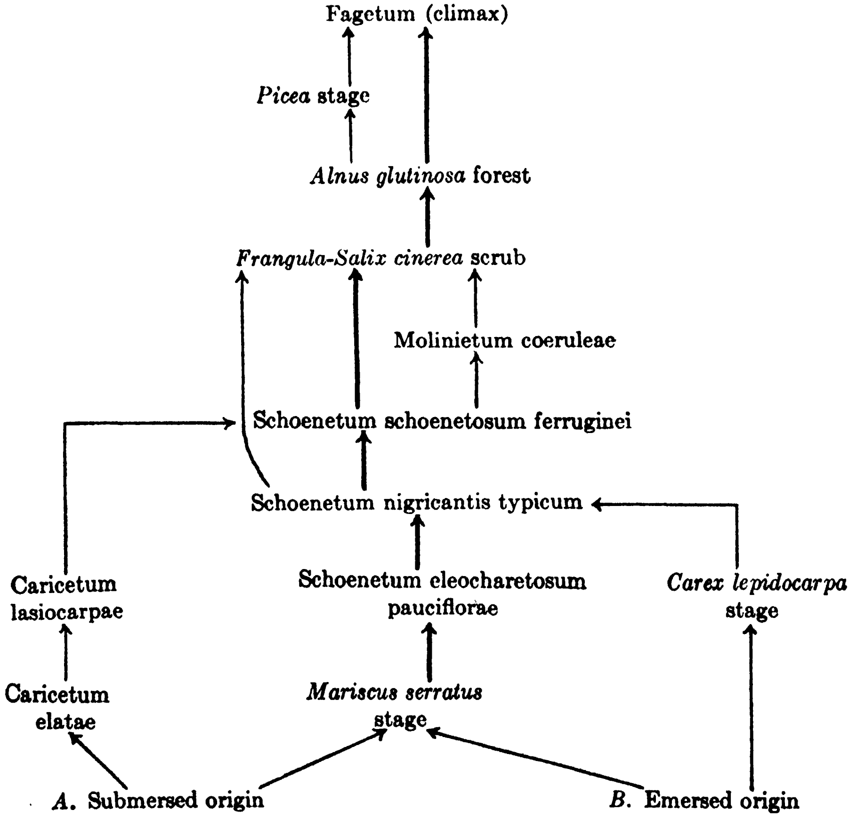
forest but rather the *P. cembra-Larix* forest, are confirmed by the prolonged study of permanent quadrats in the region.[1]

Presentation of Social Development.—In presenting material on succession the utmost simplicity and clearness are desirable. One should avoid whenever possible schemes with lines that cross one another. It is better to divide a chart than to overload it.

A common method of expressing succession is one in which arrows show the course of development, as in Table 38.

TABLE 38.—LAND-FORMING SERE OF SCHOENETUM NIGRICANTIS IN NORTHERN SWITZERLAND

(After W. Koch)



The normal course of development of this succession in northern Switzerland as it originates from calcareous springs, pools, and ponds is shown by the heavy arrows (see also Table 37).

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[1] These and other methods for studying successions have been summarized by Lüdi (1930).

Photographs taken from the same point from time to time form admirable records of the changing physiognomy of the vegetation.

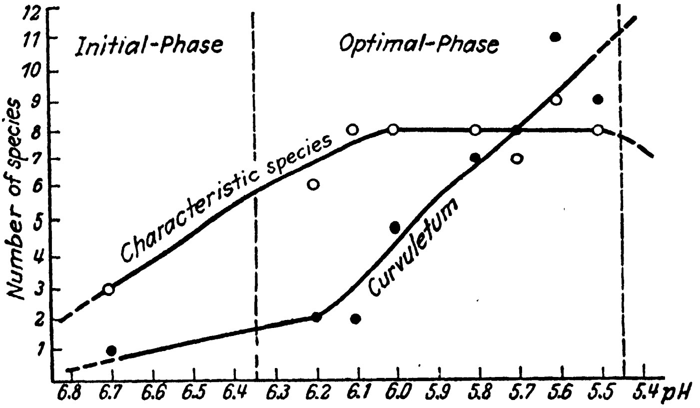

FIG. 168.—Curve of the characteristic species and the succession from the Elynetum to the Curvuletum. Single stands Nos. 2–12 in Table 4, p. 70, arranged according to pH of the soil solution. Each dot or circle represents a single stand. (*After Braun-Blanquet and Jenny.*)

Curve Diagrams.—By means of curves it is possible to express clearly the change in certain groups of species along with changes in such determining factors of the habitat as light, moisture, lime content, and acidity (Frey, 1927, 1928).

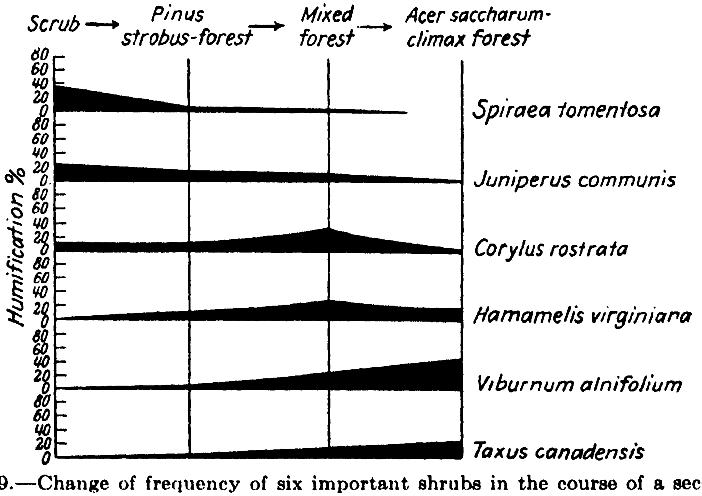

FIG. 169.—Change of frequency of six important shrubs in the course of a secondary succession. (*After Cooper.*)

Succession curves are especially adapted for precise expression of the floristic and ecological changes which take place during the development of an association. As an example, we cite the development of the more or less neutrophilous Elynetum into the extremely acidophilous Curvuletum (Fig. 168). The successive increase of the acidophilous Curvuletum species in the Elynetum, as shown by the curve of the acidophiles, corresponds perfectly with the increasing acidity of the individual stands. The terminal phase of the Elynetum corresponds with the initial phase of the Curvuletum.

Block Diagrams.—Block diagrams serve to bring out clearly the share of certain dynamically important species or groups of species in different genetically related plant societies. Using this method (Fig. 169), Cooper (1922) gives an expressive picture of the changes in abundance of six important shrubs in the secondary succession from pasture land to climax forest in New England.

Spiraea tomentosa, present in 40 per cent of the pasture plots, is absent from the climax forest, whereas *Viburnum alnifolium* and *Taxus canadensis* continually increase throughout the natural course of development, reaching their maximum in the climax forest.

4. Syngenetic Classification.—The results of more intensive studies of succession have demonstrated the need of arranging the developmental series for more ready purview. The units to be classified are the individual seres. On general principles, two arrangements are possible. One possibility is based on the conditions of the habitat, especially the beginning stages. Thus we may distinguish groups of seres on river silt, on limestone talus of alpine levels, on wandering sand dunes, in running water, etc.

The other possibility rests upon the principle of development itself and especially upon the similarities in development: type and duration of the developmental process, number of stages involved and their parallelism, and the correspondence of climax stages. This type of grouping appears scientifically more satisfying. Thus we would place first the shortest seres with the smallest number of steps, leading to the simplest terminal stages, sociologically and ecologically. The further sequence, according to the sociological progression of the groups of seres, corresponds (1) to increasing differentiation of the terminal stage (climax) through more intense competition and (2) to the larger number of stages and the consequent longer duration of the development.

Accordingly, four primary groups may be distinguished:

A. One-layered, primitive terminal communities.
  1. Competition for space only.

I. Plankton seres, floating societies of air, water, and snow.
  2. Competition for space and nutriment.

II. Communities of bacteria, fungi, and algae—inadequately known and little investigated.

3. Competition primarily for space and light.

III. Lichen seres. In high mountains above the limits of grasses and in arctic regions lichens often form the climax community.

IV. Moss seres. In cold, moist regions such as parts of Siberia, Lapland, and the Faroe Islands and Spitzbergen, moss communities may form the climax *Rhacomitrium* heath (*cf.* Fig. 17, p. 38).

B. Two- or more-layered terminal communities.[1]

4. Competition for space, light, and food (root competition).

FIG. 170.—*Artemisia* steppe (*Artemisia barrelieri*, *Thymus capitatus*, etc.), between Alicante and Elche. Chamaephyte sere or climax. (*Photo by Uehlinger and Braun-Blanquet.*)

V. Therophyte seres. Common on desert and desert steppe, probably also as climax.[2]

VI. Turf seres. The climax of the alpine heights of many mountainous regions, savanna and natural prairie.

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[1] Root layers included.

[2] An association of *Aristida acutiflora* and *Echium humile* in the sands of the Sahara near Nefta, southern Tunis, contains 74 per cent therophytes, 14 per cent chamaephytes, 7 per cent hemicryptophytes and tussocks, and 5 per cent bulb geophytes.

VII. Euchamaephyte seres. The climax in steppes of the warmer region with mostly alkaline soils and in cold unfavorable regions on mostly acid soils (dwarf-shrub heath, etc.) (Fig. 170).

VIII. Shrub seres. Shrubby climax communities often lie just above the tree line on mountains, forming a shrub zone. They are also found in the north and in hot, dry regions as a transition between steppe and desert (low scrub). Chaparral, *Chamaerops* scrub, garigue, and sibljak of the Mediterranean climates are not climaxes but rather transition societies (Figs. 144 to 146).

IX. Forest seres. The natural terminal stage of vegetational development in the temperate, warm, and torrid zones is forest, whenever the water supply is sufficient.

In naming and defining seres one may use the especially striking phenomena of the course of succession, based upon the habitat (moor seres, snow-soil sod seres, *solontschak*-shrub seres, dune-forest seres, subarctic moss seres, equatorial forest seres, etc.) or upon the nature of the succession (land-forming, sod-forming seres, etc.). Our knowledge of the dynamics of vegetation is still far too scanty, however, to permit more than a preliminary outline of the above group of seres.

5. History (Synchronology) of Vegetation.—Of the rise and decline and the genetic relation of prehistoric plant societies very little can be said, owing to the lack of adequate fossil records. Paleontological research, be it ever so carefully executed, can give at best only fragmentary cross sections, momentary glimpses, of a floristic sequence of inconceivable duration. These glimpses follow one another with little continuity. The sequence is interrupted by enormous breaks, during which climate and habitat may have suffered many changes. The few fossil beds we have give only rarely an imperfect picture of a definite plant community. All too often the fossil remains have been washed together from far and near or collected by the wind or (in the latest Quaternary beds) brought together by man. It requires a good imagination to reconstruct from such a jumbled mixture of species a definite association or to tell its genetic sequence. Of course, we must not ignore the fact that the indicator value of the species, as expressed by fidelity, may be available for synchronological uses.

