PRACTICAL
PLANT BREEDING

by W. J. C. Lawrence
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FOREWORD

by SIR DANIEL HALL, K.C.B., F.R.S., LL.D.

THERE can be few men better fitted than Mr. Lawrence, the author of this book, to introduce the practical gardener to the scientific principles that should guide him in attempting to raise new varieties by breeding. Mr. Lawrence began life as a gardener, he is now the highly qualified curator of the John Innes gardens. He has learnt his science by long collaboration with men working at plant breeding from the standpoint of pure science, until he was able to begin investigation on his own account and, by his studies of fruit, *Dahlia* and *Streptocarpus*, to add something to the general body of knowledge.

But he never lost the outlook of the gardener; he knows the requirements of the practical man and can appreciate his difficulties. The science of genetics, created as it has been during the present century, cannot off-hand resolve all the difficulties of the practical breeder nor offer him a short cut to success. But it is providing him with a systematic method; year by year it is furnishing him with new clues to progress; it can often enable him to calculate the chances of success, and it can warn him of what is impracticable if not impossible. Many improved varieties begin with a chance plant observed to exhibit some difference from others in the batch. The scientific method can then inform the discoverer how he can best proceed to "fix" the new form, or indeed if it will be possible to fix it.

To both the technique and the procedure that constitute the working equipment of the plant breeder Mr. Lawrence's book provides a sound guide, informed with the most recent results of science.

I would ask the readers not to allow themselves to be put off by what is at the outset a strange vocabulary. Chromosomes, polyploidy, look formidable words, but each stands for something definite that can otherwise only be set out in many words. Such words soon become familiar and offer no more difficulty than *Eschscholtzia* or *Penicillium*.

PREFACE

ALTHOUGH the practice of plant breeding is as old as civilization, little advance has been made in the methods employed until the last decade or two. For years the simple traditional and empirical methods have been used, sometimes, let it be said, with considerable success. An era is now dawning, however, in which the demands for new and better forms of flowers, fruit, and vegetables become ever more insistent and exacting, and the breeder who wants to keep abreast of these demands must needs improve his knowledge and technique.

The laws of heredity depend in part upon chance, therefore chance is an inseparable factor in plant breeding. The breeder who is crossing and selecting his plants in ignorance of the laws of heredity (and chance) is gambling against heavy odds. He is wasting money, time, labour and material. The aim of this book is to show how wastage and the chances against success may be reduced to a minimum; and to inform the practical breeder who wants to produce something new and better what possibilities there are, what precautions he must take and what errors he must avoid.

First I have dealt with the structure of flowers, what happens when they are pollinated, and the general technique of self- and cross-pollination. Next follows a simplified account of the laws of heredity and the mechanism by which they work. This knowledge is largely unfamiliar to the great majority of those who need it. The average gardener, amateur or professional, has heard of atoms and molecules but not of genes, while the name chromosome is Greek to him. This ignorance is rarely from choice. It is my experience that people who hear the story of chromosomes and their genes for the first time are intensely interested in the new conception of heredity presented to their mind's eye. The laws are not difficult, though their unfamiliarity may make them a little strange at first. Actually they are simpler to work out than many everyday calculations, e.g. the cost of several hundred flower pots at so much a cast. In the last part of the book I have dealt with the various methods, problems and results of plant improvement and indicated in what ways the science of plant breeding is likely to be of importance in future practice. Throughout the book technical terms have been omitted except where it was essential to use them.

There are excellent books for the research-station plant breeder and the man engaged in the large plantation industries. There is also a very good popular handbook on Mendelism. As far as I am aware there is no book written from the point of view of the amateur gardener and nurseryman, or for the student who is beginning to specialize.

The object of this work therefore is to outline in simple terms the scientific background of plant breeding, and to provide a concise and reliable guide for the practical man.

My thanks are due to colleagues and friends for their helpful advice and criticism, to Dr. K. Mather for the figures of Tables IV and V, to Miss Brenhilda Schafer for assistance in the preparation of the manuscript, and to Messrs. H. C. Osterstock and A. F. Emarton for the preparation of the illustrations. I am also indebted to the authors acknowledged for the use of text-figures.

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CHAPTER I

THE STRUCTURE OF FLOWERS

A FLOWER is a structure or mechanism specially designed to reproduce the species: and in plant breeding we make use of this mechanism in an attempt to determine the kind of progeny the plant shall have.

In its essence the mechanism is relatively simple, but during the evolution of flowering plants there has arisen an immense variety of flowers, in which the parts of the mechanism have been altered in countless ways. Necessity, that is competition for existence, was the mother of these many inventions, all of them designed to secure the greatest efficiency in reproduction, according to the special requirements of each plant. The number of inventions, however, is apt to be a little bewildering to the would-be plant breeder, and in order to understand them we shall first make a rapid survey of a few of the modifications in flower structure. In particular we shall observe the various modifications of the reproductive organs, since recognition and correct manipulation of these is the first requirement in plant breeding.

The chief parts of a flower are of four kinds, usually arranged in successive rings or whorls. The outermost whorl consists of the *sepals* (together called the *calyx*) which form a protective covering around the flower bud. Next comes the most conspicuous part of the flower, the *petals* (together called the *corolla*) whose chief function is to attract insects. The calyx and corolla together form the *perianth*. In a typical flower the sepals are green and easily distinguished from the delicate and more brightly coloured petals. Modifications of this order occur, however. Thus in some of the grasses and in such trees as the willow (*Salix*) and alder (*Alnus*), the perianth is entirely lacking; in the daisy family (*Compositae*) the calyx is often absent; in *Clematis* and *Anemone* the petals are lacking and the sepals are coloured; the sepals in the tulip and bluebell are coloured as brightly as the petals. Union, to a greater or lesser extent, of some of the parts of the flower is found in most plants. Examples are the morning glory and potato, where the petals are completely joined, though not to form a wide tube as in the snapdragon (*Antirrhinum majus*). *Salvia*, *Chrysanthemum*, *Streptocarpus*, sweet pea (*Lathyrus odoratus*), gentian (*Gentiana*) and *Calceolaria* are other examples in which the petals are united in various degrees and in various ways.

The Reproductive Organs

Enclosed by the perianth are the most important parts of the flower, the reproductive or sexual organs, namely the *stamens* and *pistils*. The stamen is the male organ and usually consists of a two-lobed *anther* borne upon a stalk or *filament*. Contained within the anther-lobes are numerous tiny rounded bodies called *pollen-grains*, which are the male germ-cells. When the anther is mature it opens and liberates the pollen, usually in the form of a fine yellow powder or meally dust. In some plants, notably the orchids, the pollen is not powdery, but the grains adhere to form a sticky mass. The number of pollen-grains carried by an anther may vary from so few as 32 as in the marvel of Peru (*Mirabilis jalapa*) to as many as 60,000 as in borage (*Borago officinalis*), while in size they may be so small as 1/30,000 in. as in the plane tree (*Platanus orientalis*) or as large as 1/100 in. as in hollyhock (*Althaea rosea*). In the great majority of plants the individual pollen-grains are too small to see and there are many hundreds to each anther.

The number of stamens in a flower may vary considerably. For example, Indian shot (*Canna*) has only one stamen, lilac (*Syringa*) 2, *Iris* 3, snapdragon 4, primrose (*Primula acaulis*) 5, lily (*Lilium*) 6, horse chestnut (*Aesculus Hippocastum*) 7, *Daphne* 8, mignonette (*Reseda odorata*) 10–20, while poppy (*Papaver*), apple (*Pyrus*), buttercup(*Ranunculus*), and many others have more than 20 stamens to each flower.

The shape of the stamens may also vary a lot. The anther may be boat-shaped, conical, round, curved, coiled (as in the pumpkin *Cucurbita Pepo*) or in the form of a spiral, may bear queerly shaped appendages, or even be branched (as in the castor-oil plant (*Ricinus communis*)). The filament too may vary considerably, being strap-, spindle- or club-shaped or forked, varying greatly in length, and sometimes being wholly absent. For example, the lily has six stamens, two of which are slightly longer than the others and mature later. The snapdragon has two pairs of stamens, one pair shorter, the other longer than the pistil. In the cabbage family (*Cruciferae*) two of the stamens are short and four long, while in the primrose the style is either half as long as the corolla tube with the stamens at the mouth of the tube, or the style is as long as the corolla tube and the stamens situated halfway down the latter. Adjacent stamens may be joined together, either by their filaments (e.g. pea (*Pisum sativum*)) or by their anthers (e.g. *Compositae*). The filaments of the stamens may be partly fused with the style or with the petals.

The anther, when mature, opens in various ways to liberate the pollen, either before or after the flower-bud opens. In the heath family (*Ericaceae*) the pollen is discharged through two short spouts or pores at the upper end of the anther. More frequently splitting is lengthwise or crosswise in varying degrees. For example in tomato and snowdrop small clefts are formed near the free end of the anther; in *Cyclamen* the whole of the top of the anther gapes open; in some members of the rose family (*Rosaceae*) transverse splitting occurs, while in the barberry family (*Berberidaceae*) little valves or trap-doors in the anther-wall open to liberate the pollen. In the orchids the pollen-grains are united into a mass by a waxy substance. Usually the splitting of the anther occurs quietly, so that the pollen is only discharged when the anther is touched or shaken. In a few cases however the opening of the anther is instantaneous and explosive in effect.

The wide range in the size of the stamens is well illustrated by the kangaroo thorn (*Acacia armata*), in which the anther is as small as a full stop on this page, and *Lilium auratum*, with its giant anthers 1¾ in. long and ⅜in. wide.

The *pistil* is the female or seed-bearing organ. It consists of a swollen lower part, the *ovary*, the tip of which is continued in the form of a stalk or *style*, and terminates in a special organ, the *stigma*. The ovary is hollow and contains the *ovules*, or seeds to be. The number of ovules ranges from one as in the grasses up to many thousands as in the orchids, according to the species. As in the case of the stamen, the number of pistils in a single flower may range from one, e.g. sweet pea, to several dozen, e.g. strawberry (*Fragaria*), and they may be free or joined together in part or whole. All three parts, ovary, style, and stigma, may differ considerably in size and shape. The style in some cases is wholly absent (e.g. poppy (*Papaver*)), and in others extremely long (e.g. angel's trumpet (*Datura suaveolens*)). It may be simple or compound. Thus in the primrose the stigma is round, in the horse chestnut pointed, split into two in the gentian and *Dahlia*, umbrella shaped in *Sarracenia*, funnel-shaped in saffron crocus (*Crocus sativus*), cross-shaped in the evening primrose (*Oenothera*), or split into three in *Freesia*. The stigmatic surface may be smooth or rough, hairy, covered with papillae, banded, lobed, depressed, convoluted, and so on.

Despite the great diversity of form of both stamens and pistils they are generally easily recognized, the stamens by their pollen, the pistils by their ovaries with the immature seeds in them.

In the great majority of flowering plants, stamens and pistils are found to occur in every flower. Flowers in which both sexual organs occur together may be conveniently described as *bisexual*. In some species however the stamens and pistils are borne separately by different flowers of the same inflorescence (*Begonia* species), or the whole of one inflorescence may bear staminate flowers and the whole of another inflorescence pistillate flowers (*Begonia*, maize, oak (*Quercus*)). Flowers which in this way are wholly male or wholly female may be termed *unisexual*. In certain species individual plants are either completely male or completely female (red campion (*Lychnis dioica*)). This condition is commoner among trees and shrubs, e.g. butcher's broom (*Ruscus aculeatus*), holly (*Ilex*), willow, than in herbaceous plants.

Finally, stamens and pistils may fail to develop properly, all degrees occurring from full development to complete abortion. Thus the reproductive organs of a plant may be so poorly developed that they are obviously incapable of performing their normal function. On the other hand the reproductive organs may appear superficially to be normal, and yet be incapable of producing pollen or yielding seed. Such flowers are therefore virtually male or female, according to which organs are suppressed or impotent, and at least one case is known (the raspberry (*Rubus idaeus*)), in which the flowers may be neuter, owing to the partial suppression of both pistils and stamens. Double flowers,

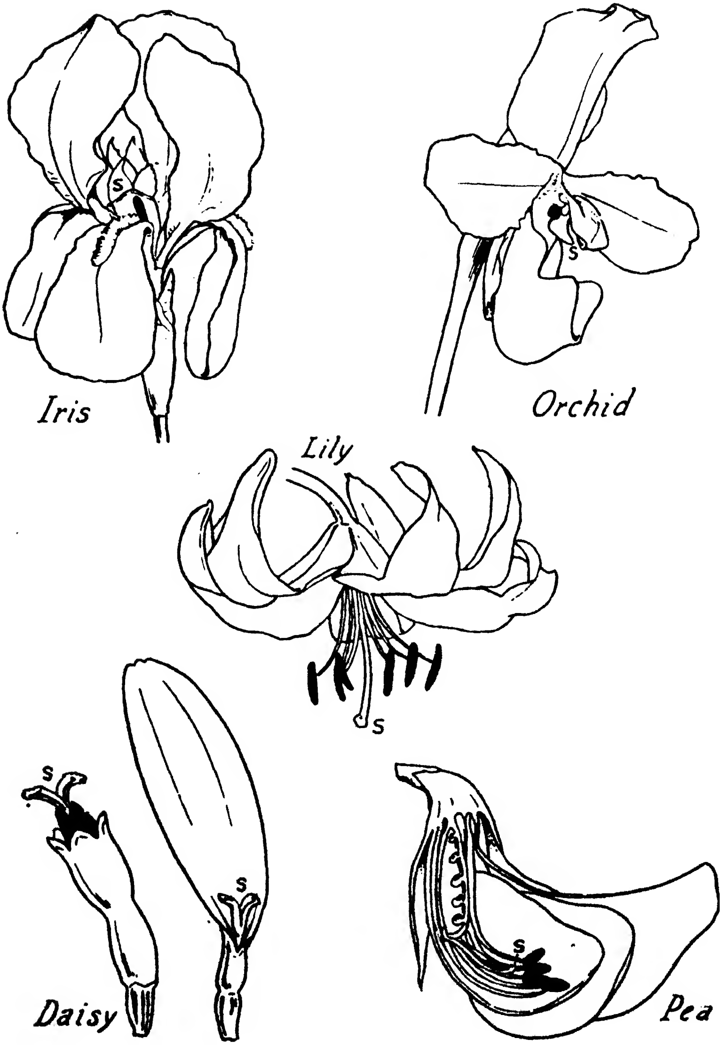


FIG. 1

in which the stamens and pistils have all been changed into petals, may be included in this neuter class. The ray florets of many members of the daisy family (e.g. *Dahlia*, *Chrysanthemum*) are neuter. In plants such as aster (*Callistephus*), *Dahlia*, *Chrysanthemum*, scabious (*Scabiosa*), and thistle (*Carduus*), what is ordinarily spoken of as a flower is really a cluster of flowers, called a *head*. The flower head consists of two kinds of flowers, the *disc* and the *ray* flowers. The disc contains small tubular flowers crowded together in the centre of the head. The ray flowers surround the disc, and each one bears a strap-like corolla closely resembling a typical petal. Other "flowers" which are really flower-heads are clover (*Trifolium*), sea-holly (*Eryngium*), and *Mimosa*.

Flowers may be borne singly, as in the iceland poppy (*Papaver nudicaule*), tulip and water-lily (*Nymphaea*), or on branching stems carrying two or more flowers, collectively known as the *inflorescence*, e.g. snapdragon, *Verbena*, grape hyacinth (*Muscari*), carrot (*Daucus Carota*).

As we have seen, the structure of flowers varies immensely, but the plant breeder who is observant will almost always be able to recognize the reproductive organs (Fig. 1). The perianth matters little to him compared with the stamens and pistils, nevertheless its form may determine the precise technique to be used in breeding and for that reason has merited our consideration.

Fig. 1.—Stigmas (marked S) and stamens (in black) in flowers of different structure. Middle: Lily, a simple flower for comparison. The stigma in Iris is the upper surface of the little ledge immediately above the stamen. The orchid is *Cypripedium*; the daisy is a *Chrysanthemum*, a bisexual disc floret on the left, a female ray floret on the right. The pea flower is drawn in section to show the stamens and stigma within the keel

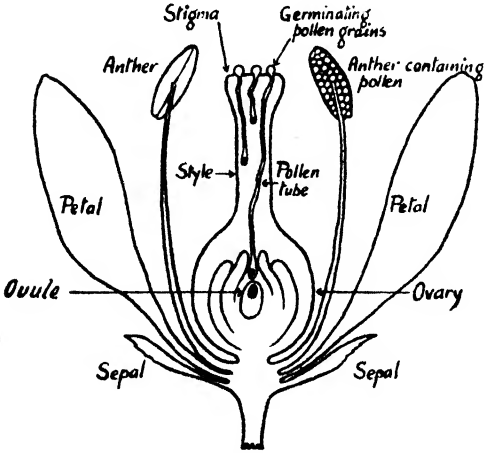
CHAPTER 2

POLLINATION AND FERTILIZATION

POLLINATION is the act of putting pollen upon the stigma, whether that is achieved by wind, insects, floral mechanisms or human intervention. A flower is said to be *self-pollinated* if pollen comes from any flower of the same plant, and *cross-pollinated* if the pollen comes from a different plant.

Under favourable conditions, shortly after the pollen reaches the stigma it pushes out a delicate pollen-tube, which begins to grow down the tissue of the style to the ovary, just as a seed sends out a root into the soil. Pollen will not germinate on the stigma unless the stigma is *receptive*. In those species like *Crocus* with compound stigmas, the approach of this stage is indicated by the opening or unfolding of the stigmatic branches. In some plants the receptive stage may be recognized by the shining appearance of the stigma caused by the secretion of a sticky, sugary fluid. This fluid not only enables the pollen-grains to adhere to the stigmatic surface, but is essential for their germination. On the other hand in some orchids and in the carrot family (*Umbelliferae*) the stigmas are sticky some time before other changes permit the germination of pollen. Many of the variations in the shape of the stigma and its surface (see p. 18) are designed to retain the pollen once it is deposited. Not every part of the stigma however is capable of germinating pollen. The monkey-flower (*Mimulus luteus*) has a two-lobed stigma, but only the inner surface of the upper lobe is receptive. In aster only the extreme edge of the branching stigma is receptive.

The distance the pollen-tube may have to grow down the style to the ovules is as little as a tenth of an inch in some plants, e.g. the calla lily (*Richardia*) and beet (*Beta*). By contrast in maize the distance may be as much as a foot and a half. Further, the rate of pollen-tube growth varies immensely in different species. Thus in some oaks the tube takes nearly a year to grow a tenth of an inch; in the autumn crocus (*Colchicum autumnale*) it takes 6 months to grow over 10 in. At the other extreme, in the true crocus the tube grows 4 in. or so in two or three days.



FERTILIZATION

FIG. 2. Showing how pollen grains germinate on the stigma and send out tubes which grow down to, and fuse with, the egg-cell or ovule. The uniting of the materials carried by the pollen tube and the ovary is the act of fertilization

When the pollen-tube reaches the ovule, material which it carries passes out and unites with similar material in the ovule. Thus every individual is a *double* thing derived from hereditary material received from the male and female parents. *This uniting of the materials of pollen and ovule is called fertilization.* (Fig. 2). The fertilized ovule develops into a seed, which in turn, when it germinates, gives rise to a new individual.

It should be noted here how very narrow is the bridge between one generation and another. No matter how large or complicated a plant is, the only connection between it and its progeny is one tiny cell and whatever is passed on in the process of inheritance must be carried in this cell.

The number of pollen-grains falling upon a stigma may be hundreds or even thousands, a great many of which may germinate and grow down the style. However many ovules there may be, only one pollen-tube can penetrate each ovule, and it is purely a matter of chance which of all the pollen-tubes penetrates a given ovule. *Fertilization is at random.* This is a very important fact for the plant breeder since, as we shall see later, it bears on the laws of inheritance.

Successful pollination is sometimes indicated by visible changes in the stigma, style, and other parts of the flower. In some members of the potato family the whole style drops off the ovary an hour after pollination, while in rose and *Fuchsia* the petals soon fall. A change in the position of the style; browning of the stigmatic surface; closing of multilobed stigmas (*Freesia, Dahlia*); the rapid fading and collapse of the flower (e.g. tulip, stock, (*Matthiola*) and *Pelargonium*) are often symptoms of successful pollination.