Synchronology is better handled as a branch of syngenetics, to which it is obviously closely related, rather than as a subject by itself. We have then the study of present-day changes in vegetation, on the one hand; and secular (Christ, 1879; Gams, 1918) or paleogenic successions, *i.e.*, paleosyngenetics, on the other.

The investigation of moors and peat bogs has yielded considerable information for the most recent geologic period, the Quaternary.

Methods of collecting and identifying remnants of fruits, seeds, and leaves found in the peat have been developed by Swedish investigators represented by Von Post and his followers. As early as 1896, G. Anderson gave directions for collecting and determining peat fossils. For such work it is important that the peat samples never get completely dry. They are to be separated by washing in water. Clearing of the darker peats with a little nitric acid facilitates the separation of materials. Plant remains like seeds, leaves, etc., may then be picked out with brush or forceps. For identification of wood, microtome sections are often necessary.

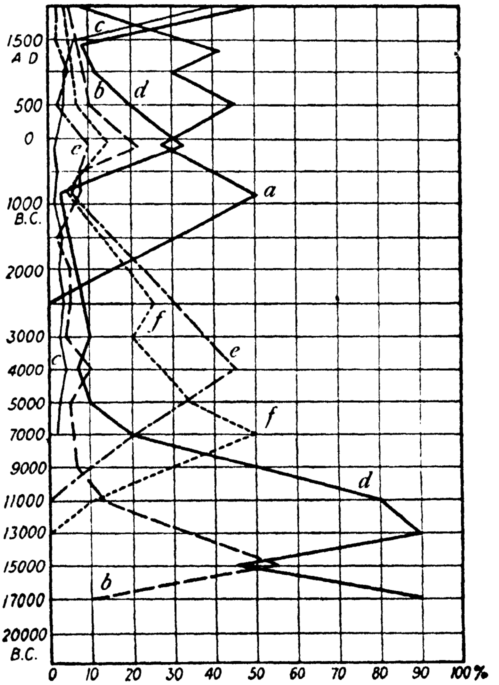

FIG. 171.—A pollen diagram from deposits in south Germany. (*After Bertsch.*) Beech (*a*), birch (*b*), spruce (*c*), pine (*d*), mixed oak (*e*), and hazel (*f*).

Pollen Analysis.—Secular changes in the dominant tree vegetation of a region, which often represents the climax, are best registered by pollen analysis. Acid peat has the property of preserving various parts of plants, and no structure is more resistant to decay than the cutinized outer coats (exines) of pollen grains. Peat samples are taken at depth intervals of 10 to 20 cm., and their pollen content, analyzed microscopically, yields the so-called pollen diagrams (Fig. 171), which give the proportion of each kind of pollen in each layer.

Thus the proportions of the dominant tree species for an appreciable distance around the moor can be shown with certainty.[1] The quantity of pollen produced by different trees, its capacity for distribution by the wind, and its degree of preservation in the peat are factors that are sure to influence results of pollen analysis. Some of these factors are decidedly difficult of evaluation. Pines and hazels produce large amounts of pollen, whereas *Ulmus* and *Tilia* produce relatively little; moreover, some pollens, such as those of *Fraxinus*, *Prunus*, and *Juniperus*, are not well preserved. But after considering all the possible sources of error, pollen analyses yield a rather convincing picture of tree life for a considerable distance around the locality of the peat bogs studied.

Pollen Statistics. Pollen Diagrams.—The current methods of pollen analysis go back to Lagerheim (1902) and have been described by Von Post, Erdtman, Rudolph and Firbas, Stark, Keller, Furrer, Bertsch, Lüdi, and others. Erdtman (1927, 1930) has given a very complete bibliography of the literature, and Rudolph (1931) has compiled a good summary of the results which apply to the forests of middle Europe.

The sampling of the peat in the bog is accomplished by a peat borer. Several types have been used, but one of the best is the Hiller peat auger, developed in Sweden. It has a closed chamber that may be opened at the exact depth at which a sample is desired, and with it clean samples may be obtained to a depth of 8 to 12 m. The samples are placed at once in numbered glass tubes, about 7.5 cm. long and 1.2 cm. in diameter, corked at both ends. For the pollen count a small sample (1 cc.) is taken and boiled in 10 per cent caustic potash for a few minutes and a portion placed on a glass slide, the surplus water evaporated, and a few drops of glycerin added. For counting the pollen a magnification of 250 to 500 diameters is necessary, and a microscope equipped with a mechanical stage greatly facilitates the labor. Trustworthy percentages are obtained if about 150 pollen grains are counted. The results are expressed graphically in the pollen diagrams (Erdtman, 1931).

Pollen Analysis and the Development of Vegetation.—Pollen analysis is obviously incapable of giving more than a crude outline of succession of forest trees and their relative abundance during the formation of the peat bed. One can hardly, therefore, discuss the development of vegetation, especially as the pollen is not only autochthonous (deposited in the place of its origin) but also allochthonous (brought together)

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[1] KUDRJASCHEW (*Ber. Wiss. Meeresinst.* **12**: 1925) has proved the presence of pollen of *Abies*, *Picea*, *Alnus*, and *Tilia* on the arctic island of Nowaja Semlja.

TABLE 39.—CORRELATION AND SUGGESTED HISTORY OF THE POSTGLACIAL FOREST OF NORTHWESTERN EUROPE

(After Woodhead)

	De Geer's geochronology	Blytt and Sernander's climatic periods	Munthe's Baltic lake periods	Archaeological periods	Vegetation					
					British Isles	Denmark	Sweden	Norway	Finland	Bavaria
Postglacial				Historical and Iron:	(Beech?)					
	1000 A.D. 0	Subatlantic: Moist and cold	(Mya)	British and Roman remains	Peat	Beech Hornbeam Peat	Peat	Peat	Peat	Peat
	1000 B.C. 2000 B.C.	Subboreal: Warm and dry	Limnaea	Bronze: Fragments of bronze barbed arrowheads	Yew (max.) Pine (sec. max.)	Yew (max.) Pine (sec. max.)	Yew (max.) Pine (sec. max.)	Pine		Beech fir (*Abies*) hornbeam beech
	3000 B.C. 4000 B.C. 5000 B.C.	Atlantic: Warm, moist, oceanic Climatic optimum	Littorina	Neolithic: Horn cases; *Bos primigenius*	Peat Beech linden	(*Trapa*) Peat yew linden	(*Trapa*) Peat linden maple hornbeam	Peat	Peat (*Trapa*) linden plane ash	Peat spruce alder linden
	6000 B.C. 7000 B.C.	Boreal: Warm, dry, continental or oceanic with dry summers	Ancylus	Patinated flints; late "Belgian" Tardenois Mesolithic	(*Cladium*) Mixed oak, alder, elm	Mixed oak, alder, elm	(*Cladium*) Mixed oak, alder, elm	(*Cladium*) Mixed oak spruce	Mixed oak, alder spruce	Mixed oak, elm
				Unpatinated flints: early "Belgian" Tardenois	Hazel Birch, pine	Hazel Pine	Hazel, spruce Birch, pine	Hazel Birch, pine		Hazel Pine
Late glacial	8000 B.C.	Subarctic	Yoldia	Palaeolithic:	Birch	Birch, poplar	Birch	Birch	Birch, pine	Birch, pine willow
				Developed Aurignac (La Madeleine)	Birch, willow	Birch, willow	Birch, willow	Birch, juniper		
	9000 B.C. 10000 B.C.	Arctic			Tundra with moorland species	Tundra	Tundra	Tundra	Tundra (Arctics rare)	
Glacial	11000 B.C.									

and derived from various communities which have developed at no great distance from the bog. If we find in a limited area several pollen spectra with synchronous horizons, we can determine with some certainty the sequence of forest conditions, at least in so far as the tree layer is concerned. The brilliant investigations of Von Post and Erdtman in Sweden, of P. Stark, Bertsch, Overbech, Firbas and others in Germany, of P. Keller, Furrer, Lüdi, and others in Switzerland suffice to establish for northwestern Europe the post-glacial forest periods (Woodhead, 1928) as shown on page 339.

Pollen analysis gives good bases for conclusions about the chronological sequence of the terminal societies, the forest climaxes, and therefore about changes in the general climate of extended areas. Of course, a single pollen diagram is not sufficient. When by a more or less dense network of investigations a chronological correspondence has been established between the forest periods determined by pollen analysis, then only may we assume changes of climate as the dynamic cause of the changes of forest.[1] The explanation of changes of climate should involve an evaluation of all the findings of related sciences (see also Lüdi, 1930). The above attempt to depict the forest periods of eastern Europe represents a synthesis of available prehistoric data (Table 39).

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[1] Even then, as pointed out by Furrer (1927), the differing mobility of tree species by seed distribution must be taken into account.

PART V

SYNCHOROLOGY

CHAPTER XIV

THE DISTRIBUTION OF COMMUNITIES

The aim of the study of synchorology is the concise description of the occurrence and distribution of plant communities, the delimitation of their areas, and the grouping of them into regional units. Conclusions concerning the origin, descent, and ecology of communities may be drawn from their areal configuration. These regional units are important indicators of climate and soil conditions and are indispensable for the biogeographic characterization of the great divisions of the earth. In order to understand the details of the distribution of vegetation, the smaller units (associations, alliances) or at least the association complexes must be included within the scope of the investigation.

Geographic Variants.—Every widely distributed association shows characteristic modifications in floristic composition in the different parts of its range. These may be termed geographic variants or races. These variants may be due to distributional or historical causes, as when the ranges of the species of the companion plants of the community are not coterminous with the range of the community. Under certain circumstances the interplay of external factors in two adjacent areas gives a similar but not identical sociological effect. Absolute identity between all the individual stands of an association is extremely rare, occurring only between communities which have few species or are very narrowly localized.

Different geographic variants of an association are often characterized by parallel species with similar ecological requirements. *Senecio uniflorus*, a characteristic species of the Pennine Curvuletum, is replaced by *S. carniolicus* in the Rhetic Curvuletum. The central Swiss Xerobrometum has *Anemone montana* and *Potentilla puberula;* that of the upper Rhine and northern Switzerland has *A. pulsatilla* and *P. arenaria*, with similar ecology.

Where the areas of two geographic variants come into contact, their boundary is often indistinct: they merge into one another as in the case of the Xerobrometum of Swabia and northern Switzerland and that of the upper Rhine. If they are separated by barriers, transitions are lacking, and the floristic individuality is much better preserved. This is seen in a whole series of associations of the Alps which are repeated in the Tatras with slightly differing variations. However, as long as the characteristic combination of species of an association suffers no important change in the different parts of its range and the geographic variants are distinguished only by local peculiarities, they are best grouped as one association.

The local races or variants are the subunits of which the association is composed and upon which structural, ecologic, and syngenetic investigations are made. In tabulation, therefore, the individual races are put separately so that the varying floristic differences appear at once.

The relation of the distribution of three variants of the Xerobrometum of the upper Rhine region to precipitation is shown on page 114. Allorge recognizes three geographic variants of the widely distributed *Rhynchospora alba* association: an Atlantic, an Atlantic montane, and a central European.

In tracing out the geographic variants of forest communities, only well-developed, mature stands are to be considered, not mere stages of development or bits of woodland greatly disturbed by man.

Semi-cultural communities, like permanent pastures, which are everywhere similarly treated by man, have closely similar combinations of species over wide stretches of territory. For example, the Arrhenatherion elatioris of central, southern, and western Europe may be divided into several associations and variants of almost identical physiognomy. The dominant grasses and a number of characteristic companions are everywhere the same, from the Carpathians to northern Spain.

Division According to Altitude.—Vertically as well as horizontally many associations show constant, though often slight, floristic modifications. Frequently these are due only to impoverishment, the dropping out of some characteristic or companion species, as in the high alpine Curvuletum as compared with that of the alpine pastures. The same phenomenon is seen in the Mesobrometum of northwestern Germany as one goes northwestward (Tüxen, 1930) and in many associations toward the limits of their range.

In general, if no important changes in the combination of species can be shown, these modifications may best be listed as altitudinal sub-associations or facies (*Höhenglieder*). Beger (1922) distinguishes the normally developed subalpine spruce forest (Piceetum myrtilletosum) from the Piceetum normale of lower levels as a sub-association. The extensive land-forming stands of *Carex inflata* and *Equisetum limosum* (with a few other species) of the shores of our subalpine lakes are best to be considered (following Koch, 1928) as impoverished altitudinal stands of the Caricetum inflatae-vesicariae.

Topographic Arrangement of Units of Vegetation.—The topographic arrangement, the interdigitation, the mutual penetration of plant communities are occasioned primarily by external factors, secondarily by competition of the species and communities. Such arrangements are either zonal or mosaic. In both cases the alternation or mixture of communities follows regularly. It is continually the same plant communities which meet, interpenetrate, and compete with one another. We speak of them as contact communities or contact associations.

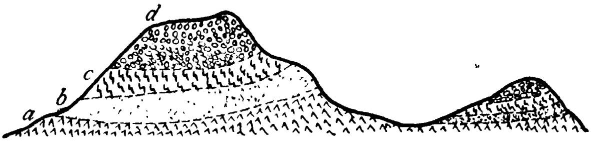

FIG. 172.—Round hillock complex at 2,010 m. in the Tatras, showing somewhat diagrammatically a girdle arrangement of vegetation due to duration of snow cover; association of *Polytrichum sexangulare* (*a*), *Salix herbacea* (*b*), *Luzula spadicea* (*c*), and the Trifidi-Distichetum (*d*). (*Braun-Blanquet.*)

Zonation.—A girdle or beltlike arrangement of the units of vegetation, whether on a large or on a small scale, is caused by similarly arranged differences of important factors of the habitat: temperature, soil moisture, salt- or nitrogen-content of the soil, duration of snow cover, wind, etc. (Figs. 172, 173). The concentric vegetation zones of the earth (not to be confused with "regions of vegetation") are due to the gradual increase in temperature from the poles to the equator. Decrease in humidity and precipitation toward the interior of continents causes zonation into belts of forest, grassland, steppe, and desert.

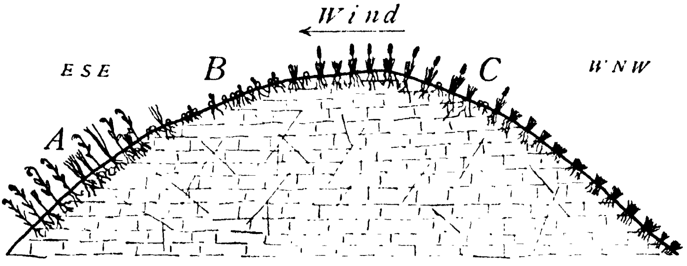

FIG. 173.—An inversion of the girdle arrangement of vegetation due to drifting of snow in the Tatoas at 2,160 m. Associations of *Calamagrostis-Luzula spadicea* (*A*), *Salix herbacea* (*B*), and the Trifidi-Distichetum (*C*).

The beltlike arrangement of communities is quite obvious in the filling up of still or flowing waters (decrease of moisture) (Fig. 174), in salt marshes (decrease in salt content) (*cf.* p. 197), on exposed ridges of high mountains (intensity of wind), in caves (decreasing light), in snowy regions of the north and of high mountains (duration of snow cover), and about bird roosts (intensity of manuring) (*cf.* p. 241). When species which spread peripherally and have rather different ecological requirements come into competition, they may form sharply bounded zones, since each species excludes the other (Fig. 91). Good examples of zonation are to be found in many recent papers on plant sociology.

FIG. 174.—Zonation of Lake Chambedaze, Auvergne. The floating *Comarum-Menyanthes* belt is followed by a *Carex lasiocarpa* belt; then follow belts of *Salix* spp. and *Betula pubescens*. (*Photo by Denis.*)

The zonation of algal associations on rocky seashores has been much studied, since Örsted (1844) called attention to it. It is of universal occurrence and is due principally to the light relation. In general, four zones are recognized (*cf.* Sernander, 1917; Kylin, 1910; Häyrén, 1914, etc.):

1. The deepest is the sublittoral or extra-littoral zone as far down as red algae extend (*Rhodomela subfusca*, *Corallina*, and *Ceramium* species, etc.).
2. The lower littoral zone or zone of brown algae, with the Fucaceae.

3. The upper littoral zone, or zone of green algae, lying between the highest flood tide and lowest ebb. This is the region of *Chaetomorpha*, *Ulothrix*, *Cladophora*, and *Ulva*.
4. The supra-littoral zone or zone of lichens, with *Verrucaria maura*, *Rhizocarpon* spp., etc., within reach of spray.

Within these principal zones more or less distinct subzones or horizons may often be distinguished. Exceptions or inversion of the usual zonation deserve particular attention, since they reflect special local conditions often slightly apparent.

Altitudinal Zones.—Different levels of altitude on mountains present an important special case of the beltlike arrangement of vegetation. As shown in Fig. 175, the different belts follow one another on the slopes of the mountain, giving by their physiognomy a quick survey of the changes of climate. Only when the slope of the land is extremely gentle may the horizontal and vertical zones merge into one another. The number of clearly marked altitudinal zones increases with the height of the mountains and with nearness to the equator. Many other factors come in, however, in opposition to this general rule, as, for example, the number and vertical extent of the climax communities of the region.

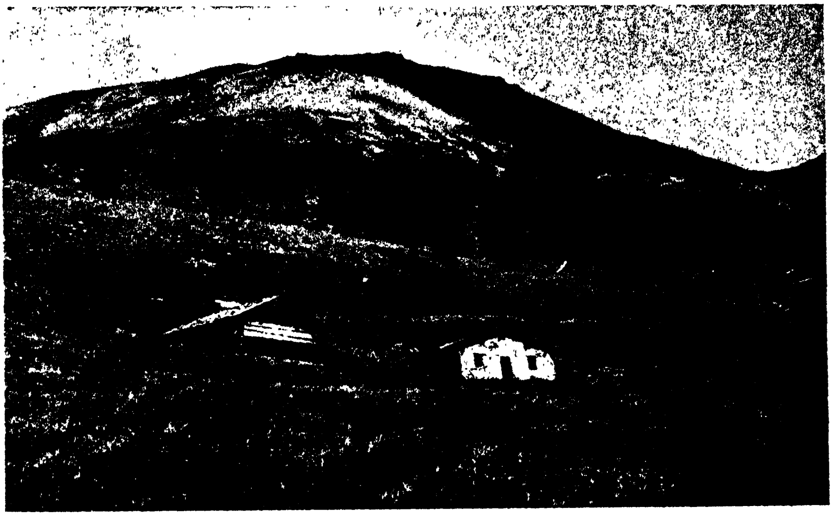

FIG. 175.—Altitudinal zones in the Swiss National Park. The *Larix-Pinus cembra* zone to 2,200 m., *Pinus montana prostrata* zone 2,200 to 2,300 m., alpine meadow zone 2,300 to 2,550 m., and the foreground of *Nardus* grassland induced by grazing. (*Photo by Heller.*)

Within the broader altitudinal zones secondary belts may be distinguished. These are best called horizons. The spruce zone of the northern Alps includes in places an *Alnus viridis* horizon. The beech zone of the Auvergne terminates upward with a narrow *Sorbus-Betula* horizon.

Bounding the Zones of Vegetation.—The distinguishing of altitude zones in mountains was one of the first activities in plant geography. It was attempted by Von Haller (1742) and Giraud-Soulavie (1783). But Sendtner in his description of the vegetation of southern Bavaria gave a stricter standard for the determination of zones. According to him, in order to determine a "plant region" (altitudinal zone), the altitudinal limits of every species of the area must be precisely given. The boundaries of the zones are to be set "where the greatest differences in the character of the vegetation come in, that is, where the largest number of new species appear and others disappear." This comprehensive method has met with scant approval. It is only apparently precise and is beset with many sources of error. It is simpler and safer to determine the boundaries of the plant communities. The boundaries of most of the species agree with the boundaries of the association.

After determining the upper and lower boundaries of all the associations in the southern Cévennes, three vegetative zones have been distinguished there (1915): (1) evergreen oaks up to 600 m.; (2) white oak up to 1,000 m.; and (3) the beech zone up to the summits. This distribution of zones corresponds to that of the climax regions (Fig. 161).

When the climax communities are relatively undisturbed in composition and distribution, as in the Alps and in the Carpathians, the altitudinal zones may be divided exactly as are the climax communities. The zones are then named after the climax communities.

General names for levels, like colline, montane, subalpine, alpine, must be used with caution. They are best combined with a vegetation name, as subalpine spruce-wood zone, alpine grassland zone. But even this cannot replace an exact definition of each zone.

Zones of vegetation are an expression of local conditions of climate —a fact that is generally overlooked. It is therefore often of doubtful value to try to point out parallels between the vegetations of widely separated mountains, as of the Alps and the Scandinavian mountains. Within the Alps there are great differences in the distribution of zones in the eastern, western, southern, northern, and central regions. The boundaries of the zones do not change in definite and corresponding directions, nor can it be said that one zone replaces another exactly.