Before leaving the subject of pollination there is one thing we must notice which is important to the breeder, namely many flowers are specially designed in regard to pollination. For instance, it is very common to find the pollen being shed before the stigma is receptive (canterbury bell (*Campanula Medium*)). In such cases it is unlikely that the stigmas will be self-pollinated, cross-pollination being the rule. Conversely, and with the same result, there are some plants in which the stigma is ready before the pollen, e.g. maize. Sometimes cross-pollination is procured by a special structure or mechanism designed to prevent pollen from reaching the stigmas of the same flower (e.g. the climbing lily (*Gloriosa superba*)). At the other extreme the floral structure or mechanism may be such that it is almost impossible for the pollen to avoid reaching the stigma (e.g. sweet pea, tomato) and self-pollination is automatic. It will be obvious from the above that the technique of breeding will be influenced to a considerable extent by the pollination mechanism of the plant concerned.

CHAPTER 3

THE TECHNIQUE OF BREEDING

UNDER natural conditions pollination is largely the work of insects or the wind, and is almost entirely a matter of chance. If full control is to be exercised in plant breeding, artificial pollination between deliberately chosen parents must replace chance pollination by wind or insects. Suitable records of these controlled pollinations must also be kept, so that the pedigree of any seedling can be quickly turned up and the inheritance of characters clearly followed.

In this chapter some of the more important points in the technique of plant breeding will be described. In practice the necessary methods will differ with the type of plant being bred and according to the precise object in view. Experience alone will determine which methods are the best, and the breeder with an inventive mind will find many small but not unimportant ways whereby his art may be perfected.

The technique of breeding is described in considerable detail in this chapter. This does not mean that elaborate equipment or methods are necessary. Good work can be done with very few and simple tools.

PROTECTION

The chief devices employed to prevent unwanted pollen from reaching the female flower are as follows:

1. *Bags*

Single flowers, or part or all of the inflorescence, may be covered with paper bags, the mouth of the bag being tied around the stem of the flower. The best type of bag for all-round use is the transparent paper

FIG. 3.—The method of protecting flowers from insect visitors by the use of transparent paper bags

bag (Fig. 3). This can be made up in any suitable size and will withstand a considerable amount of wetting. It is important that the adhesive used by the manufacturer to join the edges of the bag should be waterproof, otherwise the bags may come unstuck on exposure to rain. Quite recently cellophane bags have appeared, and these, though costing more, promise to be useful. The mouth of the bag may be closed by tying with string; or by a turn or two of *soft* aluminium wire, which is secured by twisting the ends together. For general purposes gauge 20 is suitable. Wire is superior to string in that it does not swell in wet weather and there is no need to tie. Bags should be kept bundled up in store as on exposure to air and sun they become brittle and are inclined to split.

If the stem of the flower or inflorescence is prickled (e.g. blackberry (*Rubus*)), or if special precautions are necessary, a strip of wadding must be wrapped around the stem and the mouth of the bag tied over it. Heavy flowers and large inflorescences may need support after bagging, especially in windy weather. Stout canes driven into the ground close to the flower to be bagged provide the best support, and the string or wire securing the mouth of the bag may also be taken around the cane, thus supporting the bag as well as securing it. In the case of large bags the top of the bag should be secured to the cane by an additional tie, to prevent any movement of the bag in rough weather. The mouths of small bags may be folded over once or twice and secured with a paper clip or two.

Paper bags get very hot, and sometimes moist, inside in sunny weather, and in certain cases pollinations may suffer in consequence. Small perforations made in the top of the bag with a punch will assist in cooling, although care should be taken that they are not so large as to provide an entrance for insects.

When strong growing flowers and inflorescences are enclosed, the bag should be tied as close up beneath the flower or inflorescence as possible to allow plenty of room in the bag for elongation of the shoot. Failure to observe this precaution may result in the crushing of the flowers, through overcrowding within the bag, leading in extreme cases to the rupture of the bag.

FIG. 4.—Types of cage used for covering plants in the open ground

In those cases where paper bags prove unsuitable, muslin bags may be tried. As a rule they are not so satisfactory as paper bags, since they are not so weatherproof and quickly become limp in bad weather. The muslin should be fairly coarse. If a number of bags are wanted, the material may be cut to double the width, folded over and sewn down one edge to make a long sleeve, which can then be cut up to form open-ended bags. It is better to use a cane support for large muslin bags, slipping the sleeve or bag over both cane and flower shoot and tying it to the cane both above and below the flowers.

2. *Cages*

Cages are useful for covering the whole of a plant in the open ground (Fig. 4). The frame is made of rough yellow deal 2 in. by 1 in. and 3 in. by ¾ in. as shown in Fig. 5, and covered with muslin (tarlatan, 36 in., No. 600, shade 21), using tin-tacks to secure it to the wood. Useful sizes are 1½ ft., 2 ft., and 2½ ft. high, and 1½ ft. square inside. The usefulness of the cage is considerably improved if one of the glass substitutes "Windolite" or "Flexiglas" is used instead of muslin to cover the top. These materials are not only stronger than muslin, but are watertight, thus protecting the plant from rain. A strip of wood about 1 in. square should be nailed across the top of the frame before covering with the glass substitute, in order to raise the material in the centre sufficiently to throw off water (Fig. 5). When in use, cages should be weighted with bricks placed at the top corners. Two bricks will be ample as a rule, though four may be necessary if the wind increases to gale strength.

For quite small plants, muslin may be sewn on to a framework of stout galvanized wire. If the "legs" of this wire are left on the long side they can then be driven into the ground, thus securing the cage.

3. *Insect Proof Glasshouse*

The glasshouse is made insect-proof by fixing, inside the house, wire gauze over all ventilators. For permanent structures, copper or brass gauze mounted in removable wooden frames is best. The mesh should not be smaller than thirty to the inch. Ventilator rods and other vulnerable points where wire gauze cannot be used should be shrouded with muslin, and wadding used to stuff up the space between the glass and the eaves of the house. When very large plants and trees in pots are brought into the insect-proof house it will be necessary to cover the top

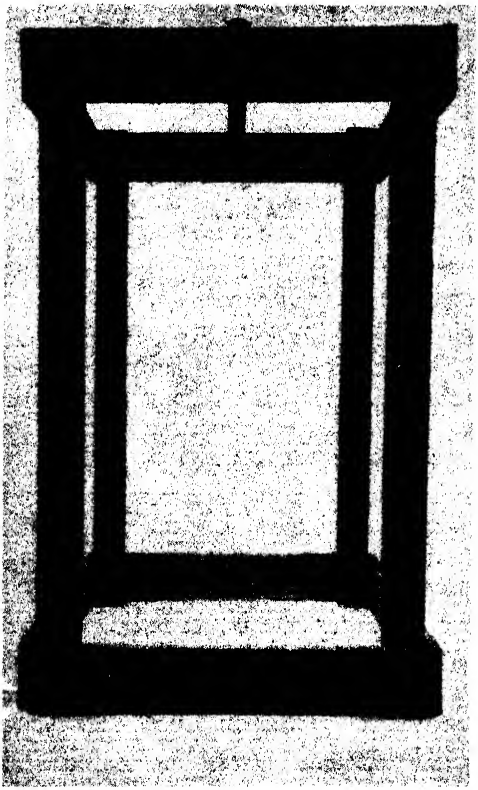


FIG. 5.—Showing the construction of the wooden framework of a cage

of the pot with muslin so that insects that hatch from the soil do not escape. Periodical fumigations will also help to keep down all insect life. In breeding houses of this kind it is important that plenty of ventilation is provided for, since the wire gauze very considerably impedes the flow of air, making it more difficult to maintain cool conditions inside the house.

4. *Isolation*

Adequate protection may often be secured simply by isolating plants. Thus outdoor flowers to be used for their pollen may be gathered in the bud stage and brought into a closed room, where they may open without fear of contamination by insects. The method of isolation is used in particular where true-breeding strains are being raised for seed. Each strain is grown as a separate block removed as far as possible from any other variety of the same species. The distance between blocks of any two strains will in the main be determined by the freedom with which cross-pollination occurs in the particular species. Thus strains of double asters can be grown fairly close together with little fear of crossing, since self-pollination is the rule in asters and the dense mass of petals prevents the free working of bees. By contrast, strains of nasturtium (*Tropaeolum majus*) need separating as far as possible owing to the high degree of cross-pollination which occurs.

Special methods of protection are useful in certain cases. For example, in the tulip the usual method is to place a loose ball of cotton-wool in the half-opened flower-bud to prevent the ingress of insects. In some members of the cucumber family a rubber band may be put around the unopened petals of the flower until it is ready for pollination, and replaced after pollination has been effected.

Whatever form of protection is adopted, care should be taken to see that all unwanted flowers are first removed.

Flowers which have shed their pollen, or whose stigmas have been exposed to foreign pollen, should never be enclosed. An inflorescence may carry more flowers than it is desired to pollinate, and these must be removed, or on opening they will shed their pollen and spoil the pollinations.

In compound inflorescences the success of pollination often depends upon the position of the flower. Thus the best results are obtained from flowers in the lower part of the flower spike of *Delphinium* and from the base of the inflorescence in the ten-week stock. In *Petunia*, the later flowers give larger and healthier seed capsules than those which open first. Differences of this kind are probably due to differences of nutrition, e.g. the terminal flowers in *Freesia* often fail to set if the basal flowers are pollinated and set seed, and the central florets in *Dahlia* set no seed if the peripheral florets are fertilized. Little is known however as to the precise causes of differences such as these, and the breeder must usually rely on his own observations and experience in regard to the choice of flowers for pollination, and select those flowers which he knows give the best results.

EMASCULATION

The majority of flowers are bisexual, and therefore the stamens of the seed parent must be removed before cross-pollinating, or self-pollination will occur. *The process of removing the stamens is called emasculation* and upon this operation the success of crossing very largely depends. The only generally satisfactory method is by means of forceps, although pointed scissors are sometimes useful. For large flowers a blunt-nosed pair of forceps will be suitable, but in the majority of cases a fine-pointed instrument is better, if not essential (Fig. 6). Forceps and fingers should be sterilized in methylated spirits before starting emasculation and as often as different varieties are handled. The spirit should be wiped off, or allowed to evaporate, before emasculating, especially when the stamens are close to the stigma, otherwise its delicate surface may be damaged if touched by the strong spirit. The flower should be emasculated as late as is safe before the bursting of the anthers. The anthers may be intact upon inspection but may burst immediately they are touched, or during their removal. If there is any suspicion of pollen having been shed during emasculation the flower should not be used. Carelessness in the observance of this precaution is likely to cause more confusion and inaccuracy in breeding than misapplication of any other part of the technique.

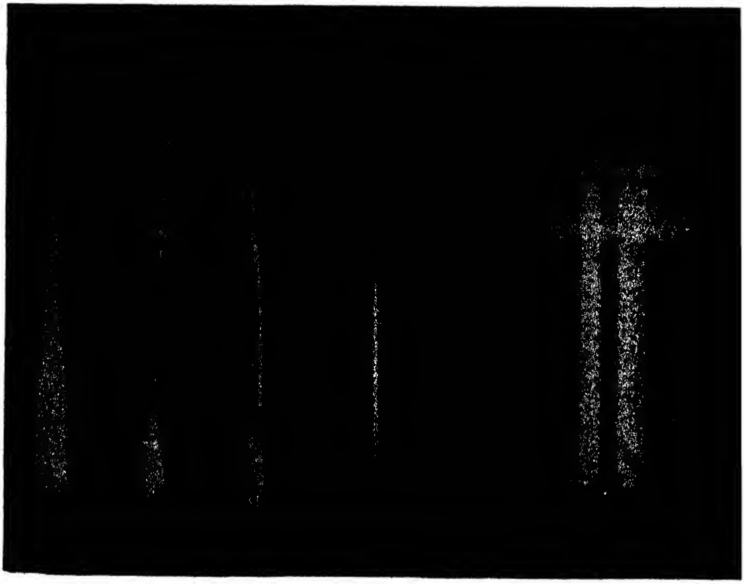


FIG. 6.—The plant breeder's tools—forceps, brush, scissors, and a wide-mouthed bottle for methylated spirit. With rare exceptions, only the fine-pointed forceps on the left, the camel-hair brush, and the spirit are necessary

In order to remove the stamens it is often necessary to remove some other part of the flower first (e.g. petals and sepals). Since emasculation is usually done in the late bud stage this means that parts of the flower which are still developing are prevented from fulfilling their normal work and the flower may suffer in consequence. For example, in raspberry the diminutive petals may be taken away with impunity, but if the protecting calyx is removed the young styles dry up and are rendered useless.

Emasculation of the specialized flowers of the pea family (e.g. sweet pea) is best made as follows. Select as large a flower as possible but before the anthers have burst. Hold it between the thumb and forefinger and fold back wings and standard, leaving the keel exposed. With a sterilized pair of pointed forceps gently slit the keel along its base (i.e. where it joins the rest of the flower) from top to bottom. The side of the keel can now be folded down under the style, securing it with the forefinger on the reverse side of the flower. In this way the stamens may be removed without taking the keel right off. After emasculation fold back the keel, wings, and standard as nearly as possible to the original positions to prevent the stigmatic surface from drying up. Emasculated flowers should be covered with waterproof bags, otherwise contamination may occur. Although the stigma is not receptive until thirty to forty hours after emasculation, pollination may be effected immediately after emasculation if desired, thus saving time and labour.

Occasionally plants are found in which, curiously enough, the mere removal of the anthers, even when other parts of the flower are untouched, causes the flower stalk to break off shortly afterwards. Such cases as this are rare, however, and generally if care is taken to do the minimum amount of damage to the flower, emasculation is successful. In contrast to the above examples, in some of the plants with tubular flowers pollinations are successful even though the whole of the corolla is pulled off, leaving the style naked (e.g. *Verbena, Streptocarpus,* forget-me-not (*Myosotis*)). If, when this method is employed, the stigma dries up and makes fertilization impossible, a short length of soda or drinking "straw" (those made of paper, not the real straws) may be slipped over the style, the top end of the straw being folded down to seal it. As an alternative to removing the corolla, it may be slit along a part of its length and the stamens removed through the side of the tube.

Curved scissors with fine points are sometimes of assistance in removing perianth parts, and a dissecting needle may occasionally prove useful. The edges of forceps may also be sharpened so that they serve for slitting corolla tubes, etc.

Precautions should be taken while emasculating to see that pollen is not shaken from other flowers on to the selected flower. In the open ground vigilance is necessary in regard to bees and other winged insects or they will alight in the boldest fashion and with great rapidity on the flower being handled.

POLLINATION

(*a*) *Self-Pollination*

Many plants will pollinate themselves without the aid of insects or wind, the relative positions of stamens and stigmas being such that pollen is bound to reach the stigma when the anthers burst. In plants such as these, all that is necessary in order to get seed from self-pollination is to protect the flowers from visiting insects. In not a few plants, however, self-pollination is rarely achieved for one reason or another, and artificial pollination thus becomes a necessity or little seed will be obtained. In such cases, if the stigma is not ready when the pollen is shed, pollen must be obtained from a flower opening later *on the same plant*. The technique for self-pollination is covered by the section on cross-pollination which follows.

(*b*) *Cross-Pollination*

In cross-pollinations the flower selected as female must be emasculated and protected until ready for pollination, and the flower selected as male also covered, the two flowers being of such an age that the stigma of the female flower will be receptive about the time that the anthers of the male flower burst. Pollen may be conveyed to the seed flower in a variety of ways. The pollen flower may be broken off and carried to the seed flower, the perianth stripped back until the stamens are exposed and the pollen dusted directly on to the stigma. If the structure of the flower is such that this cannot be done, pollen may be conveyed on the tip of the finger, or with a camel-hair brush. The chief use of the brush is where large numbers of flowers of the same variety have to be pollinated; its chief drawback is that it takes a considerable time to dry thoroughly after sterilizing in methylated spirit, though if several brushes are available this difficulty is largely overcome.

Another way is to use narrow V-shaped pieces of blotting paper, torn (not cut) to shape so that the pointed ends are fluffy. The soft tip of the blotting paper if used properly will not damage the stigma. A fresh piece of paper may be used for each pollination, which avoids the necessity for sterilizing. Stamens may also be broken off by gripping their filaments with forceps, holding them thus and lightly touching the anthers on the stigmas.

Flowers which have been bagged for their pollen are best detached with the bag still on and carried in it to the seed parent.

The ideal method of applying pollen is to allow it to fall in quantity on the stigmatic surface without touching the stigma with finger, brush, or stamen. If this is done it is impossible to damage the stigma, which should always be touched very lightly indeed. The pollen should be applied evenly over the whole of the receptive surface, or the full number of seeds may not be obtained. Although the pollen should as a rule be applied in quantity, there are a few cases where too liberal application of pollen leads to the breakdown and rotting away of stigma and style. On the other hand, in certain plants (e.g. plum (*Prunus domestica*), cherry (*Prunus avium*), orchids) the whole of the anther may be stuck on the stigma as soon as that organ is sticky, and left there.

As a rule pollination should be done at the earliest possible moment. This may actually be before the stigma is receptive; early application of pollen is successful so long as the pollen will lie in quantity on the stigmatic surface, since it will usually germinate as soon as the stigma becomes receptive. The advantage of early pollination is that the pollen tubes have the maximum time to grow down the styles, and in some crosses, especially species crosses, this growth is so slow as to render fertilization impossible unless pollination is done at the earliest moment. Instances are known where pollinations made in the bud stage are the only successful ones (Fig. 7). Pollen which lives for a very short while cannot of course be applied in this way. If after pollination a fair amount of pollen does not remain on the stigma the pollination should be repeated after a day or two. In composite flowers like *Chrysanthemum* with female ray florets and bisexual disc florets, only the ray florets are used for cross-pollination. To prevent self-pollination the disc florets must be cut off with a pair of curved scissors below the anthers just before they burst. Alternatively on some plants the disc florets can be pulled right out without endangering the success of cross-pollination. Next, the petals of the ray florets are cut off just

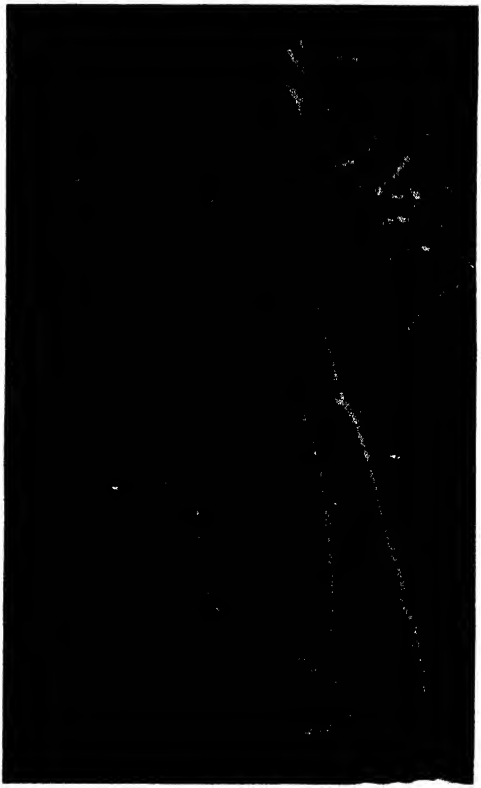


FIG. 7.—Bud pollination in the radish (*Raphanus sativus*). The inflorescences to the left were pollinated when the flowers opened. The inflorescence to the right was pollinated when the flowers were in the bud stage. Note the difference in the seed set

From Kakizaki and Kasai, "Journal of Heredity"

above the stigma. By the time the stigmas are receptive the lengthening of the styles will have caused the stigmas to protrude sufficiently from the base of the flower to make pollination an easy matter.

There are a number of plants which, though fertile, do not set seed from self-pollination, hence emasculation is unnecessary. When this condition is found in a composite flower like *Dahlia*, cross-pollination of the disc florets is easily effected by lightly rubbing together the discs of fully expanded flower-heads.

Apart from the application of pollen to the stigma, the success or failure of a pollination depends on several factors. The use of old pollen should be avoided, as the best results are obtained by using pollen from freshly burst anthers. If the seed parent is unhealthy or starved the seed vessels may never survive to maturity, or if they do the seeds may be incapable of germination. Similarly if the pollen parent is improperly grown the pollen may be bad or may die quickly. The pollen is more liable to suffer harm than the ovules through wrong cultural conditions. By "wrong cultural conditions" is meant over-feeding as well as under-feeding. Thus a "specimen" plant may be a poorer pollen parent than a "starved" one. Too high or too low a temperature may also spell failure, but in the great majority of cases average cultural conditions are quite good enough to ensure a high percentage of successful pollinations. It is probable that pollinations will be more likely to succeed if made in sunny weather when the air is fairly dry. The time of day is occasionally an important consideration, better results being obtained at one time than another. This is especially true of those plants in which the anthers burst early each day and whose pollen is at the same time very short-lived.

The length of life of pollen varies immensely. For example, in dry air the pollen of maize will only last about one day, most grasses two or three days at most, whereas pollen from the date palm has been successfully used after ten years.

In Table I is shown the length of life of pollen of various species. Longevity is considerably increased (see col. 2) if the pollen is kept in perfectly dry air. This is done by choosing anthers which are about to burst, putting them in a screw of tissue paper, placing this in a small, corked receptacle at the bottom of which is calcium chloride (Fig. 8). This substance rapidly absorbs moisture from the air, hence if the large vessel is air-tight, practically all moisture is removed from the air within the vessel. Pollen from most plants can be kept for several days in small cardboard pill-boxes if a warm, dry room or glasshouse is available. The anthers should be placed in the box just before they are ready to burst. Boxes must be sterilized by dipping them quickly in methylated spirits before using them again. The drier pollen is kept, the longer it lives. The adverse effect of moisture on pollen is also shown by the fact that under dry conditions pollen of the garden nasturtium (*Tropaeolum majus*) remained alive for eighty-eight days, whereas a similar sample after wetting for two minutes and then drying only lived for two days.

TABLE I

Species	*In normal dry conditions* days	*In perfectly dry air* days
Grasses	1–2	1–2
Mimulus luteus	10	65
Papaver Rhoeas	14	97
Cyclamen persicum	18	185
Lathyrus odoratus	23	45
Rhododendron indicum	47	—
Paeonia albiflora	56	157
Narcissus poeticus	72	—
Pinus sylvestris	74	279
Colchicum autumnale	92	229
Prunus domestica	180	—
Helianthus annuus	386	—

The fact that the pollen of many plants may be kept for quite long periods is highly important, since it enables the plant-breeder to hybridize species which normally flower at different times.

Immediately the flowers have been pollinated they should

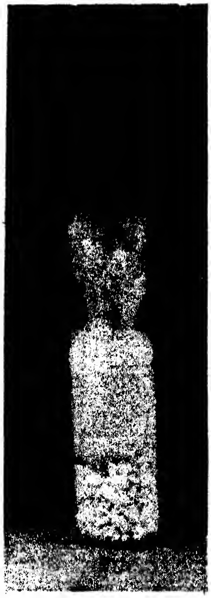


FIG. 8.—A method of keeping pollen. At the bottom of the glass tube is calcium chloride covered by a loose-fitting plug of cotton wool. The mature anthers are placed in the screw of tissue paper. The tube should be corked and labelled

be protected by replacing the bag or cage. In many cases it is possible to recognize successful pollinations within a day or two after the pollen is applied (see p. 24). Indications of fertilization such as these may be useful, since if they are not seen when expected, the pollination may be made again at once without waiting to see if the seed is developing, thus saving days or even weeks. It is a good plan always to make reciprocal pollinations, as some pollinations succeed better one way than the other.

If bags and cages are kept in place until the seed is ready for gathering, they may serve to keep it safe from birds. Not infrequently, however, ripening of the seed-vessels is retarded and even endangered if the bag is kept on, mainly on account of the excessive moisture which forms within it. As a general rule it is better to leave the seed vessels until quite ripe before gathering them. Some seeds will germinate while still "green," or if gathered "green" they will germinate after they have ripened in the seed packets. In most cases, however, the seeds keep longer and germinate better if allowed to ripen naturally on the plant. Care must be taken, however, to see that they are harvested before there is any danger of their being spilt from the seed vessel. Ripening may be finished by placing the seed pods in pans or paper bags or any other convenient and safe receptacle.

Records

It is desirable that records should be kept at each stage of progress. Uncertainty in plant breeding is deplorable, since it indicates bad workmanship and also lessens the interest of the experiment. Records need not be elaborate, indeed they should be as simple as possible. The amount of detail will be determined by the nature of the experiment. For critical work the records should enable each step to be checked with certainty, and should include descriptive notes of the relevant characters of parents and offspring. For simple breeding, the records should enable the pedigree of any seedling to be traced accurately.

Labelling

In all but the very simplest work labels must be used at some point or other. Thus if a branch or one or two flowers only have been pollinated then these must be labelled, since if this is not done they will either be lost to sight or the details of the pollination forgotten. The best way of marking pollinations on a plant is to use thin cardboard tags with strings. The most useful sizes are $\frac{1}{2}$, $\frac{3}{4}$, and 1 in. (Fig. 9). For all flower colours except yellow, yellow tags are the best, since they contrast well with foliage and leaves, and are easily seen. For yellow-flowered plants white tags may be used, though medium red will probably be more distinct.

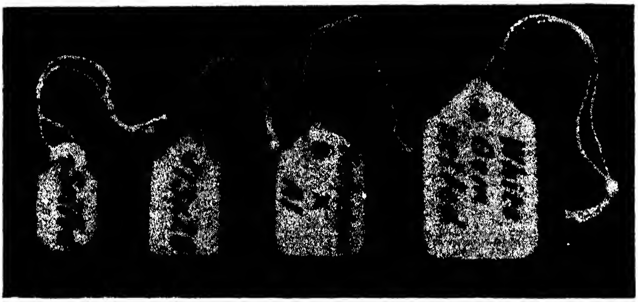


FIG. 9.—Marking-tags for labelling pollinations. The date of pollination may be written on the reverse side

The tags are hung round the stalk of the pollinated flower by passing the tag through the loop of the string, thus making it more secure. It is an advantage in some cases to hang the blank labels loosely over emasculated flowers—slipping the string through properly when the pollination has been completed. By this means the blank labels serve as markers in locating emasculated flowers. The tag should be placed where it is least likely to slip, as near to the pollinated flower or branches as possible so as to direct attention later to those seed vessels which must be watched and gathered.

On the label is written as briefly as possible particulars of the pollinations: "White Gem selfed," "Perfection × *A*1," "13 × 28," etc. *In crosses, the female parent should always be written first*, both on the labels and in the record book. The date of pollination may be written on the reverse side of the label. By referring to this when harvesting the seed, the time between pollination and harvesting is easily reckoned. In pollinations where bags have been used the label should always be tied on the stem *outside* the bag. By so doing, pollinations which have been completed are readily seen and reference can be made to the label without untying the bag.

Where the details of breeding work are important a record book is indispensable. In this the parents, date of pollination and any other notes and observations may be jotted down at the same time that the pollination is made. Later, the success or failure of the pollination may be recorded, the number of seeds set and similar details. Tie-on labels together with the notes and the record book will ensure great accuracy and possibly provide valuable information for future reference.

HARVESTING

When the seed vessel is ripe, it is carefully gathered, and usually placed entire along with the tag within a seed packet of a suitable size. Seed packets may be kept open standing upright in a suitable box, fastened with paper clips, or stuck down immediately, according to circumstances. If necessary the details of pollination and date of harvesting may be written on the outside of the seed packet, which need not then be opened to find out what is in it. Seed packets should always be stuck down with care, especially where small seeds are concerned, or they will escape at the corners of the packet. When very minute seeds are being handled (e.g. *Begonia*) it is better to put them first in a small seed packet, and then enclose this in a larger one. Seeds which are borne in fleshy fruits like tomatoes, raspberries, etc., must be removed from the fruit pulp, cleaned and spaced out on paper to dry. On no account should moist or wet seeds be sealed in seed packets. The seeds should be stored in a cool, dry place; heat and moisture are both likely to shorten the life of the seeds, if they do not permanently damage them. If the seeds are not cleaned before packeting they should be cleaned before sowing, seed which is obviously bad being discarded with the chaff.

PEDIGREE NUMBERS

If a number of different pollinations have been made and there are several families to be raised, some system of numbering will be necessary. Without such a system the tracing of descendants will be hindered and the labelling made an unnecessarily complicated business.

The simpler the system the better. The simplest way is to number consecutively all the plants of a genus as they are used and raised. Thus the first two parents would be 1 and 2, and if from them were raised fifty plants these would be Nos. 3 to 52. Each new parent introduced and each new seedling raised would be given the next available number, as described. Thus every individual has a different number and by means of the record book, in which the numbers occur in order, parents and progeny are readily traced. Moreover the minimum of writing is necessary for pollination tags and wooden family labels.

Another method is to start with No. 1 each year for each genus being bred, distinguishing the year by adding the last two figures of the year 1/37 or $\frac{1}{37}$ or 1–37. By this method members of the same family bear the same number and are distinguished by index numbers, e.g. $1^1/37$, $1^2/37$, $1^3/37$, etc., or 1/1/37, 1/2/37, etc. The chief advantage of this system is that it shows in some measure the relationship of the seedlings. The plant breeder will be able to work out his own system from the examples given above. Whatever the system adopted, the details on the wooden family labels should be copied on to the seed packets if they are not already there.

SCORING

As far as possible the breeder should watch his seedlings with the closest scrutiny right through their life, for two reasons. First, because not only will he be able to note the more obvious qualities such as relative vigour and rate of development of the different families, but he will be storing up in his mind an invaluable fund of knowledge regarding a multitude of facts too numerous to detail in the record book, which nevertheless go to build up that experience by which a man knows almost unconsciously the best course of action to take. As parents know in the most intimate way all the hundred and one characters and qualities revealed as their children grow to maturity, so the breeder should know intimately the characters and qualities of his plant subjects from germination to maturity. In practice, this ideal may not always be achieved. It is worth attempting, however.

Secondly, if an outstanding form is seen as soon as it flowers, there may be time to use it at once for further breeding work, whereas if the breeder does not visit his seedlings until they are all well in flower it may be too late to use the outstanding form in the current season. At the least this means that a whole year is wasted; at the worst, in the case of an annual form, it may mean the total loss of a promising seedling.

Though frequent visits are desirable, the main scoring should be done when the majority of the plants in a given family are all in flower together, since by so doing comparisons are more easily made and the relative merits of the seedlings readily seen. In this connection it should be remembered that first blooms are rarely typical in all respects, especially in form and size. In plants which it is the normal practice to "stop" this should be left undone, so that the true shape and true time of flowering of the seedling may be seen.

Care should be taken to miss nothing which may be of importance or useful. It is better to score the plants of a family individually at first and then add a note as to the character of the family as a whole, i.e. analyse, in the particular, before attempting to generalize. Points which should be specially noted are: flowering time, habit, resistance to pests and diseases, wet or drought; size and quality of leaves, flowers or fruits; fertility.

In the open field, especially promising plants may be marked with canes and sticks, so that they may be easily located on future visits.

CHAPTER 4

THE LAWS OF INHERITANCE

WE now come to the most important part of plant breeding, how characters are inherited. It is certainly possible to breed plants with some success without any knowledge of the laws of inheritance. But *no one can appreciate the possibilities of plant breeding or estimate the particular line of action most likely to lead to success until a working knowledge of the laws of inheritance has been acquired.*

The laws are extremely simple. They are unfamiliar to most people, however, and for this reason the reader will probably find a little practice necessary before he can apply them with facility. Only the most elementary knowledge of arithmetic is required, plus as much ability to reason as is demanded by, say, an easy cross-word puzzle. Provided each point is thoroughly grasped before proceeding to the next, the essential principles will be readily understood.

We shall begin with broad generalizations as they refer to the simplest sort of plant. Later there will be qualifications to make, but for the moment we are concerned with simple cases of inheritance.

If a self-pollinated plant gives seedlings identical with itself and they in their turn also give identical plants, then we may say that such a plant *breeds true*. This term, as well as referring to a whole plant, may also be used in regard to one or more characters, e.g. a plant may breed true for flower colour, though varying in other respects; or a plant may breed true for size of flower and quality of fragrance together; and so on. Now we have already seen (p. 24) that the germ-cells constitute a very slender bridge between generation and generation. Any hereditary character or material which is passed on must be carried by the germ-cells, the pollen and ovules.* If a plant breeds true then it means that its germ-cells are all alike in respect of the particular characters concerned. An easy way of picturing this is to use letters to indicate the plant characters. For example, suppose we have in mind a plant that breeds true for red flowers. We can say that all its pollen-grains carry something which controls the colour of the flowers, and this "something" we may represent by the letter *R* (for red). Similarly all the ovules carry the same "something," that is they carry *R*. It is obvious at a glance that if an *R* ovule is fertilized by an *R* pollen-grain then the individual that results from fertilization will be *RR*. Such a plant will breed true in regard to flower colour, since it can only pass on *R* to its germ-cells. We can summarize this and say that plants which breed true for a given character must have received the same hereditary material (in this case *R*) from both male and female parents.

If a self-pollinated plant gives seedlings which do *not* breed true then we say that it *segregates*. Just as a plant may breed true for one or more characters, so it may segregate for one or a number of characters. For example, a red-flowered plant self-pollinated might give progeny some with red and some with white flowers. Now we have already seen that the germ-cells of a plant that breeds true are all alike. Therefore the germ-cells of a plant which does *not* breed true must differ. Or to use our letter symbols, instead of all the ovules and pollen carrying *R*, some of them are, let us say, carrying *W* for white flower colour. If one of these white-flowered individuals should be found to breed true for flower colour, we should suppose that all its germ-cells carried *W*, and the hereditary constitution of all its progeny would be *WW*. All *WW* plants would breed true.

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* The ovules are the bodies which contain the female germ-cells.

The Gene

This "something" which is carried by the germ-cells from one generation to another is called a *gene*. No one has ever seen a gene, just as no one has ever seen an atom. Nevertheless, a great many experiments on the behaviour and effects of genes (and atoms) have been carried out which have told us quite a lot about them. As far as we are concerned in this book, we may say that genes are tiny specialized particles of living matter which govern the growth and development of the plant in every kind of way. One gene may control flower colour, another leaf-shape, a third the stature of the plant, while others again govern the time of flowering, sex, and the thousand other characters which go to make up the identity of the individual plant. At a moderate estimate there are between five and ten thousand genes controlling the development and inheritance of the average flowering plant. Usually a gene affects at least several characters. Thus when we talk about the gene *R* for red flowers we are really identifying it by its most striking effect. Actually it may control a number of other characters. Conversely, a character may be controlled by a number of genes, some having large and others small effects upon it. If we think over the last few sentences we shall see that the plant is a very finely balanced piece of mechanism, the appearance and working of which at every stage of its life depends upon the play and interplay of thousands of genes. *A gene, then, is the unit of inheritance which is passed via the germ-cells from generation to generation to produce its characteristic effect.* Each germ-cell, it will be noted, carries many hundreds of genes.

Because each plant is a double thing, part of its heredity material coming from the male and part from the female parent, genes usually occur in the plant in pairs, one of the pair being contributed by the female and the other by the male parent. In wild species the members of each pair of genes are usually identical, e.g. AA, BB, CC, etc. At rare intervals however a gene may change or *mutate*. We may represent the wild type gene by a capital A and the mutant gene by a small a. We shall call genes such as these, which are related in origin, *related genes*.

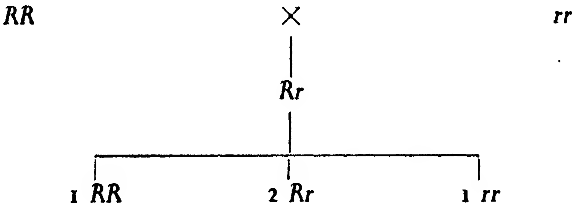
Related genes control the same sort of character though not necessarily in the same way.

Thus in the garden pea there is a pair of genes which govern the height of the plant. The effect of one of these genes is to produce a plant about 1½ ft. high. The effect of the other gene is to increase the height to 5 or 6 ft. We can use any symbols we like to represent the genes, e.g. D for dwarf and T for tall. The letters D and T, however, do not tell us that the two genes are related to one another, a very necessary thing to know, as we shall see. Hence we usually represent related genes, that is, members of a pair, by capital and small letters, T for tall and t for dwarf. Examples of the effects of gene-pairs are: hairiness/smoothness, colour/no colour, annual habit/biennial habit, entire leaves/compound leaves, wrinkled seeds/round seeds, double flowers/single flowers, early maturing/late maturing, etc.

MENDELISM

We must now see how genes are inherited and how they behave. For our first example of inheritance we will take two pure-breeding snapdragons, one red-flowered and the other ivory-white-flowered. As we have seen, all the germ-cells of the red snapdragon will be carrying the gene R, while all the germ-cells of the white variety will carry the gene W, or as we shall now call it, r. If we cross the red and white snapdragons, using the white form as the pollen parent, we find that the hybrids all have *pink* flowers, i.e. they are intermediate in colour. What has happened? In terms of genes, the R ovules of the red-flowered plant have been fertilized by the *r* pollen-grains of the white-flowered form. All the progeny therefore are of the constitution *Rr* and since they are all pink, we may conclude that the genes *R* and *r* together always have a more or less equal effect. It will be noted that the constitution of the three colour varieties is red *RR*, pink *Rr*, and white *rr*.

If a pink-flowered plant is now self-pollinated we find that the progeny are of three kinds and that they occur in definite proportions. *Approximately half of them will be pink, a quarter red, and a quarter white*, i.e. 1 red : 2 pink: 1 white. It does not matter which pink-flowered plant we test, they all behave in the same way; the same result is obtained if we cross-pollinate any two of them. The reason for this is easier to see if we make a plan of what has happened, putting letters to indicate the genes.



What, from these results, can we infer about the constitution of the pink-flowered hybrids? The fact that reds, having the constitution *RR*, were obtained from selfing a pink (*Rr*) means that some of the ovules and some of the pollen of the pink hybrid carries *R* genes. Similarly to obtain whites, *rr*, some of the ovules and some of the pollen of the pink hybrid must have carried *r* genes. The pink (*Rr*) forms therefore produce both *R* and *r* germ cells. Since the constitution of the pinks is *Rr* it seems logical that some of their germ cells should carry

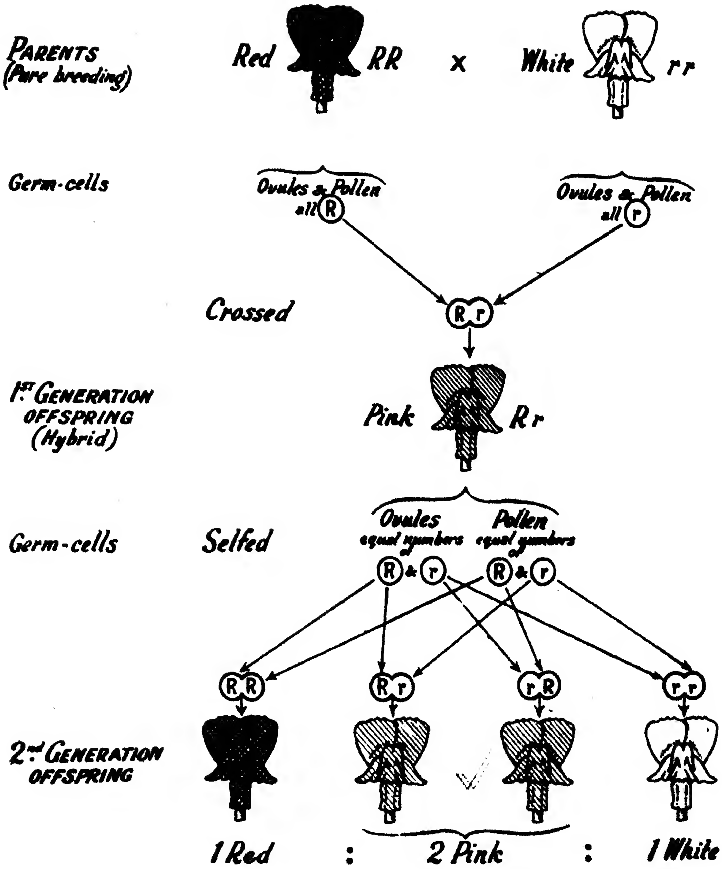


FIG. 10.—Diagram showing the inheritance and expression of a pair of genes, *R* and *r*, controlling flower colour in the snapdragon (*Antirrhinum majus*). The hybrid from crossing red- and white-flowered snapdragons is *intermediate* in colour (pink) and upon selfing gives one-fourth red, one-half pink, and one-fourth white-flowered plants in the next generation. Compare with Fig. 11

R and others *r*. We have still to explain, however, why pink selfed gives approximately one red, two pink, and one white. The explanation is simple and discloses the two fundamental principles of inheritance.