Inversion of Zonation.—An inversion of the zones of vegetation is found occasionally in narrow canyons or on very steep shaded slopes. The upper reaches of such places receive more light and heat than the

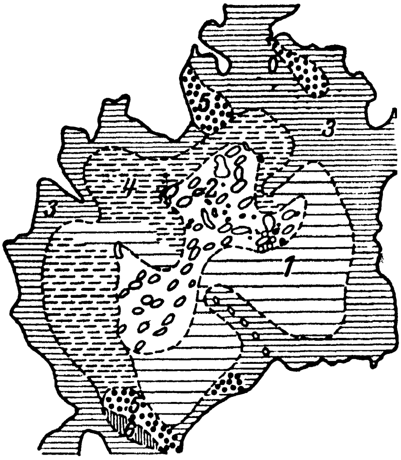

FIG. 176.—Association complexes in a Swedish moor 1:2,500. (*After H. Osvald.*) 1, Regeneration complex; 2, pond complex; 3, margin complex; 4, stabilized complex; 5, erosion complex; 6, grass moors.

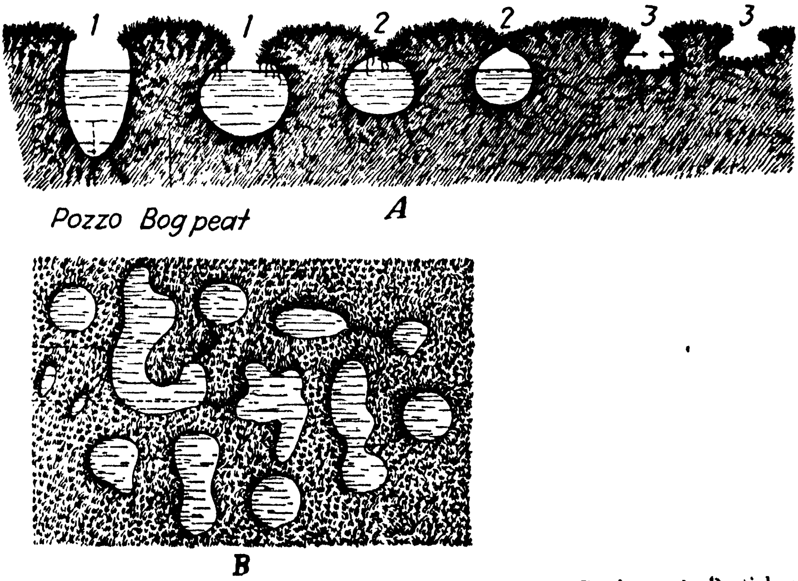

FIG. 177.—Association complexes of a "Pozzine" in Corsica. *A*, Partial cross section through a pozzine showing pits in the peat (1) with plankton and *Heleocharis acicularis* associations; overgrowth of pits by Caricetum intricatae (2); and filled pits occupied by Caricetum intricatae (3). *B*, Pozzine seen from above. (*After De Litardière and Malcuit.*)

lower. According to Beck, *Karstdolinen* that are long covered with snow have at top a spruce forest and farther down *Pinus pumilio* and scrub, then *Rhododendron* and alpine rock plants, and finally moor.

Community Complex.—Among dunes, on high moors, on recent alluvium, and on snow land the vegetation often appears as a promiscuous mixture of associations and fragments of associations. On closer examination there is an unmistakable regularity in the arrangement, in that very definite social groups occur repeatedly. The whole community complex, topographically limited, often forms a genetic unit (sere) and has a pronounced physiognomic unity. Moors and swamps were among the first community complexes to be studied (Fig. 176).

The "Pozzines" of the alpine levels of Corsica present a very characteristic land-forming complex. Their sociological composition and development were explained by De Litardière and Malcuit (1926) (Fig. 177).

Various complexes are to be distinguished in the high mountains, depending on the altitude and the substratum. There are wind-erosion complexes, snow-soil complexes, flood-plain complexes, etc. Well-defined community complexes of considerable extent are readily shown by means of maps. This method is especially useful to geographers.

Migrations of Plant Communities.—Natural displacements of area proceed very slowly. They are due either to changes in the habitat or to plant migrations still in progress. The work of Scandinavian scholars shows that the spruce forest is gradually creeping over the watershed from the Swedish to the Norwegian side of the Scandinavian mountains. The investigations of Lewis and others seem to demonstrate that in the park land of Alberta, willow scrub and stands of *Populus tremuloides* have recently invaded the adjoining grassland.

Displacements of the area of whole plant communities are often related to the advance or retreat of constructive or destructive species of high dynamogenetic power. The spread of a *Fagus* association is due to migration of *Fagus* itself. A Curvuletum can appear only where *Carex curvula* has become established. The contact of communities in well-vegetated regions gives rise to an intense struggle the outcome of which determines the entrance or the disappearance of numerous satellites.

The sudden appearance of natural associations, as in quarries, on floating rafts of débris, on the bottoms of drained ponds, and in artificial water reservoirs, is always evidence of a feeble interrelation of the species and very little mutual dependence among the different members of the community. Entire associations or fragmentary associations may be carried from one place to another on the feet of water birds or in the wool of sheep. Kreh (1929) studied the establishment of a Bidentetum tripartiti after the artificial drainage of a little lake near Stuttgart. In 1927 the lake bed was, for the first time, dry during the entire summer. In 1928 this very peculiar association was well developed; and in 1929 it was at its optimum.

The changes of climate which began at the close of the glacial period resulted in great migrations of vegetation in Central and northern Europe and, indeed, in all the northern hemisphere. Almost all of the plant communities in these regions are either of recent origin geologically speaking or have immigrated in very recent geological time.

Origin of Communities.—We cannot hope to know with certainty the origin and history of more than a very few plant communities. Paleontologic records and pollen analyses yield quite inadequate data. In most cases we must be content with analogies and with searching for the existing centers of distribution and lines of travel.

On general principles, the center of distribution of an association is to be sought where the association attains its best development, its greatest extent, and its richest floristic composition, where it varies into numerous facies, and where characteristic species are present in largest numbers.

On this basis one can explain the poverty of species and the lack of characteristic species of many water and moor communities found in the inner alpine valleys, while the same associations are richly developed in the alpine foothills and are well supplied with characteristic species. The Molinietum so widely distributed all over northern Switzerland and southern Germany dies out at Zizers (540 m.) in the Rhine valley. At this point only *Iris sibirica*, *Gentiana pneumonanthe*, and *Pulicaria dysenterica* remain as characteristic species.

The center of distribution of the familiar *Carex firma* association should be sought in the southeastern Alps. There it is most richly and luxuriantly developed and teems with characteristic species. The farther we follow it toward the north and west the fewer are the characteristic species, until in the Bernese Oberland it is all but gone (Braun-Blanquet, 1926, p. 235).

There is a community of western origin in northern Switzerland on leached high-terrace gravels. It is mostly very fragmentary, containing *Quercus pedunculata*, *Q. sessiliflora*, *Calluna*, *Genista germanica*, *Deschampsia flexuosa*, *Carex pilulifera*, *Hypericum pulchrum*, *Centaurea nigra*, etc. Even at the edge of the Black Forest, which bounds the

Swiss area on the northwest, this community covers large areas. Here it is mixed with more distinctly Atlantic species such as *Galium hercynicum* and *Digitalis purpurea.* But in northwestern France it reaches its full development as the *Q. sessiliflora-H. pulchrum* association, as described by Gaume (1924) from the forests of Orléans.

Along with this pronouncedly Atlantic outlier there are in south-central Europe other very fragmentary communities of distinctly northern origin, such as the *Carex limosa,* the *C. lasiocarpa,* the *Sphagnum fuscum,* and the *Isoetes echinospora* associations.

On the other hand, there are everywhere in northern Europe, according to Cajander (1921, p. 26), many associations which occur only in the most favorable soil conditions and are derived from communities that are much better developed farther south.

This is true also of the forest communities dominated by *Fagus silvatica.*

The data of geology, paleontology, and pollen analysis all indicate that the beech forest in relatively recent geologic time penetrated into central and northern Europe. Fossil leaves show that the beech was at home in central and southern France both in late Pliocene time and at the close of the glacial period. Nowhere do we find the beech associations better developed as climaxes and richer in important characteristic species than in southwestern and southeastern Europe. These were the postglacial centers of distribution of the beech associations. The north German and Scandinavian beech forests, with their raw humus and meager companion flora, give a wholly inadequate idea of the vigor, the richness, and the abundance of species of the original southeastern and southwestern beech associations. Whether the beech forests of southern Sweden are really climax communities is therefore very doubtful (*cf.* Tamm, 1921, p. 246).

Pioneer and Relict Communities.—From the standpoint of distribution in both time and space we distinguish aggressive, advancing pioneer associations and restricted, retreating relict communities. In regions of young topography pioneer associations predominate (*cf.* Cooper, 1923).

Among relict associations are those described by W. Christiansen from the oak scrub of Schleswig-Holstein and the remnants of high moor in southern Germany and in southern Europe generally. Such also are the communities of geologically ancient regions, like Madagascar (Perrier de la Bathie, Humbert), Cape Town (Marloth, Adamson), the mountains of the Sahara and the Sahara Atlas (Battandier and Trabut, Maire), and Corsica (De Litardière and Malcuit, 1926). Geographic and climatic isolation are essential for the preservation of relict communities. They are ill adapted for combat with the ubiquitous immigrants brought in everywhere by cultivation.

The rock-crevice associations of the headlands of the Mediterranean coasts from the Pillars of Hercules to Crete and Cyprus are relict associations of Tertiary origin. They are due to edaphic conditions and are rich in remarkable endemics. Maire and Braun-Blanquet have described a very local edaphic relict association in the Andryaletum mogadorensis of the island of Mogador. As the island is in process of destruction by the waves of the sea, the fate of this association is sealed. The forests of *Pinus silvestris* described by Schmid (1929), strictly limited by the rocky and gravelly substratum of limestone and dolomite, constitute relict associations (see also Braun-Blanquet, 1932).

The question of whether a given association is a pioneer or a relict acquires a special interest on the boundary of a climax region. The answer may indicate probable changes of climate. Are the forest islands in the alpine levels, or in the Podolian steppes, and the steppe associations in Bohemia and Moravia to be regarded as pioneers or relicts? When this is decided, we can calculate the extension of one climax region and the reduction of the other.

The difficulties which attend the answering of such questions, especially where human influences have disfigured the original vegetation till it is unrecognizable, are shown by the endless differences of opinion among North American investigators as to the natural boundaries of forest climax and prairie in the midwestern states.