The first principle is that a germ-cell cannot carry both R *and* r*; it can only carry one of them at a time.*

The second principle is that R *and* r *germ-cells occur in equal numbers.*

However many ovules or pollen grains are formed in the ovary or anthers of the flower, half of them will carry *R* and half *r*. These are the principles discovered by the Austrian monk, Gregor Mendel,* and once they are grasped by the reader the inheritance of genes is readily worked out. Thus, with the two principles in mind we will turn again to our example of the snapdragons and see why it is that the ratio in the second generation is 1 red : 2 pink : 1 white. The scheme on the facing page illustrates our point.

All the germ-cells of the red parent carry the gene *R*, and all those of the white parent carry the gene *r*. Therefore when the two parents are crossed together the hybrid is *Rr*. From the two principles we see that the germ-cells of the hybrid will be of two kinds, those carrying *R* and those carrying *r*; and there will be equal numbers of each.

Now on page 24 we learnt that when the pollen tubes grow down the style, it is entirely a matter of chance which one fertilizes any particular ovule. This being so it follows that an *R* ovule stands as good a chance of being fertilized by an *R* pollen-grain as by an *r* pollen-grain. Similarly the chances are equal that an *r* ovule will be fertilized by an *R* or an *r* pollen-grain. In other words there are four possibilities:

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* The three principles mentioned in this chapter are given in simplified form and not as originally announced by Mendel.

An *R* ovule fertilized by an	*R* pollen-grain gives a plant	*RR*
R	*r*	*Rr*
r	*R*	*Rr*
r	*r*	*rr*

A glance at the last column will show that the result is 1 *RR* : 2 R*r* : 1 *rr*. What we have really done is to combine

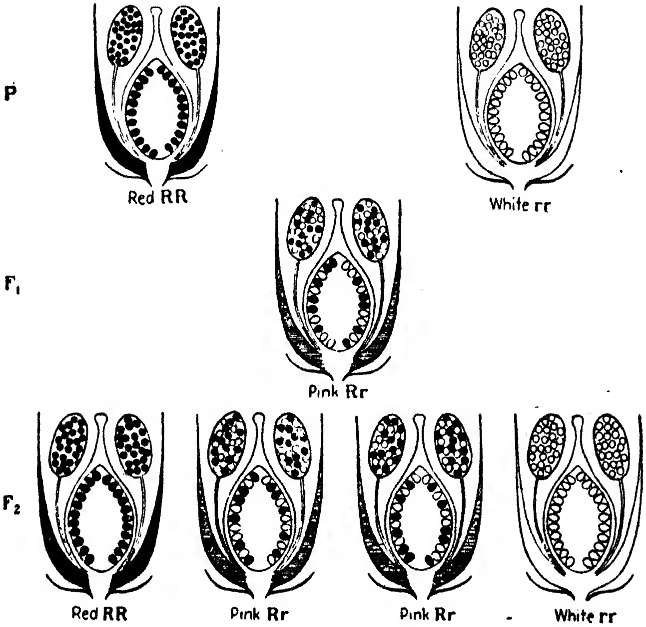

FIG. 11.—A panorama of the germ-cells through two generations after crossing red- and white-flowered snapdragons. In the diagram the black germ-cells (pollen and ovules) carry the gene for red and the white ones that for white. Although the F_1 has pink flowers the germ-cells are not pink, but half carry the red gene and half the white. In the F_2 one-fourth of the plants are red-flowered, one-half pink, and one-fourth white. Red-flowered plants always carry the red gene only, and breed true. White-flowered plants always carry the white gene only, and breed true. But the germ-cells of pink-flowered plants are always of two kinds, half carrying the red gene and half the white, and on selfing, the offspring are of three kinds—red, pink, and white in the proportions 1 red : 2 pink : 1 white
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R and *r* ovules in every possible way with *R* and *r* pollen-grains.

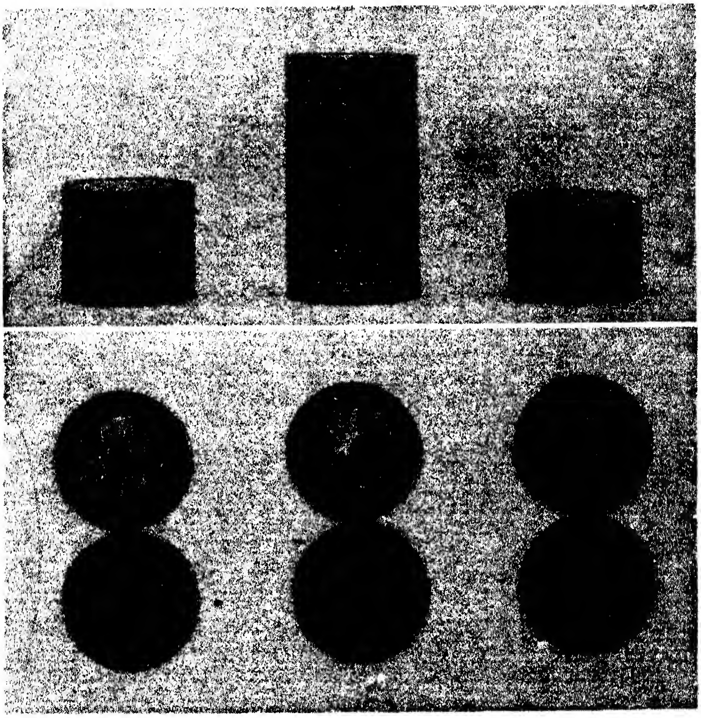

Fig. 12.—The author took two pennies and tossed them together 60 times. Fifteen times they both fell heads, 32 times one fell heads and the other tails, and 13 times both fell tails. The most probable result was 15 heads-heads, 30 heads-tails, and 15 tails-tails, or 1 heads-heads : 2 heads-tails : 1 tails-tails. This illustrates the principle of the 1 : 2 : 1 Mendelian ratio resulting from random fertilization

The inheritance and segregation of genes *R* and *r* is shown in the aggregate in Fig. 11.

A simple way of proving the truth for ourselves of the above statements regarding the combination of *R* and *r* is to take two pennies—one to represent ovules and the other pollen-grains. Heads and tails occur in equal numbers (i.e. one of each) on each of the two pennies. If we now toss the two coins together and note how they fall, say fifty or sixty times (the more the better) we shall find that "heads-tails" will occur about twice as frequently as "heads-heads" or "tails-tails," i.e. the most probable result is that we shall get a ratio of approximately 1 *HH*: 2 *HT* : 1 *TT* (Fig. 12). The laws which govern inheritance are concerned with the laws of probability.

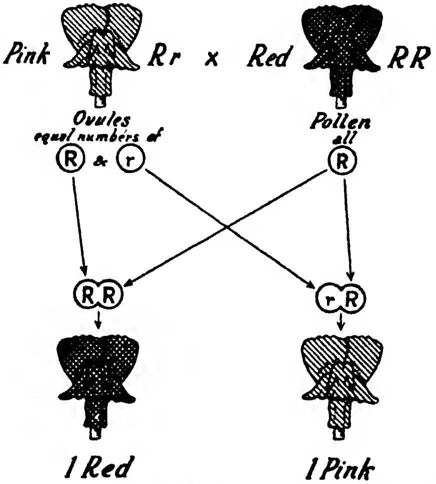

FIG. 13.—The result of back-crossing the pink-flowered hybrid snapdragon with the pure-breeding *red*-flowered parent

We have now seen the method by which the scientific plant breeder investigates the laws of inheritance. He makes crosses between plants differing in one or more characters and observes whether the characters appear in succeeding generations and if they do, the frequency with which they appear. In other words he counts (1) the *kinds* of characters and (2) the *proportions* of the kinds, and from his results deduces the hereditary constitution of the parents and progeny.

To illustrate the point let us turn again to our snapdragon. We started by crossing true-breeding red and white plants. The first generation or F_1* plants were all pink, and on selfing these we got the second generation (F_2)* comprising red, pink, and white forms. By adopting the two principles of inheritance we were able to explain the 1 : 2 : 1 ratio in F_2. Now if the principles are true then we ought to be able to say what the results would be if we cross the F_1 plants with each of the parents.

First let us examine the cross pink × red.† The pink hybrid produces equal numbers of R and r germ-cells and the red parent only R germ-cells. There are only two possible combinations: R ovules fertilized by R pollen $= RR$, and r ovules fertilized by R pollen $= Rr$. The result therefore of this *back-cross*, as it is called, is

$$1\ RR : 1\ Rr$$

or equal numbers of reds and pinks (Fig. 13). Similarly if we cross the F_1 pinks (Rr) with the white-flowered parent (rr) there are only two possible combinations: R ovules fertilized by r pollen $= Rr$, and r ovules fertilized by r pollen $= rr$, that is

$$1\ Rr : 1\ rr$$

or equal numbers of pinks and whites (Fig. 14). Many thousands of experiments of this sort have been made on

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* F_1 = first generation after crossing, F_2 = second generation after crossing, and so on.

† As a rule, in back-crossing it is better to use the hybrid as the female parent.

a great variety of plants, and the results prove the truth of the principles of inheritance. *These two ratios,* 1 : 1 *from back-crossing and* 1 : 2 : 1 *from self-pollinating the* F_1, *are the basic Mendelian ratios.* From them the reader can work out by ordinary multiplication nearly all other ratios.

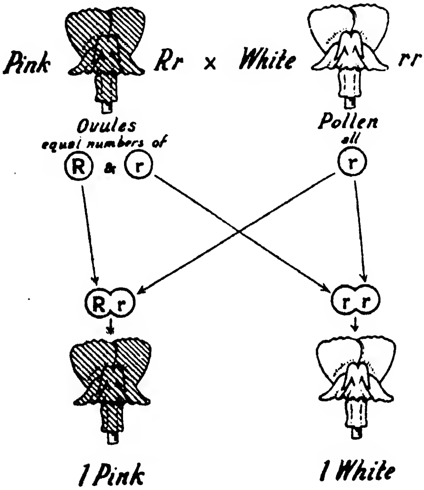


FIG. 14.—The result of back-crossing the pink-flowered hybrid snapdragon with the pure-breeding *white*-flowered parent

DOMINANT AND RECESSIVE CHARACTERS

We have now become acquainted with the fundamental facts governing heredity in all higher organisms, both plants and animals. If these were all the facts, the inheritance of characters would be very easy to trace; but it is usually more complicated. We must see therefore what factors modify inheritance. There are two. The first is that *related genes have different powers of expression, some having a strong, others a weak effect.* In our snapdragon example we saw that *RR* plants had red, *rr* white, and *Rr* pink flowers. Since pink is a colour intermediate between red and white, we concluded that the action of the genes *R* and *r* was about equal; neither had the advantage. Now usually this is not the case, the members of a pair of genes having unequal powers of expression. Red and white-coloured flowers in sweet peas are examples of this. Red-flowered plants (*RR*) crossed with white-flowered plants (*rr*) give, not pink flowers as in the snapdragon, but all red-flowered plants (*Rr*). Although the hybrid plants carry the gene *r* for white flowers, its effect is completely masked by that of *R*. The red-flowered character dominates the white-flowered, hence we refer to redness as a *dominant* and whiteness as a *recessive* character. It should be noted that the terms apply only to related genes, e.g. *R* and *r*. We cannot say *R* is dominant over *A* or *a*, any more than we can say that a pound is heavier than a foot or an inch.

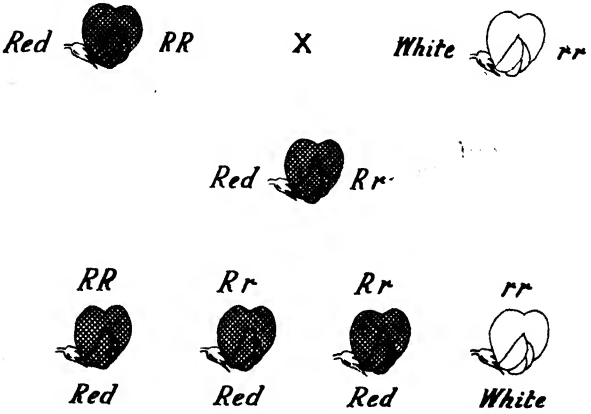


FIG. 15.—Diagram showing the inheritance and expression of a pair of genes, *R* and *r*, controlling flower-colour in the sweet pea (*Lathyrus odoratus*). The hybrid from crossing red- and white-flowered sweet peas is red, not intermediate, in colour; redness is completely dominant in expression. The red hybrid selfed gives three-fourths red and one-fourth white flowered plants in the next generation. Compare with Fig. 10

Now if one character is masked by another it is obvious that our ratio will be modified. For example, we know that three sorts of individuals are obtained from selfing a hybrid of the constitution *Aa*, viz. 1 *AA* : 2 *Aa* : 1 *aa*. But if *A* is completely dominant over *a*, then *AA* and *Aa* plants will be indistinguishable from one another and our 1 : 2 : 1 ratio becomes three dominant types (1 *AA* + 2 *Aa*) to one recessive. The genes are inherited in exactly the same way as before, but their different powers of expression modify the results. Thus, in the case of the sweet pea, instead of three sorts of individual (e.g. red, pink, and white) there are only two (red and white) and instead of the ratio being 1 : 2 : 1 it is 3 : 1 (Fig. 15). We can put this in another way and say that the difference in the degree of dominance has modified the ratios.

Dominant characters are very common. Sometimes one character completely masks the other, when dominance is said to be complete. Sometimes one character only partially masks the other, and in this case it is said to be incompletely dominant. This difference in the power of expression of related genes is one way in which the inheritance of characters is modified.

The second way in which inheritance is modified is due to the effect of unrelated genes upon each other. This is called *gene interaction*. It is probably true that all the genes affect each other in various subtle ways. Sometimes, however, gene interaction results in a conspicuous effect, and it is to this we now refer. Hitherto, however, we have only considered the inheritance of one pair of genes. Therefore before we can see the way in which gene interaction modifies the inheritance of characters we must first learn what sort of segregation and ratios we get when more than one pair of genes is involved.

INHERITANCE OF TWO PAIRS OF GENES

Let us take two plants *AABB* and *aabb* each of them breeding true for two pairs of genes. What genes will their germ cells carry? Our first principle says that each germ-cell can only carry one gene of each pair. Therefore all the germ cells of the *AABB* parent will contain one *A* gene and one *B* gene, i.e. they will be *AB*. Similarly with the other parent; its germ-cells will all be *ab*. Thus when these two parent plants are crossed together the hybrid will be $AB + ab$ or putting the *A*'s and *B*'s together, *AaBb*. What will the germ-cells of this hybrid be? Our first principle says that a germ cell can only carry one of each pair of genes. If *A* is carried by one germ-cell, then *a* must be carried by another. And here we come to the third principle of inheritance. *Pairs of genes are inherited independently of each other.*[*] Whatever happens to the gene pair *Aa* in inheritance has no effect on the pair *Bb*, or vice versa. Consequently both *A* and *a* germ cells may also carry *B* or *b*. Thus there are four possible types of germ-cell, *AB*, *Ab*, *aB*, and *ab*, and these, as we have seen from the second principle of inheritance, occur in equal numbers. Thus the answer to our question "What will be the germ-cells of the hybrid *AaBb*?" is

1 *AB* : 1 *Ab* : 1 *aB* : 1 *ab*.

Having ascertained the germ-cell ratio of the F_1 hybrid we shall now see what the results are from back-crossing and selfing.

It will be seen that on crossing the hybrid by the recessive parent each of the four types of germ-cell, *AB*, *Ab*, *aB*, and *ab*, produced by the hybrid will be fertilized by an *ab* pollen-grain and since the germ-cells occur in equal numbers the back-cross ratio will be 1 *ABab* : 1 *Abab* : 1 *aBab* : 1 *abab* (Fig. 16) or collecting the *A*'s and *B*'s together 1 *AaBb* : 1 *Aabb* : 1 *aaBb* : 1 *aabb*.

When an F_1 *hybrid is back-crossed to the bottom recessive* (the individual which is recessive for *all* the particular genes

[*] There is an important exception to this rule, see p. 81.

we are concerned with) *the ratio of the different kinds of progeny to one another is always* 1 : 1. Thus *Aa* × *aa* gives 1 *Aa* : 1 *aa*; *AaBb* × *aabb* gives 1 *AaBb* : 1 *Aabb* : 1 *aaBb* : 1 *aabb*; *AaBbCc* × *aabbcc* gives 1 *AaBbCc* : 1 *AaBbcc* : *AabbCc* : 1 *aaBbCc* : 1 *Aabbcc* : 1 *aaBbcc* : 1 *aabbCc* : 1 *aabbcc* and so on, according to the number of gene pairs involved. Back-crossing the F_1 hybrid to the *recessive* parent is an invaluable method of analysing the genetic constitution of a hybrid plant, since the character of the progeny directly reveals all the different kinds of germ-cells of the F_1 and the ratio in which they occur.

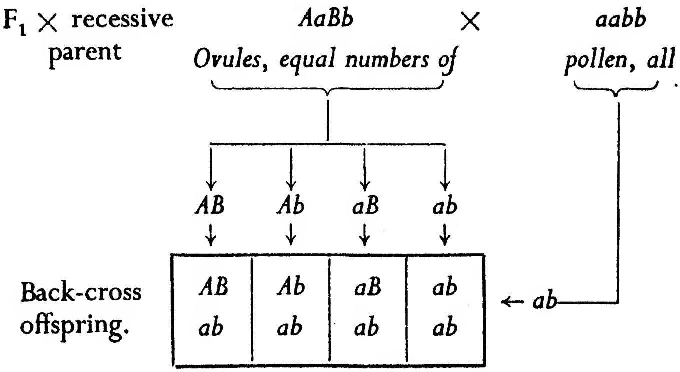
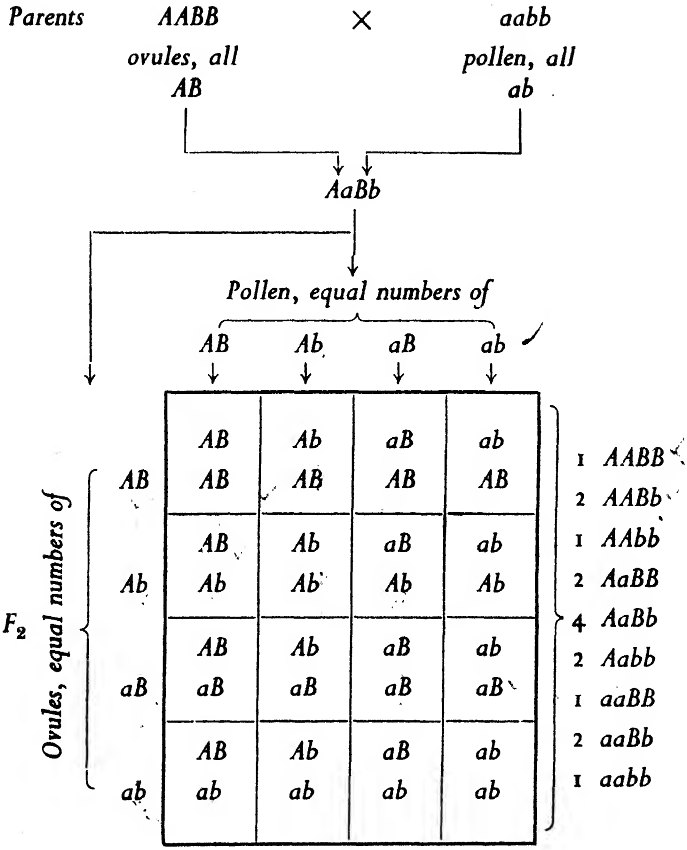


FIG. 16.—The inheritance of two pairs of genes, *Aa* and *Bb*, when an F_1 hybrid is back-crossed to the recessive parent. The offspring consist of four classes in equal numbers. It should be noted that the ratio from back-crossing to the *recessive* parent shows all the different kinds of germ-cells and the proportions in which they occur. The back-cross to the recessive parent therefore is an invaluable method for analysing the genetic constitution of a hybrid individual

Finally we must see what sort of ratio we get from self-pollinating a plant of the constitution *AaBb*. As we have seen, the pollen and ovules of such a plant will be of four kinds, produced in equal numbers, *AB*, *Ab*, *aB*, and *ab*. An *AB* ovule stands an equal chance of being fertilized by an *AB*, *Ab*, *aB*, or *ab* pollen grain. Similarly *Ab*, *aB*, and



	AB	Ab	aB	ab
AB	AB AB	Ab AB	aB AB	ab AB
Ab	AB Ab	Ab Ab	aB Ab	ab Ab
aB	AB aB	Ab aB	aB aB	ab aB
ab	AB ab	Ab ab	aB ab	ab ab

Fig. 17.—Diagram showing the inheritance of two pairs of genes, *Aa* and *Bb*, through two generations. The sixteen possible combinations between pollen and ovules are shown in the square. Some of these are identical, and the column on the right shows the number of *different gene combinations* (nine) and the proportions in which they occur. The number of different kinds of *plants* in the F_2 will depend upon the expression of the genes. Compare with Fig. 18

ab ovules stand an equal chance of being fertilized by any one of the four kinds of pollen. Thus the number of possible combinations is 4 × 4 or 16.