There is a special group of very striking relict associations which at present are found only on artificial habitats of human origin. They have no known natural habitat. The elegant Centunculo-Anthoceretum punctati of clayey, non-calcareous stubble fields, with *Delia segetalis, Montia minor* and *Myosurus* has no natural habitat, in Switzerland or in the upper Rhine country (Koch, 1926, p. 25). Also the well-characterized miniature association of *Cicendia* and *Stereodon arcuatus*, which Allorge (1922) and Gaume (1924) have described from little-traveled wood roads in western and northwestern France, seems to occur only very rarely in natural habitats.

Vegetation Territories.—Synchorologic synthesis culminates in the definition and description of natural vegetation territories. This geographic concept has arisen from the related idea of floristic regions, rather independently of the findings of plant sociology (*cf.* Braun-Blanquet, 1919).

After the first attempts of Willdenow (1797), Treviranus (1803), and Humboldt (1805, 1807), the Danish scholar Schouw (1823) and the Swiss Auguste Pyramus de Candolle (1820) were leaders in establishing "botanical regions." Their regions were founded upon purely floristic materials, namely, the distribution of the families, genera, and species of the vegetable kingdom. The son of the last-named botanist, Alphonse de Candolle, subjected these floral regions to a sharp and trenchant criticism. He recommended also the division of the large and unwieldy regions into subregions, provinces, and districts, "down to the localities, the smallest recognizable geographic units."

The leaders of the plant-geographic movement during the last decades of the last century—Engler and Drude, Flahault, Beck, and others—followed the course outlined by De Candolle and extended his nomenclature.

A division of the earth on a purely floristic basis leaves wholly untouched a great many very important questions of plant sociology and biogeography. The vegetational zones of Grisebach, physiognomic in nature, are today easily located. But they are far too superficial. They leave out of consideration the very important data of plant sociology resulting from the investigations of the past decade.

The plant communities themselves furnish the one natural basis for a division of the earth for plant sociology. The associations and their subdivisions—the alliances, orders, and classes of communities—are the essential units.

But since all phytosociological classification rests upon a floristic foundation, it is exactly in this classification that systematic botany is of the highest service. All geographically limited species, genera, and families are related to certain communities, and these communities indicate the boundaries of vegetational regions. In delimiting these regions, both the purely sociological and the systematic viewpoint can and must be used. Thus it comes back indirectly, by way of the plant communities, to the position taken by Drude and others: the necessity of combining the floristic and phytosociological bases of classification.

In discovering and bounding vegetational regions thus conceived, the following characteristics must be considered:

1. The presence of unique or almost unique plant communities, their taxonomic rank, and their ecologic and floristic specialization, *i.e.*, degree of organization of the communities and the relation of these communities to the climax.
2. The presence of extensions of foreign vegetational territories and the dominance, suppression, or absence of certain communities or ecologic units (synusiae, formations).
3. The taxonomic position, number, and degree of development or ecological specialization of the unique, or almost unique, species of the region (endemism).
4. The presence of less minutely localized, disjunct species and the dominance, suppression, or absence of certain species or races.

A preliminary attempt to define vegetational regions on this phytosociological basis appeared in 1923 in "Origine et Developpement des Flores dans le Massif Central de France." The outline and definitions of the regional units used therein (first propounded in 1919) have been made available to the general public by being quoted almost verbatim in De Martonne's classic "Traité de Géographie" (vol. III. pp. 1284–1286).[1]

Following the floristic divisions of Engler, Flahault, Diels, etc., we recognize six regional units of different ranks: region, province, sector, subsector, district, and subdistrict. The content of these terms is as follows:

Region.—The region is the most comprehensive unit, characterized by numerous well-defined climax communities and many peculiar transition communities. It shows long-standing endemism in groups of high taxonomic rank (families, subfamilies, sections, etc.). The unity of the region is shown by the occurrence throughout, or nearly throughout, of identical or closely allied species of high sociologic importance (examples: Euro-Sibiric-North American region, Mediterranean region, Capetown region, oceanic (thalassic) region).

Province.—The province is a subdivision of the region characterized by at least one climax community and by various edaphic communities. It exhibits endemism of species and genera, and has genera which are only feebly represented in neighboring provinces (examples: Central European, Illyrian, and circumboreal provinces. The subalpine-alpine levels of the Alps and Carpathians would be a subprovince of the Central European province).

Sector.—An area without any peculiar climax community of high rank (alliance). The special climatic or edaphic communities and geographic variants are usually without generic endemism but often have notable endemic species (examples: Alpine, Carpathian, north European, Baltic, north Atlantic sectors).

Subsector.—Less clearly marked by communities and endemism (microendemism); possessing mostly some peculiar geographic races of more widely distributed communities, as well as species and communities which are lacking in the neighboring areas (examples: mountains of south-central Germany; Jurassic, north Alpine, central Alpine, south Alpine subsectors).

District.—Characterized by the presence of communities and species which are rare or lacking in adjacent areas, *e.g.*, district of the low plains of the upper Rhine, of the Mainz basin; *Ilex* district and *Erica cinerea* district of the European north Atlantic sector (Holmboe, 1913; Wille, 1915).

Subdistrict.—This lowest synchorologic unit is characterized by the mere dominance or suppression of edaphic or biotic communities and by the presence or absence of distinctive species (precinct of the Schaffhausen basin of Hegau, of the upper Danube).

The above definitions are given rather as an outline than as a finished plan. In striving to make the vegetational regions comparable and the units of equal rank, some kind of outline must be followed,

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[1] A still more inclusive biogeographic classification could well be built up on that foundation.

else we shall never get out of the present unhappy confusion into which an arbitrary handling of synchorologic terminology has led us.

The vegetation of Europe is diagrammed below (Fig. 178).

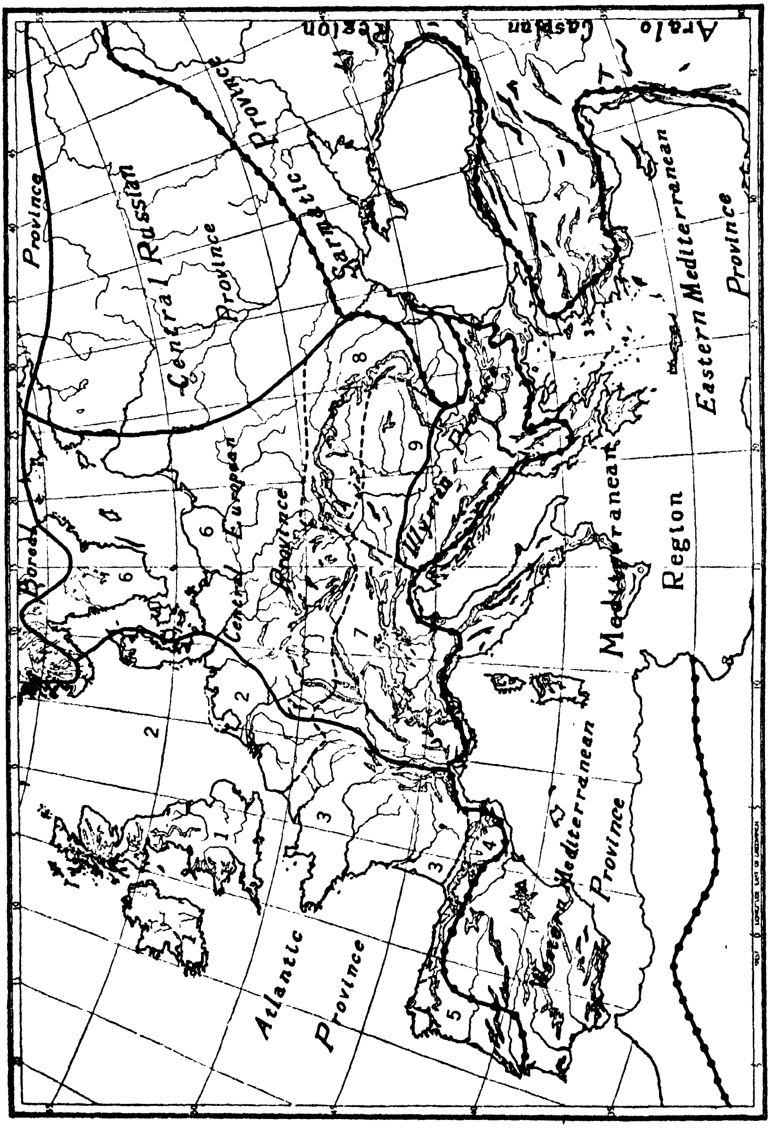

FIG. 178.—Map of the principal floristic and vegetational regions of Europe. Atlantic Province comprises (1) British Sector, (2) North Atlantic Sector, (3) Aquitanian Sector, (4) Pyrenees Sector, and (5) Iberian Sector: the Central European Province includes (6) the Baltic Sector, (7) the Alpine Sector, (8) the Carpathian Sector, and (99) the Pannonian Sector. (*After Braun-Blanquet.*)

Cartograpny.—Mapping of the smallest units—the associations or their subdivisions (subassociations or facies)—is possible only when large-scale base maps are available. But it is possible to enlarge existing maps by photography and to make records on the enlargements. Even these must be diagrammatic. In any case, the boundaries of the community must be exact, and this requires exact observation.

The higher social units, such as alliances and orders, are more easily mapped, since they usually occupy large, continuous areas. They are best shown by strongly contrasting flat tones. It is difficult to bring out the distribution of the larger units of vegetation by means of cross hatching. This has been admirably done by Luquet (1926) in his vegetation map of the Mont Dore massive (1:80,000). An internationally accepted color scheme would be very desirable.

Communities with zonal distribution are easily and satisfactorily shown by sketch maps with boundaries and shading in black and white (Figs. 105, 161, 176).

If there is interdigitation or mosaic arrangement of communities, whole association complexes (the regularly recurring, intermingling groups of associations) may be shown in one color or in one style of cross hatching.[1]

Observations of vegetation and photographs from airplane are not to be ignored as a means of geobotanic cartography. Stamp (1925) has used this method successfully in the delta of the Irrawaddy.

Line Transects.—Following the example of foresters, the approximate proportion of area occupied by plant communities of a uniform region may be obtained by line transects. Parallel straight lines are run through the area by means of compass and tape line, and the length of these lines in each community recorded. The Finnish foresters have determined the distribution of forest types in all Finland by means of line transects 26 km. apart.

Belt Transects.—For the study of gradual changes in vegetation, as in profiles or the transition zone between two communities, the belt transect is useful. This is a continuous series of quadrat areas running across the profile or transition zone. In certain cases it is sufficient to take one area in each well-defined zone of vegetation along the transect.

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[1] Scharfetter (1928) has discussed in detail methods of mapping vegetation, giving a good bibliography; and Brockmann-Jerosch (1931) has proposed an international color scheme.

PART VI

SYSTEMATICS OF PHYTOSOCIOLOGY

CHAPTER XV

THE CLASSIFICATION OF COMMUNITIES

A system which is scientifically sound presupposes a knowledge of the material to be classified. The study of plant communities is not at present far enough advanced to supply the minute details for a strictly natural and therefore permanent classification, but the fundamental outlines of a system that will express natural affinities may be pointed out. These outlines can even now be used to advantage in treating the communities of a well-studied area.