Perhaps the easiest way of performing the multiplication is to use the "chequer-board" method. We draw a large square and divide it into sixteen small squares (Fig. 17). Along the top we write the four different kinds of germ-cells, one opposite each column. These represent the *pollen* of the *AaBb* hybrid. Down the left side we write the four germ-cell types in the same way. These represent the *ovules* of the hybrid. The sixteen squares can now be filled in as shown below, by writing in the upper half of each small square the letters above each vertical row of squares, and in the lower half of each small square the letters to the left of each horizontal row of squares.* This formula for deriving the constitution of the F_2 generation is the most important of all Mendelian formulae. Reference to the figure will show that some of the sixteen combinations are identical, so that there are really only nine *different* combinations, as shown to the right of the square in Fig. 17.

By referring to this formula we can calculate most of the ratios we shall ever want to know as practical plant breeders. The genes *A*,*a*,*B*,*b*, can stand for any pairs of related characters we like, e.g. tallness, dwarfness; coloured, white. In using gene symbols, however, it is an advantage to choose those letters which suggest the characters concerned, e.g. *T*, *t* for tall and dwarf, and *C*, *c* for coloured and white.

The ratio will depend entirely on the way the genes express themselves. Thus if *T* and *t* have equal effects and *C* and *c* also, there will be talls, intermediates, and dwarfs,

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* For those who are familiar with algebra, the calculation is simply $(AB + Ab + aB + ab)^2$.

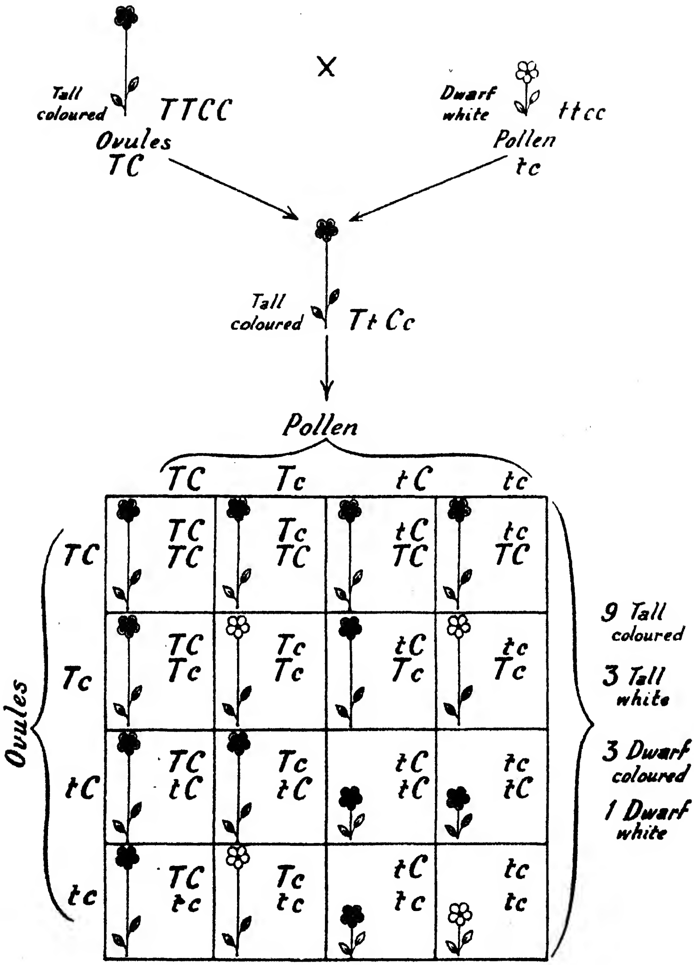


FIG. 18.—This diagram is the same as Fig. 17 except that different gene-symbols are used and *T* and *C* are supposed to be completely dominant over *t* and *c*. As a result, although there are still nine different gene-combinations as in Fig. 17, there are only four kinds of plant in the F_2 and these occur in the proportions 9 : 3 : 3 : 1

and full-coloured, tinged and white in the F_2, and the ratio will be exactly as given in Fig. 17, i.e. 1 : 2 : 1 : 2 : 4 : 2 : 1 : 2 : 1. But if *T* is dominant to *t* and *C* to *c* (Fig. 18) then our ratio becomes

9 tall with coloured flowers	1 *TTCC* 2 *TTCc* 2 *TtCC* 4 *TtCc*
3 tall with white flowers	1 *TTcc* 2 *Ttcc*
3 dwarf with coloured flowers	1 *ttCC* 2 *ttCc*
1 dwarf with white flowers	1 *ttcc*

RECOMBINATION

It is important for us to notice that by selfing the individual *TtCc* derived from crossing the forms *TTCC* and *ttcc* two new types, unlike the parent or grandparents, appear in the second generation, namely *TTcc*, tall with white flowers, and *ttCC*, dwarf with coloured flowers. These new types are due to the *recombination* of the genes which were carried by the grandparents separately. No new genes have been introduced, but the old ones have been combined in a new way. This will help us to see why offspring are like their parents, but not so very like. Snapdragons always give snapdragons because they pass on those genes which in the aggregate result in a plant with characters we recognize as belonging to snapdragons. But there are different kinds of snapdragons because there is a sorting out (segregation) of genes when the germ-cells are formed, leading to new combinations of genes in the progeny so that they differ somewhat from one another. Heredity is the principle that like begets like. Recombination is the process which modifies the principle and says "but not so very like."

Recombination also explains the phenomenon called *reversion*, i.e. "throwing back" to an ancestral wild type. Some characters depend upon the complementary effect of two or more genes, e.g. neither *C* nor *R* has any effect by itself but together they produce an effect (see Fig. 20). If genes *C* and *R* become separated in different strains or varieties during the history of a plant, so that one strain carries *C* and the other *R*, then the crossing together of the varieties carrying *C* and *R* will lead to the reappearance of the character in the progeny in which the genes *C* and *R* have been brought together again.

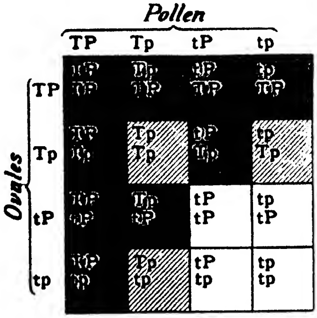


FIG. 19.—Diagram showing the results in F_2 of the interaction of the genes *T* and *P* in raspberry, giving a 9 : 3 : 4 ratio

GENE INTERACTION

We are now in a position to see how the interaction of genes modifies inheritance. Two examples will be given. The first is in raspberry (*Rubus idaeus*) in which the expression of spine colour is controlled by two genes *T* and *P*. *T* produces a tinge of reddish pigment in the spines, while *P* increases the intensity of pigmentation to reddish-purple. *P* produces no pigment by itself. What then will the ratio be from selfing an individual of the constitution *TtPp*? Referring to Fig. 19 and remembering that types *T*

TABLE II

The most useful ratios resulting from the inheritance of one to three pairs of genes are given below. Reciprocal crosses give the same results. By substituting *A* for *a* and *B* for *b* *throughout* each horizontal line, other combinations can be readily ascertained. In the last part of the table dealing with three pairs of genes the constitution of the *progeny* is shown in abbreviated form, recessive symbols being omitted (except in the case of the bottom recessive) and dominant symbols shown only once, e.g. *AABbCc*, *AaBBCC*, and *AaBbCc* are all given as *ABC*.

Parents		*Germ-Cells (in equal numbers)*		*Progeny*
Female	*Male*	*Female*	*Male*	
ONE PAIR OF GENES				
aa	*aa*	*a*	*a*	all *aa*
Aa	*aa*	*A*, *a*	*a*	1 *Aa* : 1 *aa*
Aa	*Aa*	*A*, *a*	*A*,*a*	1 *AA* : 2 *Aa* : 1 *aa*
AA	*aa*	*A*	*a*	all *Aa*
AA	*Aa*	*A*	*A*, *a*	1 *AA* : 1 *Aa*
AA	*AA*	*A*	*A*	all *AA*
TWO PAIRS OF GENES				
aabb	*aabb*	*ab*	*ab*	all *aabb*
aaBb	*aabb*	*aB*, *ab*	*ab*	1 *aaBb* : 1 *aabb*
aaBB	*aabb*	*aB*	*ab*	all *aaBb*

Aabb	*aabb*	*Ab*, *ab*	*ab*	1 *Aabb* : 1 *aabb*
AaBb	*aabb*	*AB*, *Ab*, *aB*, *ab*	*ab*	1 *AaBb* : 1 *Aabb* : 1 *aaBb* : 1 *aabb*.
AaBB	*aabb*	*AB*, *aB*	*ab*	1 *AaBb* : *aaBb*
AAbb	*aabb*	*Ab*	*ab*	all *Aabb*
AABb	*aabb*	*AB*, *Ab*	*ab*	1 *AaBb* : 1 *Aabb*
AABB	*aabb*	*AB*	*ab*	all *AaBb*
aaBb	*Aabb*	*aB*, *ab*	*Ab*, *ab*	1 *AaBb* : 1 *aaBb* : 1 *Aabb* : 1 *aabb*
aaBB	*Aabb*	*aB*	*Ab*, *ab*	1 *AaBb* : 1 *aaBb*
AaBb	*Aabb*	*AB*, *Ab*, *aB*, *ab*	*Ab*, *ab*	1 *AABb* : 1 *AAbb* : 2 *AaBb* : 2 *Aabb* : 1 *aaBb* : 1 *aabb*
aaBb	*AaBb*	*aB*, *ab*	*AB*, *Ab*, *aB*, *ab*	1 *AaBB* : 1 *aaBB* : 2 *AaBb* : 2 *aaBb* : 1 *Aabb* : 1 *aabb*
aaBB	*AaBb*	*aB*	*AB*, *Ab*, *aB*, *ab*	1 *AaBB* : 1 *AaBb* : 1 *aaBB* : 1 *aaBb*
AaBb	*AaBb*	*AB*, *Ab*, *aB*, *ab*	*AB*, *Ab*, *aB*, *ab*	1 *AABB* : 2 *AABb* : 1 *AAbb* : 2 *AaBB* : 4 *AaBb* : 2 *Aabb* : 1 *aaBB* : 2 *aaBb* : 1 *aabb*
THREE PAIRS OF GENES				
AaBbCc	*aabbcc*	*ABC*, *ABc*, *AbC*, *aBC*, *Abc*, *aBc*, *abC*, *abc*	*abc*	1 *ABC*, 1 *AB*, 1 *AC*, 1 *BC*, 1 *A*, 1 *B*, 1 *C*, 1 *abc*
AaBbCc	*AaBbCc*	*ABC*, *ABc*, *AbC*, *aBC*, *Abc*, *aBc*, *abC*, *abc*	*ABC*, *ABc*, *AbC*, *aBC*, *Abc*, *aBc*, *abC*, *abc*	27 *ABC*, 9 *AB*, 9 *AC*, 9 *BC*, 3 *A*, 3 *B*, 3 *C*, 1 *abc*

and *P* will be purple, those carrying *T* tinged, and *tP* and *tp* types green-spined, we find that the F_2 will comprise 9 purple : 3 tinged : 4 green. Thus as a result of gene interaction there are now only three kinds of plant in F_2 instead of four, and the 9 : 3 : 3 : 1 ratio is modified to 9 : 3 : 4. If a *TtPp* plant is back-crossed to the recessive *ttpp* form, the ratio will be found to be 1 purple : 1 tinged : 2 green.

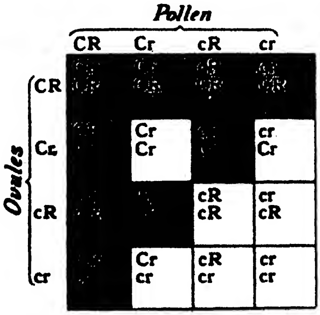


FIG. 20.—Diagram showing the results in F_2 of the interaction of the genes *C* and *R* in sweet pea, giving a 9 : 7 ratio

The second example is in sweet pea where two genes, *C* and *R*, are necessary for the production of purple flower colour, individuals with *C* or *R* alone having white flowers. What will the F_2 ratio be from selfing the type *CcRr*? Referring to Fig. 20 and remembering that only the types carrying both *C* and *R* will have coloured flowers, we find that there are 9 purple : 7 white. If a *CcRr* plant is back-crossed to the recessive form *ccrr*, the ratio will be found to be 1 purple to 3 white.

Other ratios obtained from the interaction of two pairs of genes in the F_2 are 12 : 3 : 1, 13 : 3, and 15 : 1.

All the most useful ratios resulting from independent inheritance of one to three pairs of genes are given in Table II.

We have now completed our survey of the way characters are inherited. The essential facts are summarized below:

I. The characters of plants are controlled by genes.
II. The genes are the units of inheritance which are passed on unchanged from generation to generation.
III. Genes occur in pairs, one member of a pair being derived from the female and the other from the male parent.
IV. When the members of a pair of genes differ in their effects upon a character, the plant is called a hybrid.
V. A germ-cell carries only one member of each pair of related genes.
VI. Therefore when a hybrid forms germ-cells, half of them will carry one gene of a pair and the other half the other.
VII. Different pairs of genes are for the most part inherited independently.

It will be seen from the above facts that the principles of inheritance are exact and orderly, characters being inherited from generation to generation according to very definite rules. Only by orderly methods based on exact knowledge can these principles be used to the best advantage.

CHAPTER 5

THE MECHANISM OF INHERITANCE

IN the last chapter we learnt that the many characters of a plant are determined by the genes it carries; that the genes are the units of inheritance passed on from one generation to another; and that they always occur in pairs except in the germ-cells, where they are single.

Now all this is founded on hypotheses which, though they have been well tested by experiment, are, nevertheless, based only on deductions. It is clear, however, that such orderly behaviour as we find in inheritance must be the result of a very accurate mechanism. Can this mechanism be seen? For if it can take the place of the rather abstract juggling with figures which gives us our Mendelian ratios, we shall be able to picture to ourselves exactly what is happening—a much more interesting thing. The answer is "Yes—the mechanism can be seen, and a very beautiful piece of mechanism it is too." And when we have seen it we shall understand much more than how genes are inherited; we shall have some idea of how new plants are evolved.

The Body Cells

Let us begin with the new individual, the fertilized cell, which results from the union of ovule and pollen-grain (p. 23). With a microscope to aid us we see that this cell, like most other growing cells, contains a semi-fluid, transparent substance. Embedded in this is a rounded, somewhat denser body, the *nucleus* of the cell. By suitable treatment the nucleus can be seen to consist of a number of long fine threads with tiny globules of matter distributed along them like beads on a thread. Actually these fine intertwined threads are chains of genes.

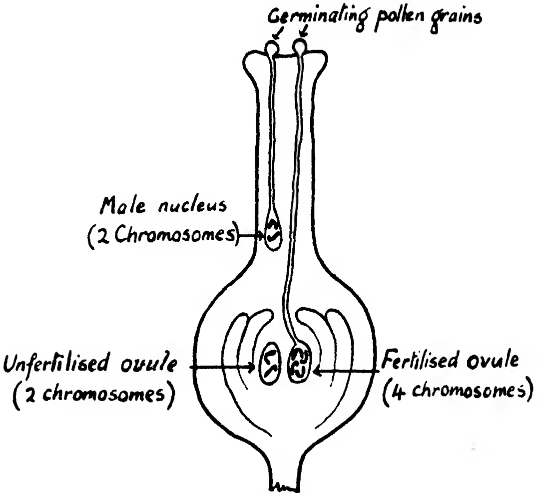
Ordinarily the genes would be quite invisible because they are so small, but a certain amount of living material accompanies each one and joins it to the next. Thus, although we cannot see the individual genes, we can, with the aid of a powerful microscope, see the "houses" they live in (Fig. 21). Every gene has a definite position in the chain, therefore the genes are always in the same linear order and by certain indirect methods it is possible

FIG. 21.—Two chromosomes, one from the female and one from the male parent, lying close side by side in preparation for the formation of germ-cells in the crown imperial (*Fritillaria imperialis*). Note that the two chromosomes correspond exactly in the sequence of the globules (gene houses). Magnified 2,800 diameters

From Darlington, "Proceedings of Royal Society"

to locate a good many of the genes in their proper order. The gene-chains are called *chromosomes*, and if we look at our fertilized cell more closely we shall see that the chromosomes differ in length, in the number, size, and spacing of the "beads" and in other ways. If we look very closely we shall notice that there are two chromosomes of each kind. Actually there are two *sets* of chromosomes, one set having been contributed by the ovule and the other by the pollen-grain which gave rise to our fertilized cell, i.e. one set of chromosomes came from the female and one from the male parent (Fig. 22). The chromosomes are distributed quite haphazardly in the nucleus.

Such is the appearance of the chromosomes just after the mechanism starts to move. Presently the chromosomes begin to contract, growing shorter and shorter until they look like stumpy rods or sausages in which the beads are so crowded as to be indistinguishable (Fig. 23, *a*). At this stage a new movement begins. The chromosomes arrange themselves in a plane across the middle of the cell, *each one "splits" along its length into identical halves* (Fig. 23, *b*), and the half-chromosomes move to the opposite ends of the cell (Fig. 23, *c*). A new cell-wall now grows across the middle of the cell, with the result that there are now two cells in place of one, *each with exactly the same number and*



FERTILIZATION AND CHROMOSOMES

FIG. 22.—Each germ-cell (pollen-grain or ovule) receives one complete *set* of chromosomes from the parent plant, i.e. it has one of each kind of chromosome. (In the diagram the pollen and unfertilized ovule have one V-shaped and one hook-shaped chromosome each.) Hence when fertilization takes place the fertilized ovule will have two of each kind of chromosome, i.e. two sets of chromosomes, one set from the male parent and one from the female

kind of chromosomes as before (Fig. 23, *d*). The two cells enlarge, their chromosomes lengthen and grow to full size, and the whole process is repeated, again and again. Thus the single fertilized cell becomes two cells, these two four, the four eight, and so on. In this way the plant grows by cell-division, and the important thing we must notice about this simple mechanism is that it results in every cell having the same number and the same kind of chromosomes, which is another way of saying that each cell has exactly the same genes as every other cell.

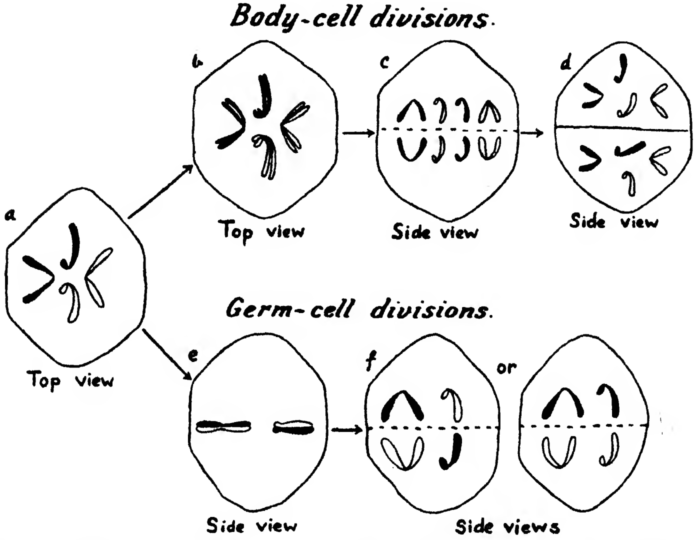


FIG. 23.—All the cell-divisions in a plant are the same until the germ-cells are formed. In the diagram two pairs of chromosomes are shown, those from the female parent in black, those from the male parent in outline. Starting from *a* (a body cell) the behaviour of the chromosomes in body-cell divisions is shown in *b–d* and in germ-cell formation in *e*, *f*.