Attempts at a classification of plant communities reach well back into the last century. The changes this classification has suffered remind us of the history of systematic botany. The first grouping was based upon obvious but purely superficial characteristics: physiognomy. Later Warming based his division upon one of the most cogent causes of physiognomy: the water relation. He distinguished three great classes:

Hydrophytes, communities with a high water balance.
Mesophytes, communities with a medium water balance.
Xerophytes, communities with a low water balance (Diels, 1918).

The individual plant communities are arranged under these principal classes.

Schimper's classification (1898) is based more upon the development of vegetation. The climatic terminal communities are distinguished from the beginning and transition stages and are grouped under the headings: forest, grassland, and desert.

Following out the dynamic-genetic principle of classification, Clements (1916) worked out a system of plant communities, but it was overloaded with hypothetical assumptions.

Of the newer classifications, mention should be made of Graebner's division of communities according to the nutrients of the soil and also the physiognomic-ecologic divisions of Brockmann-Jerosch and Rübel (1912), Vierhapper (1921), Du Rietz (1921), and Rübel (1930).

Physiognomic-ecologic Systems.—Physiognomic-ecologic systems aim to arrange the floristically defined associations, or other natural and regularly recurring combinations of life forms in a series of externally related (physiognomic) "formations" (*cf.* p. 302). They do not attempt to arrange the fundamental units of vegetation, the associations, according to affinities based on their intrinsic characteristics or to place them in a logically incontestable series of group concepts. They aim at a system "which can be used without extensive study" (Brockmann-Jerosch and Rübel, 1912, p. 13). Obviously, such a system is possible only by making many concessions, and everyone must admit that his own arrangement is just as far from being "natural" as any other, in that it cannot give a clear picture of the situation to the student (Warming-Graebner, 1918, p. 341).

Some of the most ardent supporters of the physiognomic-ecologic method are beginning to doubt its adequacy. "It seems practically hopeless," writes Du Rietz (1924, p. 130), "to get plant sociologists to agree on a unified system of formations. And one must admit that in this grouping into formations, associations that from every other consideration are very closely related must often be classed in different formations."

To make things worse, the Brussels Congress (1910) gave this archaic classification its official benediction.

Meanwhile, influential voices have spoken against the Brussels pronouncement. "Would we," remarked Pavillard (1912, p. 13), "place white sheep and white rabbits in one genus just because they are white? The preliminary arrangement of associations according to their appearance is an expression of laziness, without philosophic grounds. Nothing could be more illogical than to create in this way *ecologic genera* whose *species* are the floristically defined associations."

Floristic Systems.—The most recent grouping of plant communities according to similarity in floristic composition proceeds from confirmed observation that every species—indeed, every race—has a definite, greater or lesser, indicator value. The species are used as signs of certain synecologic, syngenetic, and synchorologic relations. Similarly, therefore, the combination of species of two communities shows similarity in their life conditions in the widest sense. Since we combine floristically related communities into higher units, we are uniting, by floristic characteristics, units which should be united also on ecologic and historic grounds.

However, floristic criteria cannot be applied mechanically. Floristic coefficients of similarity, however carefully obtained, are not adequate if used alone.

Coefficients of Community.—Jaccard (1912) used the term coefficient of community for the similarity of the species lists of two regions, expressed in percentage. The concept is equally applicable for the comparison of two communities.

As the basis of comparison, one may use the entire list of species of two associations or the lists without the accidentals or only the characteristic combination of species.

Supposing that the number of species in association A is 100 and in B 150 and that 60 species are common to both; the coefficient of the community is:

$$\frac{60}{150} \times 100 = 40 \text{ per cent.}$$

The application of this method is limited, because only two species lists can be compared at once.[1]

It must be noted that the species are not to be reckoned merely as figures in a statistical comparison. Because of their entire sociologic relation they must be evaluated as social units of differing importance.

Evaluation of the Characteristics of Communities.—Universal rules for the systematic evaluation of floristic characteristics of communities cannot be laid down. As in systematic botany, now one, now another, character takes a leading place. Undoubtedly, fidelity is of supreme diagnostic importance. But in every case the summation of the floristic characteristics must determine the systematic relations. In doubtful cases the summation of all the floristic, ecologic, syngenetic, and synchorologic characteristics of the community must be decisive.

If one holds the usually accepted view that the association is defined by its combination of species and that it is the fundamental unit in the classification of communities, the affinities of the communities should be derived from a study of the association tables. The vast labor involved in the exact floristic analysis of associations proves useful, therefore, for community systematics.

1. Higher Community Units.—With the acceptance of the floristic principle of classification which forces itself irresistibly upon modern research, the general plan of the system is determined.

Alliance.—The most closely related associations are united into an "alliance." The floristic relationship is shown especially by the presence of a rather large number of species characteristic of the alliance. The alliance corresponds approximately to the genus of systematic botany. Koch (1926) has admirably arranged the most important alliances of water and swamp communities of Central

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[1] Guyot (1924) proposes to use the coefficient of community for determining the floristic correspondence between the individual stands of an association. The stands would be compared with a "standard," which would be the complete combination of characteristic species (*cf.* Jaccard, 1928). The significance of the generic coefficient has been discussed by Maillefer (1929).

Europe. From his work we have taken the following table, illustrating the actual procedure in establishing alliances:

TABLE 40.—ALLIANCE OF THE NANOCYPERION FLAVESCENTIS

Associations	Eleocharetum ovato-atropurpureae	Centunculo-Anthoceretum	Cyperetum flavescentis
Characteristic species of the association........	*Eleocharis ovata*	*Anthoceros levis*	*Cyperus flavescens*
	Eleoch. atropurpurea	*A. punctatus*	*Carex distans neglecta*
	Fimbristylis annua	*Sagina apetala*	*Juncus compressus*
	Lindernia pyxidaria	*S. ciliata*	*J. tenuis*
	Schoenoplectus supinus	*Juncus capitatus*	*Trifolium fragiferum*
		Plantago intermedia	
Characteristic species of the alliance	*Juncus bufonius*	*J. bufonius*	*J. bufonius*
	Gypsophila muralis	*Gypsophila muralis*	
	Hypericum humifusum	*Hypericum humifusum*	
	Centunculus minimus	*Centunculus minimus*	
	Gnaphalium uliginosum	*Gnaphalium uliginosum*	
	Cyperus fuscus	....	*Cyperus fuscus*
	Isolepis setacea	....	*Isolepis setacea*
	Carex oederi	....	*Carex oederi*
	....	*Panicum ischaemum*	*Panicum ischaemum*
	....	*Centaurium pulchellum*	*Centaurium pulchellum*

Just as the association is designated by attaching the suffix -etum to the stem of the genus name, so an alliance is designated by attaching the suffix -ion. We speak of the Ammophilion of the Mediterranean and Atlantic sand dunes, of a Rhodoreto-Vaccinion of the Alps, etc. Where necessary, a species name in the genitive may be added to the genus name, as Caricion curvulae. As key word we may use the designating species of one of the most important associations; or a new compound name (Nanocyperion, Magnocaricion) may be chosen. Occasionally, reference is made to the dominant life form, as in the Thero-Brachypodion of the Mediterranean region; or the geographic limits of the alliance may be utilized, *e.g.*, Potamion-eurosibiricum.

Order.—The "order" stands above the alliance. In pursuance of the floristic principle of classification, orders of communities are primarily circumscribed by their component associations and alliances. Each order has its special characteristic species. The individual orders are also ecologically characterized. To designate an order, the compound suffix -etalia is added to the root of the name of one of the most important associations, as in Molinietalia.

One of the best known orders of Central Europe, the subalpine Caricetalia curvulae of moderately to strongly acid, xeric or mesic soils, is divided as follows:

TABLE 41.—ORDER OF THE CARICETALIA CURVULAE

Alliances	Associations	Localities
Caricion curvulae	Caricetum curvulae alpinum	Alps
	Caricetum curvulae pyrenaicum	Pyrenees
	Festucetum halleri	Alps
	Trifidi-Distichetum	Tatra
Festucion variae	Festucetum variae	Southern Alps
	Festucetum alpestris	Eastern Alps
	Festucetum spadiceae	Southern Alps
	Festuceto-Chrysanthemetum delarbrei	Auvergne
	Festucetum eskiae	Pyrenees
Nardion	Deschampsietum flexuosi	Cévennes
	Nardeta (various authors)	Alps, Tatra, Pyrenees
	Nardeto-Plantagetum alpinae	Auvergne

In addition to the numerous characteristic species of the component alliances and associations of the Caricetalia curvulae, we may enumerate as characteristic species of the order: *Agrostis rupestris, Potentilla aurea, Sieversia montana, Trifolium alpinum, Gentiana kochiana, Phyteuma hemisphaericum, Leontodon pyrenaicus,* and other rather widely distributed acidophilous species of the central European mountains.

Class.—Orders which have numerous, or sociologically important, species in common may be united into "classes." These usually have a large number of species which are characteristic of the class and are, therefore, ecologically well defined.

In many cases (but not always) classes may coincide with "plant formations" which have long been physiognomically recognized, such as high moor, swamp, canebrake, heath, forest, dry meadow, and bush steppe. As far as possible they may best be designated by means of these commonly understood terms.

As a rule, however, it is necessary to give a precise geographic location. For example, the orders of the Molinietalia and Caricetalia fuscae could very well be put into the class of the Eurosibiric flat moors.

Circle of Vegetation.—The highest unit of a system or classification of vegetation on a floristic basis is the "circle of vegetation." It includes the totality of the communities and species connected with it that are confined, or largely confined, to a natural vegetational region.

It thus brings to its most comprehensive expression the individuality of vegetation, based partly upon climatic isolation and partly on floristic history.

Since we base our system of vegetation upon units (associations and species) which are strictly circumscribed in space, the spatial factor has a profound systematic importance. A division which thus rests upon the species must necessarily culminate in the regional unit of geographic and developmental history—the circle of vegetation. Consequently, in this highest unit the phytosociologic and phytogeographic divisions of the earth are the same. The areal basis of both is the "vegetational region" (*cf.* p. 355).

The vegetational region corresponds, in general, to the great life zones of our planet, the biogeographic regions. Thus, in these highest categories of the division of space, the unity of life and its organic interrelations find their most complete expression.

Similar combinations of life forms (formations, vegetation types) may occur in regions widely separated geographically, where they have never been in contact and therefore have no floristic relation to one another. These are to be classed as parallelisms, due to similarity of climate. Under similar climatic conditions similar life forms "evolved." This is the explanation of the similarity of the regions of broad sclerophyll forest in Mediterranean climates found in the Mediterranean region, California, Cape Colony, Chile, and southwestern Australia. Gams (1918) has proposed the name "isocies" for such communities; the term "homologies," used by Chodat, seems preferable.