Note.—(1) Body-cell divisions give rise to cells all having exactly the same *number* and *kind* of chromosome. (2) In germ-cell formation the chromosome number is *halved*, and the members of each pair of chromosomes pass to different germ-cells, i.e. the germ-cells differ in the *kind* of chromosome they carry. There are four kinds of germ-cells possible when two pairs of chromosomes are concerned, and the four kinds occur in equal numbers

Under the control of the genes the plant may change from week to week, but whether it be seed or seedling, half-grown or fully mature plant, in all these varied forms the number and kind of chromosomes and genes remains exactly the same in every cell. *Except once.* And that is when the germ-cells are formed.

THE GERM-CELLS

In the formation of the germ-cells the mechanism begins to move in much the same way as before, but very soon the long thread-like chromosomes, instead of being distributed haphazardly, approach one another in pairs and finally lie extremely close side by side. At this stage we can see that the two members of each pair of chromosomes are identical in structure, having the same length, and with the genes in their houses in exactly the same sequence (Fig. 21). Actually each pair is made up of a chromosome from the female and a chromosome from the male parent of the plant now producing its germ-cells; that is to say, the set of chromosomes derived from the female parent has paired with the set derived from the male parent, each one with its particular mate.

The closely paired chromosomes next contract* as in other cell-divisions, move to the equator of the cell (Fig. 23, *e*), and then without splitting along their length separate to opposite ends of the cell (Fig. 23, *f*). *But this time it is whole chromosomes that are separating and not half chromosomes.* Half the chromosomes go to one end of the cell and half to the other, and in consequence the number of chromosomes in the two daughter nuclei is reduced to *half* the number found in the body cells (Fig. 24). For this reason the cell-division which gives rise to the germ-cells is called the *reduction division.*

What are the results of this reduction of the number of chromosomes to one-half? It will be remembered that each pair of chromosomes comprises one maternal and

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* After interchange of their parts; see "Linkage," p. 81.

one paternal chromosome. At the reduction division the two chromosomes and the genes they carry go to opposite ends of the cell and ultimately into different germ-cells. Accidents apart, both chromosomes of a pair are never found in the same germ-cell, and this means that *the members of each pair of genes are always distributed to different germ-cells* (Fig. 23, *f*), which is exactly what is postulated about genes by the first principle of heredity. Moreover, each pair of chromosomes behaves independently of the rest. For example, if we consider two pairs of chromosomes *Yy* and *Zz*, the capital letters denoting those chromosomes derived from the female parent of our plant, then *Y* and *Z* might go to the same end of the cell and

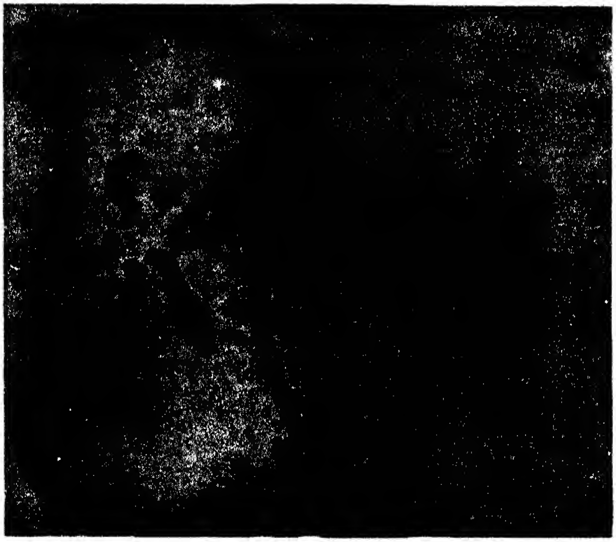

FIG. 24.—The chromosomes of *Eremurus spectabilis*: *a*, germ-cell (pollen-grain); *b*, body-cell. The germ-cell has a single set of seven chromosomes, one of which is very short. The body-cell has two sets of chromosomes (14). The two short chromosomes are seen above and below the chromosome, half out of focus, in the centre of the photograph. Magnified 2,200 diameters

From Upcott: (a) unpublished; (b) "Cytologia" therefore to the same germ-cell, while *y* and *z* go to the other germ-cell. On the other hand it is equally possible for *Y* and *z* to go to one germ-cell and *y* and *Z* to the other. Here then is independent segregation of chromosomes. Therefore if we were studying the inheritance of a pair of genes carried by the *Yy* and a pair carried by the *Zz* chromosomes, we should find that they too were inherited independently, as required by the third principle of heredity.

We can summarize the essentials of the mechanism of heredity as follows:

1. The genes are attached in long chains called chromosomes.
2. There are two of each kind of chromosome in each body-cell of the plant, one derived from the female and one from the male parent.
3. When the body-cells divide, each chromosome divides along its length into identical halves which separate and pass to opposite ends of the cell to form two new cells. Hence every body-cell has the same number of chromosomes and genes.
4. When the germ-cells are formed the paternal and maternal chromosomes come together in pairs at the equator of the cell, and then separate to opposite ends of the cell, thus halving the number of chromosomes and distributing the paternal and maternal genes to different germ-cells.

It will be seen from the above account that if the fertilized cell receives a pair of genes *A* and *a* from the ovule and pollen grain respectively, then every body-cell arising from this original cell will also carry the *A* and *a* genes, but at the reduction division *A* and *a*, being carried by the paternal and maternal chromosomes, will pass to different germ-cells. And since all the body-cells are alike, what is true for one pair of germ-cells is true of all the others; therefore half of them will carry *A* and half *a*. And this is precisely the mechanism required by the second principle of heredity.

We can now construct the full cycle of events from one generation to the next.

1. Each germ-cell taking part in fertilization contributes *one* member of every related pair of genes.
2. The *pairs* of genes are found together in every body-cell of the plant.
3. The members of each pair of genes are distributed to *different germ-cells.*

Thus the life cycle of every plant is made up of two stages, (1) the germ-cell stage where only one of each type of gene is found, and (2) the body-cell stage, where two of each type of gene are found (Fig. 24).

HEREDITY

We see then that the mechanism of heredity is such that the gene units are preserved unchanged from cell to cell and generation to generation in an unbroken line. The very existence of heredity—that is the fact that like begets like—depends on the unvarying character and continuity of the genes. Variation in inheritance is possible, however, because the mechanism permits a reassortment of the genes once in every generation when the germ-cells are formed.

LINKAGE

There is an important feature of gene reassortment to which up till now we have omitted all reference, in order that the main features of the mechanism of heredity should not be obscured. While the maternally and paternally derived chromosomes are closely paired at the reduction division, portions of their length become interchanged or crossed over. This crossing-over is shown below (Fig. 25). Owing to strains imposed on the chromosomes when they pair, breaks occur at different places at the same point in each of the two chromosomes. (Between *C* and *D* and *c* and *d* in Fig. 25.) If opposite ends join up (*C* and *d* and *c* and *D*) the result is that half of the maternally derived

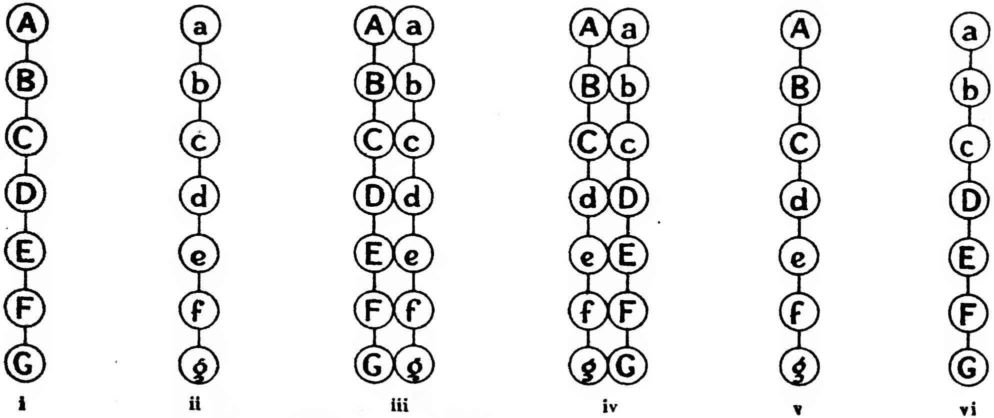

FIG. 25.—Crossing-over between chromosomes.

1 and 2.—Two chromosomes before pairing, each a chain of genes, *A–G* and *a–g*.

3.—The paired chromosomes.

4.—The chromosomes after crossing-over between *C*, *D* and *c*, *d* (see p. 83).

5 and 6.—The two new chromosomes as they will pass to the germ-cells.

Crossing-over produces new combinations of genes and hence new types of plant which would not otherwise be possible.

NOTE.—This is a simplified diagram showing the hereditary consequences but not the mechanical causes of crossing-over.

chromosome is interchanged with the corresponding half of the paternally derived chromosome. If it were not for *crossing-over*, as it is called, the genes carried on any one chromosome would always keep together in exactly the same order (e.g. *ABCDEFG*) and gene *A* would always go to the same germ-cell as genes *B* to *G*. Crossing-over, however, may occur at any point in a pair of chromosomes,* and wherever it occurs between *A* and *B* they will go to different germ-cells. The same is true of *B* and *C*, *C* and *D*, and so on. Since the breaks occur at different places along the length of the chromosome, the closer any two genes are together the less likely is it that they will be separated. This will be clear if we think of the two end genes *A* and *G*. Every break that occurs must occur between *A* and *G*, whereas in our example only one-sixth of the total number of breaks will occur between *F* and *G*, the other five-sixths occurring between *A* and *F*, i.e. there will be less crossing-over between *F* and *G* than between *A* and *G*, the degree of linkage depending upon the distance separating the genes on the chromosome (Fig. 26).

Many examples of linkage are known where a pair of characters are linked in inheritance. The "tighter" the linkage the more are the usual 9 : 3 : 3 : 1 or 1 : 1 : 1 : 1 ratios modified. A typical example of this is shown below.

TABLE III

	Dark axil Fertile anthers	*Dark axil Sterile anthers*	*Light axil Fertile anthers*	*Light axil Sterile anthers*
Actual numbers ..	1,560	38	49	500
Calculated numbers on 9 : 3 : 3 : 1 basis..	1,207	403	403	134

The example given in Table III is one of moderately "tight" linkage, i.e. about ninety-six plants out of every hundred

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* There are exceptions.

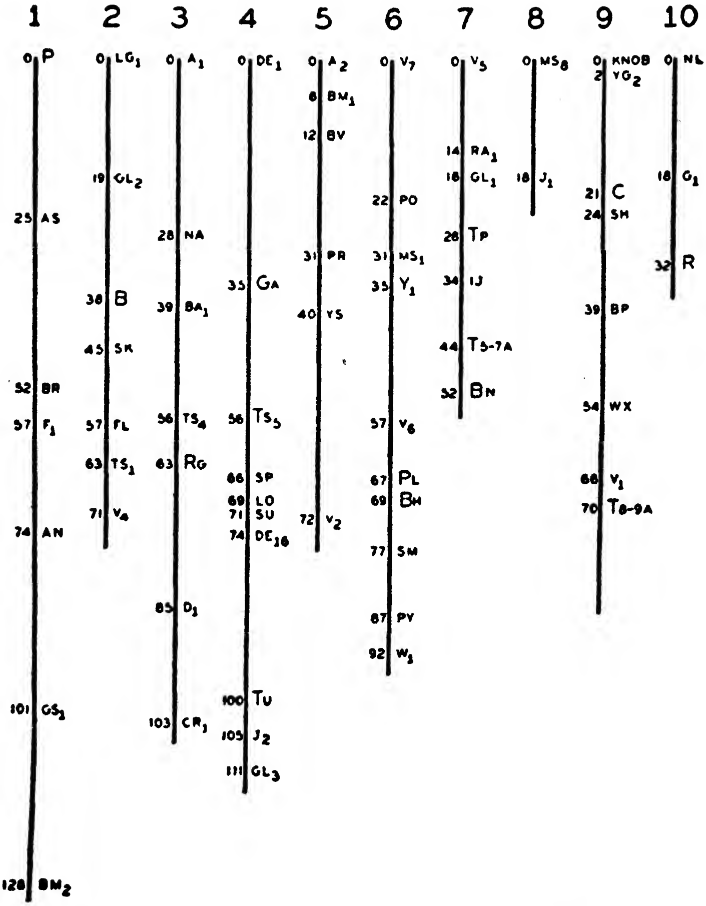

FIG. 26.—A chromosome "map" of a single set of ten chromosomes of maize. The chromosomes vary in length roughly as shown. The letters on the right of each chromosome are the gene symbols and the figures on the left the distance of the genes along the chromosomes. Thus in Chromosome 1, the genes *BR* and F_1 are 52 and 57 units from the end respectively. Genes such as these which are situated close together will be strongly linked. Genes which are far apart (e.g. *BR* and BM_2) will show no linkage

From Rhoades and McClintock, "Botanical Review" will be like the first or last classes. If the linkage were tighter still then the breeder might raise a family of a hundred or two plants and not get the particular recombination of factors that he wanted. Thus, he might have to raise a family of 500–1,000 plants in order to get the one plant required, but once obtained it would be easy to raise a plant breeding true for the pair of characters concerned.

PLANTS AND THEIR CHROMOSOMES

Having learnt something about chromosomes, let us now take a general survey of the chromosomes of plants. The first point of importance which arises is that *all the plants comprising any one species have the same chromosome number*. For example, all sweet peas (*Lathyrus odoratus*) have 14 chromosomes, that is seven pairs or two sets of seven; all tomatoes have 24 chromosomes, or two sets of 12. Other chromosome numbers are peony 10, radish 18, delphinium 32, apple 34, potato 48, strawberry 56. Because chromosome numbers vary from species to species it is possible to identify a plant by its chromosomes, especially as not only the number of chromosomes but their size and shape are characteristic for each species. Drawings of the chromosomes of a number of species are shown below, and differences in number, size, and shape will readily be seen (Fig. 27).

CHROMOSOMES AND FERTILITY

Apart from what has been said regarding chromosomes there are three ways in which they are especially important to the plant breeder.

In the first place *fertility and sterility are intimately bound up with the number and behaviour of the chromosomes*. In the great majority of cases only those species will cross which have the same number and approximately the same kind of chromosomes. If the hybrid plant is to develop normally the chromosomes must work harmoniously together, and this can only happen when the two sets of chromosomes are similar. If the chromosome sets are quite dissimilar the fertilized cell may never even divide; if the two sets are different, but in a lesser degree, growth will proceed, although it may be abnormal. If the sets are reasonably similar the plant, though it appears to develop normally, may be found to show a degree of sterility when the pollen and ovules are formed. The reason for this is that for the chromosomes to pair and separate regularly at the reduc-

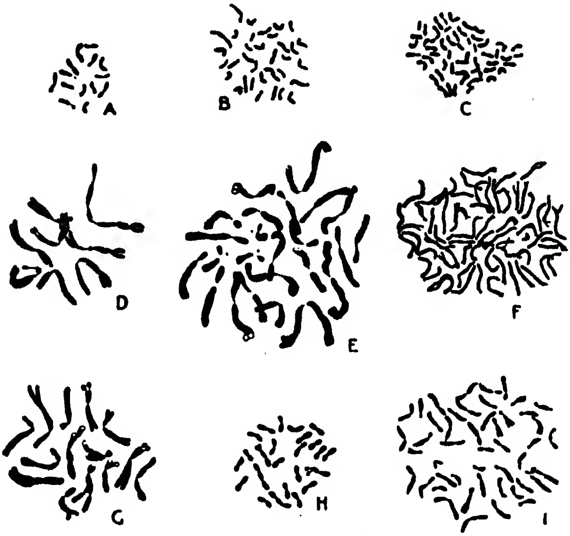

FIG. 27.—The chromosomes of some cultivated plants. *Fruits:* A, raspberry var. Superlative, 14 chromosomes; B, apple var. Worcester Pearmain, 34 chromosomes; C, strawberry var. Keen's Seedling, 56 chromosomes. *Flowers:* D, *Crocus vernus*, 8 chromosomes; E, aconite, Sparks' variety, 24 chromosomes; F, garden dahlia, 64 chromosomes. *Vegetables:* G, garden pea, 14 chromosomes; H, tomato, 24 chromosomes; I, potato, Sharpe's Express, 48 chromosomes. Magnified 1,670 diameters

From Crane and Lawrence

tion division, they must be identical or nearly so. Chromosomes which are dissimilar will not pair at all, and in between these extremes chromosomes which are to some extent alike will pair on some occasions and fail on others.

Chromosomes which have not paired do not move to the ends of the cells in a regular way as paired chromosomes do, consequently their ultimate fate is a matter of chance. They may go into one or other daughter nucleus, or be left lying about in between and degenerate later. In this way we shall get germ-cells with too many or too few chromosomes. Such germ-cells rarely work properly for long, and they often die, hence the sterility associated with species hybrids. *If a plant is to be fully fertile its chromosomes must pair and separate to the daughter cells with great regularity; and chromosomes will only pair regularly when they are considerably alike.*

There is a way, however, in which distantly related species may cross to give highly fertile hybrids. This process is of great importance to the breeder, since other things being equal the greatest number of new characters may arise when plants which are most different are successfully hybridized.

CHROMOSOME DOUBLING

If the cell-division mechanism goes wrong so that after the chromosomes of a body-cell have split lengthwise and passed to opposite ends of the cell, a new cell wall fails to grow between them, then *twice the normal number of chromosomes will be found in that cell.* By repeated divisions of this cell, a whole branch or part of a plant may arise having double the usual number of chromosomes. Should this occur in a sterile species-hybrid then the branch, if it flowers, will be fertile and produce seed. The explanation of this is quite simple. The hybrid is sterile because its two *sets* of chromosomes are too different to pair. We may represent these sets by the letters *Y* and *Z*. But if the chromosome number is doubled then there will be two *Y* and two *Z* sets (*YYZZ*). The *Y* chromosomes can now

FIG. 28.—Chromosome doubling in a sterile species-hybrid:
a. Solanum nigrum, 2 sets of chromosomes.
b. Solanum luteum, 2 sets of chromosomes.
c. S. nigrum × *S. luteum*, 2 sets of chromosomes.
d. S. nigrum × *S. luteum*, 4 sets of chromosomes.
A fruiting branch of each of the four plants is shown at the bottom of the figure.

Note.—(1) the complete sterility in the hybrid with *two* chromosome sets as compared with the fertility of the double form with *four* sets; (2) the (slight) hybrid vigour of the sterile plant; (3) the increase in size of the doubled form. The doubled form is potentially a new species, since it breeds true and will not cross with the parent plants

Jørgensen, "Journal of Genetics"

pair with *Y* and the *Z* with *Z* with perfect regularity, thus restoring fertility (Fig. 28). This fertile hybrid is virtually a new species. It differs from each of the parent species and will not cross with them except to give sterile or highly infertile offspring, as is usual in species crosses, e.g. *Primula kewensis*.

In the examples just mentioned the fertile hybrid arose through doubling of the chromosomes in a body-cell. Another way in which a fertile species-hybrid could arise from a sterile form would be for two unreduced germ-cells to unite in fertilization. Thus representing the two species as *YY* and *ZZ* the normal germ-cells would each carry one set of chromosomes, *Y* and *Z* respectively. But should reduction not take place, then the germ-cells would carry two sets of chromosomes, *YY* and *ZZ*, and if these germ-cells unite in fertilization then we have the same result as before—a fertile species-hybrid with four sets of chromosomes—*YYZZ*.

We may note in passing that inheritance in a fertile hybrid of this kind will be more complicated, owing to the interaction effects between the genes of the two species.

It is only in the more or less *sterile* species hybrid that chromosome doubling restores fertility. If chromosome doubling occurs *within* a single species then the process is reversed and the normal fertile variety becomes more or less sterile. Our symbols will make the reason clear. In the variety with two sets of chromosomes (*YY*) each chromosome has only one other that it can pair with, but if the chromosome number is doubled there are then four identical chromosome sets (*YYYY*) and every chromosome has three others it can pair with. As a result of this competition, disorder arises. The chromosomes associate in twos, threes, or fours and separate in a variety of ways to give germ-cells with different chromosome numbers, and this as we have already seen is the cause of sterility.

Doubling of the chromosome number as outlined above has proved a most important factor in the improvement of garden plants. It so happens that many of our best cultivated plants have more than two sets of chromosomes. At some time or other in their history an accident has occured to the cell mechanism, leading to chromosome duplication. Such accidents are, of course, relatively rare or heredity would not be so consistent as it is, but they have occurred from time to time in many plants and all unconsciously the gardener and plant breeder have selected those plants with more than two sets of chromosomes. In order to accommodate the increased number of chromosomes the cell size must be increased also (Fig. 28). Larger cells mean larger plants, therefore larger leaves, flowers, and fruits. Increase in size has long been one of the most sought for improvements in plant breeding, and so plants with more than two sets of chromosomes have been chosen in preference to those with only two sets. *Plants with more than two sets of chromosomes are called polyploids, in contrast to diploids with only two sets.* Polyploids are classified as triploid, tetraploid, pentaploid, hexaploid, etc., according to the number of chromosome sets.

POLYPLOIDS

A great number of polyploids are known. For example in the raspberry family the following chromosome numbers are found: raspberry 14, mahdiberry 21, veitchberry 28, loganberry 42, and laxtonberry 49 (Fig. 29). Other (unnamed) forms have been found with 35 and 56 chromosomes, so that there is a series of chromosome numbers all multiples of the *basic number*, 7, and ranging from 14 (two sets of 7) to 56 (eight sets of 7). A polyploid series such as this is the result of species hybridization coupled with, and made possible by, chromosome doubling.

Other examples of polyploid series (some of them rather complicated) are as follows. Flowers: *Aster* 18, 36, 54; *Chrysanthemum* 18, 36, 54, 72, 90; *Delphinium* 16, 32, 48; *Iris* 16, 18, 20, 22, 24, 32, 34, 36, 38, 40, 42, 44, 48, 72; *Lupin* 36, 42, 48; *Narcissus* 14, 16, 21, 28, 32, 42; *Rose* 14, 21, 28, 35, 42, 56. Fruits: apple and pear 34, 51; cherry 16, 32; plum 16, 32, 48; strawberry 14, 21, 28, 56. Polyploid series are not found in vegetables, but several species are polyploid, e.g. cabbage, potato, swede, turnip. In contrast to the foregoing plants are those in which the chromosome number is the same throughout the genus, e.g. *Antirrhinum* 16, oaks 24, *Philadelphus* 26, red and black currants, gooseberries 16, *Rhododendron* 26. Cases such as these are rare, however, at least several

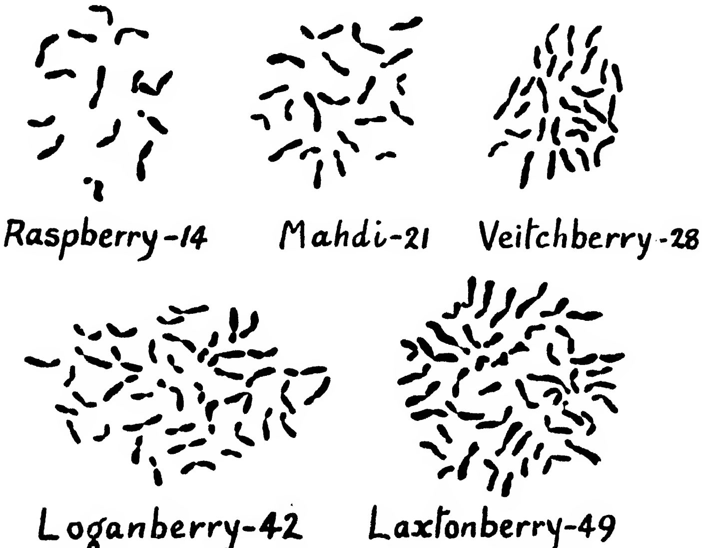

FIG. 29.—Polyploids in the genus *Rubus*, showing forms with 2, 3, 4, 6, and 7 sets of chromosomes respectively. Magnified 3,800 diameters

From Crane and Darlington, "Genetica"

different chromosome numbers being found in most genera.

Apart from the examples already given of sterility arising as a consequence of chromosome doubling there is one other case of some importance. Polyploids which have an odd number of chromosome sets are usually sterile to a high degree (Fig. 30). For example, in the raspberry family the mahdiberry with three sets (21 chromosomes) and the laxtonberry with seven sets (49 chromosomes) at the best only bear very small imperfect fruits, whereas the raspberry (14), veitchberry (28), and loganberry (42) having two, four, and six sets respectively, bear heavy crops of perfect fruit. Plants with an odd number of chromosome sets are usually highly sterile because the odd set of chromosomes has nothing to pair with at the

FIG. 30.—Sister blackberry seedlings from the same cross, *Rubus inermis* × *R. rusticanus*. (*a*) With three sets of chromosomes (21) highly sterile. (*b*) With four sets of chromosomes (28) highly fertile

From Crane and Lawrence, "Journal of Genetics" reduction division. Thus we may represent the three sets of the mahdiberry as

$AA\ A'$
$BB\ B'$
$CC\ C'$
$DD\ D'$
$EE\ E'$
$FF\ F'$
$GG\ G'$

the A'–G' set being too different to pair with the A–G sets. Since there are two of each of the A–G chromosomes they pair and go to the germ-cells in the usual way, but the A'–G' chromosomes have no corresponding types with which to pair and in consequence are left lying about at the reduction division to go entirely at random into one germ-cell or the other. Hence the germ-cells have an irregular number of chromosomes and sterility follows.

POLYPLOID INHERITANCE

Increase in size is not the only "improvement" brought about by chromosome doubling. In the first place a much greater variability in the expression of the characters is possible. For example, we have seen that if a plant carrying the genes *Aa* is self-pollinated then three types of progeny will be found, *AA*, *Aa*, and *aa*. But if the number of genes in our *Aa* plant is doubled, then it becomes *AAaa* and five types of progeny may be obtained by selfing, *AAAA*, *AAAa*, *AAaa*, *Aaaa*, and *aaaa*. If we suppose *A* and *a* to stand for red and yellow fruit colour, in a case where these genes have an equal effect, then five colours are now possible, red *AAAA*, deep orange *AAAa*, medium orange *AAaa*, pale orange *Aaaa*, and yellow *aaaa*; whereas before there could be only three types, *AA* red, *Aa* orange, and *aa* yellow. This is the simplest example of how variability is increased in polyploids. Actually, gene interaction makes the possibilities much greater than indicated here.

Chromosome doubling not only increases the number of types, but alters the ratios also. Before chromosome doubling, *Aa* selfed gives 1 *AA* : 2 *Aa* : 1 *aa* and the recessive form occurs once in four times, but after doubling the ratio is 1 *AAAA* : 8 *AAAAa* : 18 *AAaa* : 8 *Aaaa* : 1 *aaaa* and the recessive occurs only once in thirty-six times, i.e. nine times as many plants must be grown if the recessive is wanted.

Thus although polyploidy leads to increase in size and variation, it also increases the difficulties of the breeder, e.g. it takes much longer to "fix" a new character since many more genes are involved in the control of a character in the polyploid than in the diploid (see p. 127).

THE WORLD OF GENES

The botanist classifies plants by their appearance, e.g. by the shape, size, and position of various parts of the plant. We know, however, that the appearance of the plant is primarily determined by the genes it carries; therefore it may be useful to exercise our imagination and attempt to conceive the world of plants in terms of chromosomes and genes.

Each species owes its nature to a certain number of different genes, arranged in chains to form a definite number of chromosomes. Within the species a limited number of varieties may occur as a result of different combinations of the genes found in that species; some varieties may differ by one gene only, others by hundreds of genes. Those species with fairly similar gene complements constitute a larger group called the *genus*, and still higher in the scale is the *family* consisting of genera whose genes though broadly corresponding are more widely different than in the lower groups. To put it another way, the closer the relationship between any two species, the greater will be the number of identical and similar genes common to those species; and the same is true of genera and families.

Species may differ not only in the number and kind of the genes they carry, but in the arrangement of these genes. In one species the sequence of the genes in a given chromosome may be *ABCDEFG*, while in a related species the sequence may be *ABEDCFG*. Structural changes such as these, while leaving the number and kind of genes unaltered, nevertheless, have a profound effect, since by altering chromosome pairing they prevent hybridization and thus isolate forms which develop into new species.

The world of plants is then revealed to our imagination as an immense array of genes. How did they originate? In the first place all genes arise from genes. We may visualize a chromosome before it divides as a single string of genes. At a certain stage an identical row of genes is laid down by the side of the original row so that the chromosome is then like a string of twin genes. When the chromosome divides by splitting along its length the split separates the twin rows, which pass to the daughter nuclei. With unfailing regularity at every one of the hundreds of thousands of cell-divisions in the average plant this reproduction of the original gene goes on, in the parent plant and its thousands of descendants, generation after generation, millions of times—hence the constancy of heredity. Suddenly, however, the mechanism may go wrong and a gene will give rise, not to an identical gene, but to a different one. The new gene in its turn may reproduce itself for countless cell-generations until perhaps another change occurs. These gene changes, which normally occur only at rare intervals, are called *gene mutations*, and it is by reason of these changes that the great multitude of genes has arisen from a much smaller original number.

It is not yet clear what is the cause or causes of change, although X-rays for example have been used to bring such changes about. A gene which controls, let us say, the resistance of the plant to cold, suddenly mutates so that the plant is slightly more resistant to cold. This mutation may be beneficial or harmful according to the plant's environment, but if it assists in the plant's struggle for existence then the mutant gene will be handed on to successive generations, since the plants carrying the gene have a better chance of survival than those without it. Most gene mutations are recessive mutations, and only occasionally are dominant mutations found.

Gene mutation is the fundamental process by which evolution proceeds. No amount of hybridizing or selecting can give similar results, e.g. the "Spencer" Sweet Pea could not have been produced by crossing or selection. We had to wait for the mutation to occur.

If in our final look at the world of genes we could foreshorten the dimension of time we should see rarely but regularly genes mutating to give new genes and therefore new varieties. We should see parts of chromosomes being inverted or translocated, chromosomes and chromosome sets being duplicated to give new arrangements and numbers of genes and therefore new species. We should see hybridization bringing together in one individual the results of the above changes in separate individuals, and so providing new and more complex sets of genes for natural selection to work upon, favouring this type for one environment and that type for another, thus leading again to new species.

Fascinating though this ever-shifting pattern is, it is too complicated to describe adequately in so small a book as this; indeed only superficial treatment such as found here can give it any semblance of simplicity.

CHAPTER 6

STERILITY

AMONG the problems which confront the breeder from time to time, failure to set seed is one of the most important. The parent plants may be quite healthy and to all appearances perfectly normal; the pollination may be made correctly and with due care, and yet little or no seed is obtained. Or a promising hybrid has been raised but further progress is impossible since it will neither set seed with its own pollen nor when crossed with its parents. It is probably not overstating the case to say that many a promising plant or line of work has been abandoned for the reasons stated above; whereas had the breeder known the facts of the case he might have found a way round his difficulty.

Interspecific Sterility

Failure to set seed may be due to one or more of three causes. As a rule cross-pollinations between widely differing species will fail because the pollen-grains cannot germinate, grow down the style and effect fertilization in the normal way. Pollen-tubes will not, as a rule, grow down a "foreign" style, but only down one of their own species or genus. The more different two plants are, the less likely is it that normal pollen germination or pollen-tube growth will occur.

Thus if we think of a wide variety of species which we can designate by the letters *A* to *Z*, species which are closely related being indicated by adjacent letters, then pollen from species say *S* to *Z* put on *A* would probably never even germinate; pollen from *F* might germinate, but fail to grow down the style; while pollen from *D* might germinate and grow down the style, but fail to fertilize the ovules. Pollen from *C*, however, would fertilize the *A* ovules and give seeds which grow into normal plants. But the plants might be sterile because the two parental chromosome sets cannot work together in harmony—they are too different. *A* × *B*, however, would give seeds which grow into fertile offspring, since *A* and *B* are in the main very much alike in their genes and chromosomes and, in consequence, all the vital processes of growth.

The breeder may expect abundant seed and fertile offspring if he crosses varieties of one and the same species; less seed and less fertile progeny if he makes crosses between species belonging to the same genus; and little or no success if he attempts crosses between different genera. When two species have different chromosome numbers it not infrequently happens that while *A* × *B* fails, *B* × *A* gives some seed. Therefore *species crosses should always be made reciprocally*.

If in crossing it is desired to use a plant which is a poor seed setter, it will as a rule be best to employ this plant as the pollen parent, as a better set of seeds is usually obtained when this is done. The reason is that there is always a large excess of pollen, so that enough good grains should be present to fertilize the ovules, even if only 2 per cent of the grains are fertile; whereas a similar sterility on the female side would clearly bring down the number of seeds to a very low yield. For example, in the apple with normally ten seeds per fruit, 2 per cent fertility on the female side would mean that five flowers would have to be pollinated to give one pip.

STRUCTURAL STERILITY

A second cause of sterility is improper development of the reproductive parts. The pollen or ovules may be defective and the stamen or style deformed or only partly developed. In the case of defective pollen, or where little pollen is formed, change of cultural treatment will occasionally result in the production of good pollen, e.g. a lower temperature, or starvation. If the sexual organs are malformed or aborted there is much less chance of getting seed. However, in the case of double flowers where the stamens have been changed into petals, starvation and drought will sometimes result in the production of less double flowers bearing a few anthers with good pollen.

INCOMPATIBILITY

A third cause of failure to set seed, and one less familiar to the breeder, is the failure of the pollen-tubes to grow down the styles owing to the effect of a gene or genes. In such cases the pollen and ovules are perfectly normal and will function normally under the right conditions. This sort of infertility is called *incompatibility*, to distinguish it from true sterility which involves some defect in the reproductive organs or some aberration of the reproductive processes. Since incompatibility is due to the action of genes it is inherited just like any other character.

The facts of incompatibility briefly stated are as follows. Pollen carrying a gene, which we will call *I*, will *not* grow down the style of any plant the cells of which also carry the gene *I*. It will, however, grow down the style of a plant carrying *i*. Conversely, *i* pollen will not grow down the style of a plant carrying the gene *i*, though it will grow down the style of a plant carrying *I*. This means that no plant carrying incompatibility factors can set seed with its own pollen, since whatever genes are carried by the pollen are also in all the cells of the style. The plant is *self-incompatible*. For the same reason two plants which carry exactly the same genes for incompatibility, e.g. *II* × *II*, *Ii* × *Ii*, or *ii* × *ii* will be *cross-incompatible*.

Moreover, pollen from *II* cannot fertilize the plant *Ii* since all its cells carry *I*. But the *i* pollen from *Ii* could fertilize an *II* plant, since none of the latter's cells carry *i*—and so on.

These are the reasons for self- and cross-incompatibility. Their importance to the plant breeder is this. Inbreeding (i.e. self-pollination, sister-brother mating, parent-progeny mating) increases the chance of plants carrying similar incompatibility genes being crossed together. Outbreeding, on the other hand, reduces the chance of plants carrying similar incompatibility genes being crossed together and therefore makes seed-setting more certain.

Incompatibility is very common in flowering plants. Some of the more important genera in which it occurs are: *Alyssum*, *Antirrhinum*, apple, *Brassica*, cabbage, candytuft, cherry, *Cistus*, *Coreopsis*, *Dahlia*, *Eschscholtzia*, *Freesia*, *Hippeastrum*, *Lilium*, *Linaria*, mignonette, *Nemesia*, pear, *Pelargonium*, *Petunia*, poppy, radish, tobacco, *Veronica*, *Verbascum*. In some genera every species and variety is self-incompatible (e.g. sweet cherry, *Dahlia*, and *Freesia*) and in consequence cross-pollination is enforced. In such genera, many *cross*-pollinations will be incompatible and inbreeding may not only lead to reduced vigour (see p. 120) but the establishment of pure lines will be difficult.

Self- and cross-incompatibility can sometimes be overcome by making the pollinations in the bud stage one to ten days before the flower opens. This method has been successfully applied in the case of such plants as *Nicotiana*, *Verbascum*, *Petunia*, radish (Fig. 7), cabbage, and broccoli. Another method which has been used with success is to rub or macerate the stigmatic surface before applying the pollen. When the stigma has been mutilated in this way, better results will be obtained if the plant is kept in a moist greenhouse.

This is the problem then: if we inbreed we often fail to get seed; and if we outbreed our strain will not breed true. The solution is—compromise. Inbreed as close as you dare. An illustration will make the point clearer. Suppose we are growing an annual flowering plant with red flowers, all forms of this annual species being self-incompatible. Suddenly we find one plant, a sport, with white flowers. If we self-pollinate it we shall get no seed. How then can we raise a white-flowered strain? The method is, with the aid of a camel-hair brush dust the pollen from as many red-flowered forms as possible on to the stigmas of the white sport—or if we are sure the bees will cross-pollinate our plant, collect the natural seed. By using the pollen from as many other individuals as possible we are reducing the chances of cross-incompatibility. If red is dominant to white, all the plants of the next generation will be red-flowered. We know that by selfing or crossing these F_1 plants together we shall get the desired white-flowered forms in F_2. Selfing is useless, however, so we again collect seed from open pollination or make as many crosses as possible. In the next generation (F_2) a quarter of the plants will have white flowers. The red individuals are discarded and seed saved from open pollination of the whites or from cross-pollination as before. We have now got the desired white-flowered strain. In subsequent generations selection for size and qualities of flowers, etc., could be made, *so long as a fair number of whites are kept for seed and inbreeding is avoided as much as possible.*

It should be noted here that the foregoing remarks do not imply that close inbreeding is impossible in strains where self-incompatibility occurs. Actually, if the constitution of a plant for incompatibility is known, then it is possible to make continuous brother-sister or parent-progeny matings with impunity. The amateur and commercial breeder are rarely able to identify the genes for incompatibility in their stocks and must therefore follow that plan which is most likely to lead to success.

"Sterility" in species-hybrids may sometimes be due to the fact that the hybrid is the only plant of its kind—not to any inherent sterility. For example, if two *self-incompatible* species are crossed and chromosome doubling occurs in the hybrid, it will be infertile if it is still self-incompatible and there is no other plant of its kind (i.e. with the same chromosome number) to cross it with.

STERILE SPECIES-HYBRIDS

Another, and very common, example of sterility blocking the progress of a breeding programme is the sterility found in species-hybrids. The breeder crosses two species showing many desirable characters, in the hope of getting a hybrid race combining the best points of each species. Usually the hybrid is more or less intermediate in character and of little value itself. If it could be selfed, then among the progeny would be plants combining the best qualities of the parent species. The hybrid is sterile, however; or if a few seeds set they give rise to weak and worthless plants. Loth to throw away a potentially valuable plant, the breeder probably keeps the hybrid for some years (if it is a perennial or can be propagated vegetatively), relegating it to an odd corner where it finally dies and is only remembered with regrets of what it might have been.

A species-hybrid, especially when derived from selected parents, always has great potentialities and it is worth taking some trouble to bring about fertility if this is lacking. The sterility of species-hybrids is usually due to failure of chromosome pairing, the chromosomes of the parent species being too different to pair. But as we saw in Chapter 6 doubling of the chromosome number in sterile hybrids of this kind restores fertility, therefore our problem will be solved if we can induce chromosome doubling. Can this be done? The answer is, not with certainty, but there are methods which may increase the chance of its happening.

In the first place a sterile hybrid should not be discarded as useless after a few attempts to get seed, since chromosome doubling, though relatively rare, occurs naturally from time to time. In the last ten years of the author's experience he has come across quite a number of plants which have originated by chromosome doubling, including such important examples as the "John Innes" blackberry and *Delphinium Ruysii* (the red-flowered garden strain); and during the last year chromosome doubling has occurred on three separate occasions in plants of a sterile hybrid strain of considerable promise derived from crossing two *Streptocarpus* species.

Secondly, we can increase the chances of chromosome doubling by vegetative multiplication of the sterile hybrid. If we have only one plant the odds may be, say, 1,000 to 1 against its occurring in a period of five years, but with ten plants the odds are reduced to 100 to 1. Therefore the sterile hybrid should be increased vegetatively to as many plants as we think worth while, and for which we can afford space.

Thirdly, it is known that the regularity of cell-division can be upset by certain treatments, and these if applied may still further increase the chances of chromosome doubling. The most promising results have been obtained by the use of a powerful alkaloid drug, colchicine.* The

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* It is dangerous to let even dilute solutions of colchicine touch the skin.

method is to bring soft tissue in which growth, and therefore cell division, is rapidly proceeding into contact with a dilute aqueous solution of the drug. This may be done by applying drops to the growing point of a seedling or shoot, or by soaking germinating seeds in a solution of colchicine. Concentrations of from 0.05 to 0.10 per cent are the most useful, especially the former.