2. Regional and Extraregional Units.—The more complicated the structure, the more highly organized the floristically defined social units the more strictly are they confined to certain parts of the earth. Forest associations, as at present understood, can hardly extend from one vegetational region into another. If they appear to do so, they may be regarded as "outliers." The beech forests of some Mediterranean mountains are outliers of the Euro-Sibiric-North American region; the areas of *Quercus ilex* scrub of the central Rhone valley, north of Valence, are outliers of the Mediterranean region.

Water and swamp communities, on the other hand, show a much greater capacity for distribution. For example, the order of Potametalia proposed by W. Koch (1926) is found in the Mediterranean as well as the Euro-Sibiric-North American circle of vegetation. Primitive floating communities (phytoplankton) have, of course, a still broader and more general range.

In characterizing a circle of vegetation, only those communities can be used which are more or less confined to a strictly bounded geographic region, *i.e.*, regionally bounded communities. In contrast to these there are "extraregional" communities whose range extends over several vegetational regions. Plankton communities with similar composition are distributed over large portions of the earth. They are generally extraregional and of little value for characterizing divisions of the earth. The regionally defined circles of vegetation are accompanied by at least two extraregional circles, those of the air and those of the water. Probably the soil, with its microcommunities (edaphon), constitutes another extraregional circle.

3. The Taxonomy of Communities.—As a basis for taxonomy (Braun-Blanquet, 1919, 1921), for determining the sequence of the higher units, the principle of sociologic progression, rather than a phylogenetic basis, has been proposed. Each unit is placed by means of comparison with all other units and not in a preconceived series of steps. This gives rise to true concepts of relationship. It depends primarily upon the orderly relations of the objects to be classified. The arrangement is thus brought into harmony with the prevailing views of the theory of knowledge.

Sociological Progression.—The arrangement of communities according to sociological progression means according to their progressive advance in organization. The "sociologically" simplest come at the beginning; the most complex, at the end of the series. First are those of extremely primitive ecology, the rather unstable floating communities of air and water. In these, the social union, if it exists at all, is so loose that one can scarcely speak of associations or even of alliances and, indeed, can consider them only as belonging to the more comprehensive units, orders, or classes (*cf.* Pavillard, 1925, p. 432). Between the members of these most primitive unions there is no competition for space or food; and no interdependence can be demonstrated except in cases of parasitism. The constituents of these floating communities stand on the lowest step of evolution and are of extremely simple structure, without adaptations. Each is an ecologic unit. They are, in general, widely distributed. There is no genuine layering in floating communities.

At the opposite end of the series stands the tropical rain forest in its majestic splendor and luxuriance, the type of the highest possible phytosociologic completeness. In its complex, many-layered structure it presents a marvelous picture of closely knit community life. Its manifold systematic and ecologic types of plants and communities are the most highly evolved, the most minutely adapted (Fig. 179). Somewhat less complex are the climax forests of temperate regions (see Frontispiece and Fig. 180).

Syngenetically considered, the simple floating communities are always the pioneers and do not reach beyond the pioneer stage. The highly organized forest communities, in whose structure the most

FIG. 179.—Interior of the liana-filled tropical rain forest on the Amazon River. (*From Huber, Arboretum Amazonicum.*)

varied types of communal life take part, are relatively stable end stages of a very long-continued process of adaptation and selection.

From these contrasting glimpses we discern what characteristics are of use in judging sociological progression. The most important are:

1. The kind of union which holds the species and individuals together. The closeness of the union is greatly influenced by the dependence of the constituents

upon habitat. Communities strictly related to a certain habitat show a greater interdependence of species than free-floating communities or unstable or accidental rooted communities.

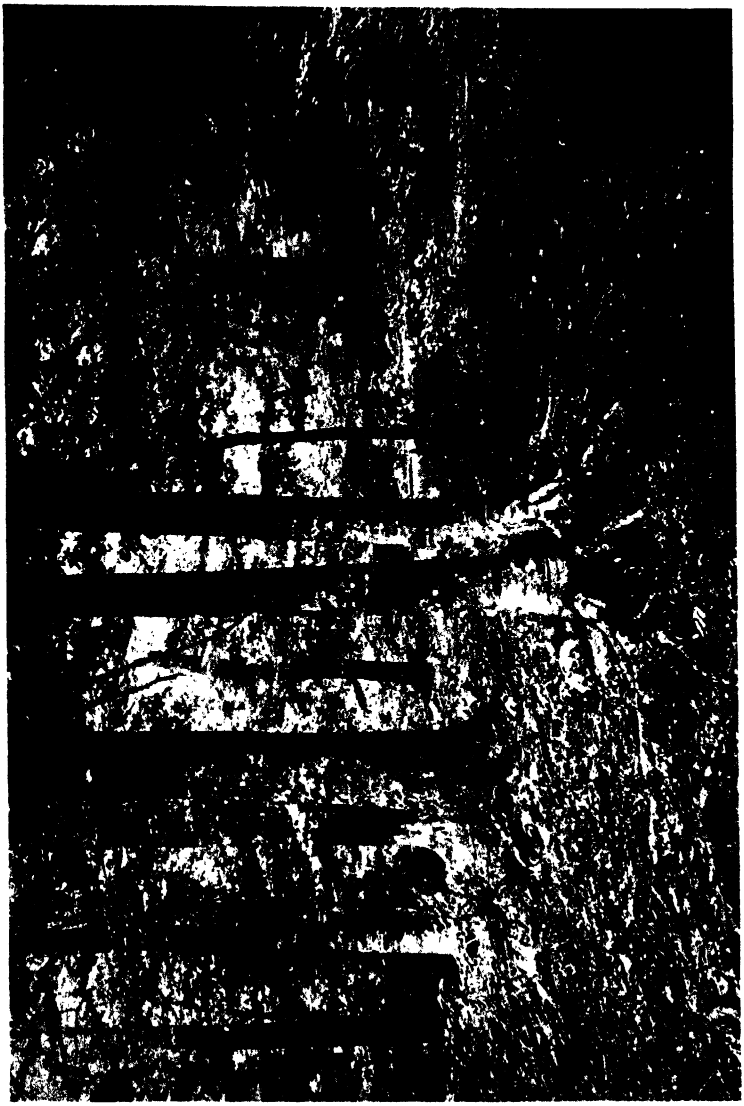

Fig. 180.—Climax forest of *Fagus grandifolia* with a small amount of *Acer saccharum*. Rome, Indiana. (*Photo by Land.*)

2. The presence of interdependence between the members of the community. Communities whose union is mere proximity are more simply organized than those with sharp competition between species and individuals. Open communities are generally simpler than closed.

3. Ecologic differentiation. The more varied the union in respect to layering, life forms and adaptations to social life the more complex and highly developed is the social organism. Communities made up of simple and ecologically similar life forms stand low in the scale of organization (therophytes).

4. The stability and duration of the communities. Simple pioneer and transition stages are of shorter duration and lower stability than the climatic climax.

5. Sociologic independence. Dependent communities, such as the algal communities of the Sphagnetum and epiphytic communities, are usually short-lived and simple in structure.

The higher units (circles of vegetation, classes, orders, alliances) offer no insuperable difficulties to classification according to sociological progression. The sequence of the circles of vegetation is determined by the level of organization of the dominant climax communities. First come the extraregional circles of air, water, and perhaps of the soil. Then follow the circles of polar regions, deserts, steppes, grasslands, and scrub; and finally those of scrub and of forest, each according to its own stage of sociological development.

In describing the plant communities of a circle of vegetation, or of any delimited area, the arrangement of the units down to alliances should be according to sociological progression. But there is little use in extending this arrangement to the associations and their subdivisions. The steps are here too close together, and the gradations too minute. Floristic relations suffice to determine the sequence of the lower units.

4. CLASSIFICATION OF PLANT COMMUNITIES ACCORDING TO SOCIOLOGICAL PROGRESSION

A. Extraregional one-layered communities of ecologically simple, similar, lowly, and unadapted organisms, with extremely loose union.

I. Floating communities of unstable composition.
  1. Composition of communities subject to rapid, often sudden, change (Aeroplankton).
  2. Composition more stable, often subject to cyclic rhythms (Hydroplankton).

II. Communities with more or less stable constituents.
  1. Populations of few species, on the surface of ice or snow, characterized by great mobility of the constituents (Cryoplankton).
  2. Bacteria, algae, and fungi of soil, often with active interdependence (Phytoedaphon).

B. Regionally delimited distinctly layered communities, mostly of rather high organisms with stronger mutual dependence.

I. One-layered communities without root competition.
  1. Free swimming (Pleuston).
    a. Oceanic. Sargassum-like communities.
    b. Limnetic. Lemnoid communities of *Lemna*, *Azolla*, *Salvinia*, etc.

2. Attached.
   a. Dependent communities growing on bark, incapable of further development, *e.g.*, Schizogonion cruenti, Graphidion scriptae, Xanthorion, Usneion, etc. (Ochsner).
   b. Communities growing on soil, with capacity for further development.
      (1) With few species, ecologically simple, on soil and rock.
         (a) Communities of soil algae and crustose lichens of short duration, often pioneer stages, *e.g.*, *Zygogonium*, *Cystococcus*, and *Stereonema* communities.
         (b) Endolithic and epilithic communities of rocks, *e.g.*, Gloeocapseta, Aphanocapseta (Fritsch, 1922), crustose lichen communities.
         (c) Submersed attached algal communities, *e.g.*, Acetabularietum, Schizotricetum (Schröter, 1902; Baumann, 1911, p. 494).
      (2) Moss and lichen heaths, with more numerous species and better ecologic organization.

II. Two- or more-layered,[1] mostly rooted communities.
   1. Open communities of slightly related commensals, involving competition for place to germinate and for food.
      a. Climatic climax communities without capacity for further development, communities of deserts and desert steppes.
      b. Edaphic; mostly pioneer communities: communities of sand dunes, talus, rock crevices, *e.g.*, Ammophilion, Potentilletalia.
   2. Closed communities. Competition for place to germinate, for space, and for food.
      a. Stability low. Constituents predominantly therophytes. Often ephemeral communities of cultivated land, ditches, etc., due to man; *e.g.*, Nanocypereto-Polygonetalia, Chenopodietalia.
      b. More stable communities with closer union.
         (1) Biologically uniform, often crowded communities of water and swamps with few species.
            (*a*) Submersed aquatic communities, *e.g.*, Litorelletalia and Potametalia.
            (*b*) Emersed communities of still waters, rooted in mud, mostly with few species; often forming extensive uniform crowds; swamp communities, *e.g.*, Phragmitetalia, Salicornietalia.
         (2) Bioecologically multiform communities of solid ground, mostly with numerous species.
            (i) Few-layered communities without dominant trees or shrubs.
               (*a′*) Aerial layering indistinct. Little influence of layers on one another. Flat moors, meadow, and tall-herb communities (grass-herb vegetation), *e.g.*, Molinietalia, Brometalia, Caricetalia curvulae, Seslerietalia, etc.
               (*b′*) Persistent double layering. More or less distinct influence of each layer on the other.
               (*c′*) Ground layer more or less open, dominated by the layer above, which is rarely absent. Dwarf-shrub communities, *e.g.*, Rhodoretalia.

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[1] Including root layers.

- (*d′*) Ground layer mostly closed (very rarely absent) dominating the layer above, *e.g.*, Spagnetalia, high moor.

(ii) Several-layered communities; lower layers more or less influenced by upper.

- (*a′*) Mostly three layered, often edaphic or biotic. Dependent epiphyte communities lacking or feebly developed. Shrub communities.
- (*b′*) Mostly more than three layered, often as climax in permanent equilibrium with the environment. Dependent epiphyte communities mostly present, *e.g.*, forest communities.

5. Classification of the Communities of Higher Plants of Bas Languedoc, France.—The following table of the plant communities of Bas Languedoc is offered as an example of the practical application of the principles of classification elaborated above. The vegetation covers a rather large area which has been intensively studied, and the table comes as the culmination of more than fifteen years of investigation. As a result of these studies, records exist of the analysis of many typical stands (30 from certain associations) taken from different parts of the area. The segregation of the associations into alliances, orders, and classes is made on the principle of floristic affinities.

Every unit, however, whether association, alliance, order, or class, has its special ecology and represents a more or less definitely circumscribed ecologic unit.

The arrangement of the higher units follows a sociological progression. It is, moreover, interesting to note that in the area under consideration this arrangement brings out at the same time a syngenetical scale which corresponds to the progressive succession. The higher parts of the scale approach more and more closely to the climax.

Attention may also be called to the fact that the groups at the base of the classification have, in general, a wide geographic distribution; in the upper groups territorial localization is more and more pronounced, so that the six final classes of shrubs and trees are almost exclusively limited to the Mediterranean region. These final classes are preeminently those which reveal the phytosociologic individuality of this region and which characterize it so wonderfully as possessing a highly specialized type of vegetation.

TABLE 42.—COMMUNITIES OF HIGHER PLANTS OF BAS LANGUEDOC CLASSIFIED ON THE BASIS OF THEIR SOCIOLOGICAL PROGRESSION

Associations	Alliances	Orders	Classes	Geographical distribution (of orders and classes)
Asplenium glandulosum-Phagnalon sordidum	Asplenion glandulosi	Potentilletalia	Europeo-Mediterranean chasmophyte communities on rocky slopes	Central and southern Europe; Mediterranean region
Alyssum spinosum-Erodium petraeum				
Parietaria ramiflora-Oxalis corniculata				
Potentilla caulescens-Saxifraga cebennensis	Potentillion caulescentis			
Polypodium-Anomodon viticulosus	Polypodion			
Adiantum capillus veneris-Eucladium	Adiantion	Adiantetalia		
Asarinetum rupestris	Anthirrhinion asarinae	Androsacetalia multiflorae		
Centranthetum lecoquii	Stipion calamagrostidis	Thlaspeetalia	Communities of calcareous gravel slides and talus slopes	Mountains of central and southern Europe
Agropyron junceum-Cyperus capitatus	Ammophilion	Ammophiletalia	Communities of maritime dunes	Western and southern Europe and Mediterranean region
Ammophila arenaria-Medicago marina				
Crucianelletum maritimae				
Diplotaxis erucoides-Amaranthus delilei	Diplotaxion	Secalinetalia	Weed communities of cultivated areas	Eurasia, northern Africa, etc.
Galium tricorne-Bunium incrassatum	Secalinion			
Scleranthus annuus-Spergula arvensis				
Bidentetum tripartiti (fragmentary)	Polygono-Chenopodion polyspermi			

TABLE 42.—COMMUNITIES OF HIGHER PLANTS OF BAS LANGUEDOC CLASSIFIED ON THE BASIS OF THEIR SOCIOLOGICAL PROGRESSION.—(*Continued*)

Associations	Alliances	Orders	Classes	Geographical distribution (of orders and classes)
Chenopodietum murali	Chenopodion murali	Chenopodietalia	Ruderal communities on soils rich in nitrogen	Very widely spread in warm, temperate regions of the earth
Silybeto-Urticetum	Hordeion murini			
Hordeum murinum-Carduus tenuiflorus				
H. murinum-Lepturus incurvatus				
Tribulus-Crepis bursifolia				
Sclerochloa-Coronopus ruellii	Polygonion avicularis			
Posidonia-Cymodocea	Posidonion	Potametalia	Submerged and floating aquatic communities of fresh and salt water of the temperate zone	Throughout the northern hemisphere
Ruppia maritima-Zannichellia pedicellata	Ruppion maritimae			
Zostera nana (sub-association)				
Myriophyllum verticillatum-Nuphar	Potamion eurosibiricum			
Potamogeton fluitans-Vallisneria				
Kochia hirsuta-Suaeda maritima	Thero-Suaedion	Salicornietalia	*Sansouires* communities on highly saline soils, wet or dry	Western Europe, the Mediterranean region, eastern Asia, etc.
Salsola soda-Suaeda splendens				
Salicornietum radicantis	Salicornion			
Salicornietum fruticosae				
Salicornietum inuletosum (sub-association)				
Salicornia macrostachya-Sphenopus	Staticion galloprovincialis			
Limoniastrum-Statice lychnidifolia				
Statice virgata-Artemisia gallica				

TABLE 42.—COMMUNITIES OF HIGHER PLANTS OF BAS LANGUEDOC CLASSIFIED ON THE BASIS OF THEIR SOCIOLOGICAL PROGRESSION.—(*Continued*)

Associations	Alliances	Orders	Classes	Geographical distribution (of orders and classes)
Scirpus maritimus-Scirpus littoralis	Phragmition	Phragmitetalia	Reed-swamp communities on the margins of fresh-water ponds and streams	Throughout North America and Eurasia, etc.
Scirpeto-Phragmitetum				
Phragmitetum isiaci (sub-association)				
Carex elata-Leucojum aestivum	Magnocaricion			
Heliosciadietum				
Preslia cervini-Heleocharis	Preslion cervini			
Isoetes setacea-Juncus pygmaeus	Isoetion	Isoetetalia	Aquatic communities of temporary fresh-water pools	Western Europe, the Mediterranean region, United States, etc.
Juncus capitatus-Isoetes duriaei				
Elatine macropoda-Herniaria glabra				
Juncus gerardi-Triglochin maritimum	Juncion maritimi	Juncetalia maritimi	Europeo-Mediterranean salt-marsh communities along the seashore	Western Europe and the Mediterranean region
Carex divisa-Lotus decumbens				
Plantago crassifolia-Schoenus nigricans	Plantaginion crassifoliae			
Holoschoenus romanus-J. acutus (subassociation)				
Trifolium maritimum-Agropyrum pycnanthum	Trifolion maritimi			
Schoenus nigricans-Holoschoenus	Holoschoenion	Holoschoenetalia	European wet grasslands on low, wet areas	Eurasia, the western portion and the mountains of the Mediterranean region
Molinietum mediterraneum				
Holoschoenus-Cirsium monspessulanum				
Juncus compressus-Trifolium fragiferum				
Arrhenatherum-Narcissus poeticus	Arrhenatherion	Arrhenatheretalia		

TABLE 42.—COMMUNITIES OF HIGHER PLANTS OF BAS LANGUEDOC CLASSIFIED ON THE BASIS OF THEIR SOCIOLOGICAL PROGRESSION.—(*Continued*)

Associations	Alliances	Orders	Classes	Geographical distribution (of orders and classes)
Anthyllis montana-Carex humilis	Bromion erecti	Brometalia	Dry grasslands of central and southern Europe, mostly closed communities	The northern Mediterranean region, southern and central Europe
Brachypodietum phoenicoidis	Brachypodion phoenicoides	Brachypodietalia phoenicoides		
B. phoenicoidis-Brometosum (sub-association)				
Poa bulbosa-Onopordon illyricum				
Sedum-Arabis verna	Thero-Brachypodion *a.* petrosum *b.* sabulosum	Thero-Brachypodietalia	Therophytic *garigue* on dry calcareous soil, open communities	Mediterranean region
Brachypodium ramosum-Phlomis lychnitis				
Ononis pubescens-Convolvulus lineatus				
Scleropoa loliacea-Statice echioides				
Barbula gracilis-Onobrychis caput galli				
Armerietum juncei	Armerion juncei	Rosmarinetalia	Shrub *garigue* on calcareous, rather impermeable soil	Mediterranean region
Phleum arenarium-Plantago arenaria				
Deschampsia media-Brunella hyssopifolia	Aphyllanthion			
Aphyllanthes-Leontodon villarsii				
Genista scorpius-Lavandula latifolia				
Rosmarinus-Lithospermum fruticosum[1]	Rosmarinion			
Astragalus narbonensis-Hedysarum capitatum[1]				
Corynephorus articulatus-Helianthemum guttatum	Helianthemion guttati	Lavanduletalia stoechidis	Mediterranean shrub heath on somewhat acid siliceous soil	
C. canescens-Nardurus lachenalii				
Erica scoparia-Lavandula stoechas	Cistion ladaniferi			
E. arborea-Adenocarpus				

TABLE 42.—COMMUNITIES OF HIGHER PLANTS OF BAS LANGUEDOC CLASSIFIED ON THE BASIS OF THEIR SOCIOLOGICAL PROGRESSION.—(*Continued*)

Associations	Alliances	Orders	Classes	Geographical distribution (of orders and classes
Salix purpurea-Salix atrocinerea	Populion albae	Populetalia albae	Flood-plain forest	
Populetum albae				
Pinus salzmanni-Quercus pubescens[2]	Pinion salzmanni	Quercetalia pubescentis	North-Mediterranean deciduous oak forest	Northern Mediterranean region and southern Europe
Buxus sempervirens-Cytisus sessilifolius	Quercion pubescentis-sessiliflorae			
Quercus pubescens-Buxus				
Quercetum cocciferae galloprovincialis	Quercion ilicis	Quercetalia ilicis	Mediterranean broad sclerophyll forest, the climax of the Mediterranean region	Mediterranean region
Quercus ilex-Q. pubescens				
Quercetum ilicis galloprovincialis				

[1] The two associations occur both with and without *Pinus halpensis* (planted).

[2] A relict group, rare, and apparently disappearing in the Cévennes.

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