The effect of colchicine at the right concentration is to prevent division of the cell, but not of the chromosomes (see page 76). Thus double the number of chromosomes are found within one cell. After the colchicine has been removed by washing with water, normal division of such a cell may ultimately give rise to a tetraploid shoot which may be propagated vegetatively; or to flowers and fruits from which tetraploid seeds may be gathered.

Where treatment has been effective, growth is often temporarily stopped and the root tips of seedlings become swollen and bulbous. Therefore the most retarded plants should be selected and nursed back to normality by growing them in a moderately high temperature and moderately humid conditions. Some of the tissue that recovers will have the normal diploid constitution, while other tissue will be tetraploid. It is not always easy to distinguish the two tissues. However, with the aid of a microscope, the tetraploid branches may sometimes be recognized by the larger stomata of the leaves, while tetraploid flowers may be identified by their larger pollen grains. The colchicine method has been used successfully on Marigold, Petunia, Zinnia, Antirrhinum, Tomato, and other species.

Fourthly, whether sterile hybrids are treated or not, every flower should be self- or cross-pollinated or left to certain open pollination—preferably the first of these three. The plants should be examined every week during the flowering season for the slightest signs of seed. *This examination must be made with great care*, since it is rarely that more than one seed vessel will be found at a time and even then it may contain only a very few seeds; and if only one seed is found, that one seed may give rise to a new and valuable strain of plants. Occasionally a whole branch or even the greater part of a plant will be found to be fertile, depending on the point in the development of the plant where chromosome doubling took place. *Delphinium* "Belladonna" is an example of a strain which first arose as a sterile hybrid and then, after many years, gave three capsules with seed from which the present fertile strain was developed.

When sterility is not complete in a species-hybrid the seeds obtained will usually give rise to weak plants of no value, having more or less the same number of chromosomes as the hybrid. In cases such as this, watch should be kept for any vigorous-looking seedling, since such a one is very likely to prove a fertile form with twice the number of chromosomes.

If a species-hybrid fails to set seed when self-pollinated, it must not be assumed that it is sterile and therefore useless as a parent. Sometimes a hybrid will fail both as seed and pollen parent in the majority of crosses with other species or hybrids, yet be successful in one or two combinations. Further, characters from species which will not cross directly can sometimes be combined in one strain by crossing with another species first and then crossing the hybrid with the desired parent. For example, it is desired to combine certain characters of species *A* and *B* but they will not cross. *A* will cross with species *C*, however, and it is then found that the hybrid *AC* can be crossed with *B*.

In such roundabout ways the difficulties of interspecific hybridization can occasionally be surmounted.

In some members of the tomato family, the *Solanaceae*, chromosome doubling can be induced by decapitation. The method is to cut down the young plant when it is 6–8 in. high, to about 3–4 in. from the soil, keeping the stump in a warm, humid atmosphere (60–80° F.). A proportion of the adventitious shoots which arise from the callus formed on the decapitated surface have double the number of chromosomes, e.g. in tomato about 7 per cent of the total number of adventitious shoots. The shoots with double the number of chromosomes are recognized by their stouter stems and thicker and broader leaves. As soon as they are large enough they should be removed and rooted as cuttings in the usual way. This method of inducing chromosome doubling has also been used successfully in sugar beet.

The method described above for tomato and sugar beet consists essentially in the production of callus which will give rise to adventitious shoots. Accidents to cell-divisions are more frequent in callus than in normal tissue. It is possible, therefore, that the use of "plant hormones" to stimulate the production of callus may prove an aid to the formation of shoots with an increased number of chromosomes.

In conclusion, it should be pointed out that sterility and incompatibility are sometimes desirable characters. Thus the double-flowered ornamental cherries are all sterile and since no fruits are ever set the whole energy of the trees is available for flower production. Self-incompatible strains of flowering plants might be worth developing for their greater freedom of flowering.

CHAPTER 7

METHODS OF PLANT IMPROVEMENT

THE breeder should always know exactly what he is aiming at in the way of plant improvement. Vague expectations may sometimes be satisfied by a haphazard cross, but only definite aims will ensure steady progress.

The breeder who knows something of the laws and mechanism of heredity; who knows his plants and keeps a careful record of their behaviour in inheritance; who has an observant eye and a mind quick to interpret his results—that breeder will soon acquire a large capital of knowledge which invested in wisely chosen programmes of work is bound to yield a good return. Even so it takes time to accumulate knowledge and experience; hence these last pages will deal with the nature of plant improvement, and special and general methods of achieving it.

A plant may be improved in two ways, (1) by a change in the conditions under which the plant grows, namely its environment, or (2) by a change in its hereditary constitution.

FLUCTUATIONS

The first kind of improvement is due to a change *outside* the plant, e.g. transplanting from a poor to a rich soil and other such changes in cultivation or climate. Improvements such as these are of a temporary nature only, and are not inherited. Thus seeds saved from a well-fed plant will, other things being equal, give progeny no better and no worse than the seeds from a starved plant, and *vice versa*. The big difference between a starved and a well-fed plant is a *fluctuation* caused by a difference of environment.

This does not mean that it is of no consequence whether the breeder saves his seed from good or bad plants of the same strain. A plant which starts life as a starved and shrivelled seed is handicapped from the beginning, even though in the end it is no different from the plant which came from a good plump seed. Rather does it mean that the breeder will not necessarily improve a strain by selecting the largest plants. A plant of a potentially large strain may actually be smaller, through unfavourable environmental conditions, than a plant inherently smaller but enjoying exceptionally good conditions. However drastic the effect of the environment upon the characters of the plant, the genes are not altered. In other words, acquired characters are not inherited.

It will be clear from the above remarks that the breeder is concerned with heritable variations only. Indeed, fluctuations will misdirect him, and obscure his results. In breeding work, therefore, it is important that the plants should be grown under uniform conditions of soil, moisture, light, and temperature, since only then can we be fairly certain that any differences observed are variations that will be inherited. At the same time the cultural conditions should be reasonably good, since it is then easier to recognize desirable variations; inferior forms in particular often doing best under poor cultural conditions and in bad growing seasons. In certain instances, however, indifferent conditions might reveal qualities masked by good conditions (e.g. the quality of drought resistance required for light sandy soils would not be apparent on a good moisture-retaining soil). Therefore in choosing his planting site the breeder must always have his particular objective in view.

VARIATIONS

The second kind of improvement is due to a change *inside* the plant (e.g. immunity to disease instead of susceptibility, or the production of large flowers instead of small), and though differences in the environment may somewhat alter the character concerned (e.g. the flowers will be smaller if the plant is starved) yet the improvement is in essence a permanent one, and is inherited. Changes of this kind we shall call *variations*. Heritable variations are of two kinds, those due to mutation and those due to hybridization.

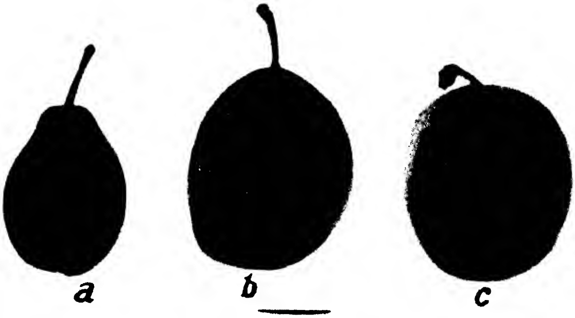

Fig. 31.—Bud variations in the plum (Prune d'Agen). (*a*) The type. (*b*) A bud variation known as Coates Prune. (*c*) Another variation which arose in California. Both of the variations equal the type in quality and cropping

Mutation

After remaining constant for many generations a character may suddenly change or mutate, e.g. a plant with mauve flowers will suddenly produce a branch bearing red flowers, seed from which breeds true to red. Changes such as these are called *sports* or *mutations* (see p. 95). Mutations are fairly common, although as a rule only the most conspicuous ones are noticed. Every sort of character may mutate, characters of form and colour, also the more obscure physiological processes. Mutations are of three kinds, due respectively to

1. change in a gene (see p. 95);
2. change in the chromosome complement (see pp. 87, 96);
3. a sorting-out of different tissues (see p. 128);

but only the first of these will as a rule concern the breeder.

Gene mutation is a very important source of plant improvement. To quote but two examples, the "Spencer" Sweet Pea and the new variety of the Chinese Primrose called "Dazzler" both arose as gene mutations. Conspicuous mutations like these are at once noticed by the plant breeder, who perpetuates them by isolating the plants and securing seed from self-pollination, or by propagation from grafts, cuttings, etc. (Fig. 31).

It must not be assumed that every sudden change in a strain of plants may be attributed to mutation. Thus, if in a true-breeding strain one plant is different from all the rest, it might have resulted from accidental cross-pollination. However, if only a portion of the plant is different, then the change is certainly of a mutant character.

HYBRIDIZATION

The second great source of plant improvement is hybridization, i.e. the natural or artificial crossing of plants which differ inherently from one another. Thus we may hybridize varieties, species, or genera and the progeny would be varietal, specific or generic hybrids respectively. *Hybridization is practised in order to combine in one individual or strain characters found in two or more individuals or strains.* Thus the breeder notices that one plant has certain desirable characters which another plant, although excellent in other ways, has not. He therefore crosses the two plants and combines in the hybrid or its descendants the desirable characters of both species. Artificial hybridization in particular has contributed to plant improvement, since species which normally grow in different parts of the world, and therefore could never cross naturally, have been brought together in gardens and hybridized by the breeder. Heritable variations then may arise from the crossing of plants or, to put it another way, *from new combinations of genes.*

It often happens that the result of crossing two desirable forms is a nondescript hybrid combining the good and bad qualities of the parents in more or less equal proportions—and this is especially true of species-hybrids (cf. *Delphinium Ruysii*, p. 142). Such a hybrid must not be regarded as a failure, however. It is only the first step in securing forms which combine the desirable qualities only. The next step, therefore, is to self- or back-cross the hybrid according to requirements.

By selfing or back-crossing a hybrid we sort out special combinations of the genes contributed by the parents of the hybrid. For example, if the constitution of the parents is *AAbb* and *aaBB* then the hybrid is *AaBb* and by selfing it we get among other forms the two new true-breeding types *AABB* and *aabb*, i.e. we have obtained new combinations of genes and therefore new plant varieties. Since no one wants to waste time and material in raising new plants the question the practical man asks is: "What is the smallest F_2 I need raise in order to get at least one of either the top dominant or bottom recessive forms?" The answer depends on how good a chance will satisfy the breeder. Probably most people would feel satisfied with a nine to one chance of success and the figures for this and even more favourable odds are given in Table IV (see p. 112).

The appearance of the hybrid is often no guide as to what it may yield in the next or later generations. Thus if *a* and *b* are genes controlling the desirable characters then the hybrid *AaBb* will be intermediate if *A* and *B* are incompletely dominant, or the desirable characters will not be seen at all if *A* and *B* are completely dominant. The breeder, therefore, should always raise a second generation. Indeed, if promising forms appear in the F_2, they should be self- or cross-pollinated and a third or fourth generation raised. The more different the original parents are, the longer will it take to sort out new gene combinations, and the longer should breeding be continued before deciding that further work is not worth while.

TABLE IV

This table shows the number of plants which must be raised in order to stand a 9 : 1, 19 : 1, or 49 : 1 chance of getting at least one bottom recessive or one top dominant plant from (*a*) back-crossing, (*b*) selfing, an F_1 hybrid.

Pairs of genes	*Chances of success*		
	9 : 1	19 : 1	49 : 1
(*a*) back-crossing:			
one (*Aa*)	4	5	6
two (*AaBb*)	8	11	14
three (*AaBbCc*)	17	23	30
(*b*) selfing:			
one (*Aa*)	8	11	14
two (*AaBb*)	35	47	61
three (*AaBbCc*)	147	191	250

Example: The breeder has crossed two plants *AAbb* and *aaBB*. By selfing the F_1 hybrid (*AaBb*) he should get in F_2 the top dominant (*AABB*) and bottom recessive (*aabb*) plants. How many plants must he raise in F_2 in order to stand a 9 : 1 chance of getting at least one of the desired types? Answer: 35.

Note.—There is no special virtue attached to the chances 9 : 1, 19 : 1, and 49 : 1. They have been selected merely as giving a fair range of odds. Thus, the breeder who is extremely anxious to get a desired result may consider a 9 : 1 chance not good enough and prefer the greater certainty of the 19 : 1 chance.

Selfing a hybrid is the best plan when each of the parents shows a *number* of desirable characters. Not infrequently, however, it is desired to cross a plant with many good qualities but one specifically bad one (such as susceptibility to disease) with another plant whose only merit is that it possesses the character needed to correct the fault (e.g. resistance to disease). In such cases the hybrid is usually inferior, revealing many of the poor qualities of the second parent. We may represent the parent and hybrid as follows, the recessive gene *d* conferring disease resistance (it does not matter which plant is used as female):

$$\begin{array}{c} aabbccDDee \times AABBCCddEE \\ | \\ AaBbCcDdEe \end{array}$$

Now the particular plant wanted is one combining the good qualities of the female parent with the disease resistance of the male parent, that is to say a plant of the constitution *aabbccddee*. In our example the chances of getting this in the F_2 from self-pollination are over 1,000 to 1 against, and the breeder might be unable to accommodate so many plants. What is the best thing to do, then? The answer is, back-cross the F_1 to the high-quality parent and raise a fair number of plants. From these select several of those individuals *which are most resistant and at the same time most like the high-quality parent.* On the average every other one of these plants will be hybrid for resistance* (*Dd*), therefore if several plants are selfed and the seed sown separately, one or more will be found to give resistant forms like the female parent. The scheme is shown on p. 114. This method of transferring one or two desirable characters from an otherwise inferior plant by back-crossing the hybrid to the desirable parent is much quicker and more effective than continued selfing. In complex cases back-crossing may have to be carried on for 4, 5, or 6

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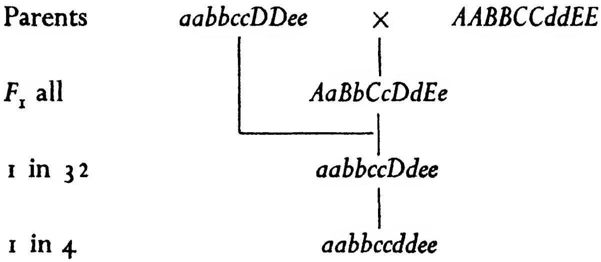
* If susceptibility is completely dominant, the back-cross generation will all be susceptible to disease, though half of them will be carrying the gene for resistance.

generations, selecting in each generation that plant which is most resistant and most resembles the high-quality parent and back-crossing it to the high-quality parent. This method will eventually yield progeny identical with the high-quality parent but hybrid for the character being transferred (in our example, disease resistance). The desired new form will then be obtained on selfing.

If the character being transferred is recessive, then self-pollination will be necessary before each back-cross to ensure that the plant or plants selected for back-crossing carries the hidden recessive character.



Most breeders' hybridizing programmes are restricted through lack of space for all the plants they would like to grow. It is useful, therefore, to know the rules governing the size of F_1, F_2, and F_3 progenies necessary to secure certain results.

In the first place, *if the parents breed true the* F_1 *will be uniform, every plant being genetically the same as every other, and only a small* F_1 *need be raised.* The size of the F_2 in such a case should be governed by the degree of difference between the two parents. If they differ only by one or two characters then only a small F_2 need be raised. The greater the difference between two true-breeding parents the larger should be the F_2.

Secondly, we have to consider the size of F_1 and F_2

progenies required when the parents do not breed true. The rule is, *the greater the hybridity of the parents, the larger should be the F_1*. In regard to this rule, in practice only rough estimations are possible, though if the breeding performance of the parents is known from other pollinations, this will be helpful. In the main, therefore, a breeder will have to rely on his experience in calculating the size of F_1 required. The size of each F_2 family, though smaller than F_1, will be proportional to it.

The size of progenies from back-crossing will be determined by the combined degrees of hybridity of the parent and the F_1 plant used.

APOMIXIS

A source of error which may be the cause of much perplexity to the breeder is apomixis, i.e. the production of seed without fertilization. The breeder crosses two plants and obtains apparently normal seed which germinates, only to give progeny *all of the same type as the female parent*. Thus one of the parents appears to be completely dominant over the other. It is not uncommon to find apomixis occurring when species and species-hybrids are self- or cross-pollinated. For instance, in experiments the author was making with *Streptocarpus* it was found that *S. Rexii* crossed with various species gave plenty of seed and normal hybrid progeny, whereas *S. Rexii* × *S. Holstii* gave little seed and the progeny, though weaker at first, were identical with *S. Rexii*. Similar results have been obtained in breeding blackberries. Apomixis has been recorded in *Rubus*, *Rosa*, *Hieracium*, *Allium*, *Ochna*, *Erigeron*, and numerous other plants. It is, of course, a definite block to plant improvement in the ordinary sense. However, in propagating a good type apomixis might be useful since apomictic seedlings are usually genetically identical with the mother plant and therefore form a pure line or *clone* (a clone is a group of plants derived from asexual propagation, e.g. cuttings).

Maternal inheritance *not* due to apomixis is sometimes found in plants with variegated or yellowish leaves. In the marvel-of-Peru (*Mirabilis jalapa*) varieties occur with leaves mottled green and white, and these variegated plants sometimes bear green shoots and white shoots also. Seeds saved from the selfing of flowers borne on the green, white, and variegated shoots give progeny with green, white, and variegated leaves respectively. If flowers on green shoots are fertilized by pollen from flowers on white shoots, then all the progeny have green leaves, like the mother. Conversely, if flowers on white shoots are fertilized by pollen from flowers on green shoots then all the progeny have white leaves, like the mother. Thus in respect to both cross- and self-pollination the progeny always resemble the female parent. The explanation of this is as follows. The green colour of leaves is due to the presence of numerous minute bodies, called chloroplasts, in the cell-plasm which surrounds the nucleus of the cell. The cell-plasm of the egg-cells normally carries the bodies which give rise to chloroplasts, which the male germ-cells never do. In consequence, chloroplasts are only inherited from the female parent. If the egg-cells arise from green tissue then green chloroplasts are passed on to the progeny, but if the egg-cells arise from white tissue then colourless plastids are passed on.

MASS SELECTION

Not all mutations constitute improvements of value to the breeder, and not all the results of hybridization are desirable and worth perpetuating, hence the breeder must always be selecting, saving the good and better forms and using these as parents in turn.

The simplest form of selection is by "rogueing out" or destroying all inferior and undesirable types from the crop, and saving the mixed seed from the remainder. This is called mass selection. It is usually practised when seed of those annual and biennial plants which are usually propagated from seed is wanted in large quantities for trade purposes. The seed thus obtained is from open (chance) pollination—i.e. from self- or cross-pollination according to the pollination mechanism of the plant—hence the male parent is normally uncertain or unknown. Rogueing should be done if possible before flowering begins, so that no pollen from the inferior plants takes part in fertilization. In certain cases rogueing can be done at very early stages. For example, in a number of species forms with red or bluish flowers also have reddish pigment in their leaves and stems (unless the flower colour is very pale), e.g. *Aquilegia*, *Dahlia*, *Antirrhinum*. Thus it is an easy matter to distinguish such coloured flowers from the white or yellow kinds, even in the earliest seedling stages. If the breeder is observant he will notice from time to time correlations between juvenile and adult characters as described above and will be able to save himself much time and labour.

In order to keep stocks true to type and maintain improvement, rogueing should be scrupulously carried out *every* year; otherwise the strain will soon deteriorate, rogues usually being dominant forms.

A better method of mass selection is to save the mixed seed from the choicest plants only, but as before there is still no control over the pollen parents, which might be inferior forms. A still better method, therefore, is to destroy all of the maincrop except the choicest plants, saving the mixed seed from these alone. If the number of selected plants is few, or if they are rather scattered, artificial pollination might be necessary to ensure good seed setting. In this last method of selection there is some control over the pollen parent and the strain may be considerably improved. The method is particularly useful in the case of self-incompatible plants (e.g. *Brassica*) and those species in which the sexes are borne on different plants (e.g. asparagus).

SINGLE PLANT SELECTION

The best form of selection is single plant selection, in which one plant only is used to perpetuate the strain. The results of this selection, however, are very different, according to whether the plant is naturally self- or cross-pollinated.

i. *Naturally Self-Fertilized Plants*

The effect of self-fertilization is to sort out and reveal the dominant and recessive genes. For example, *Aa* selfed gives the types *AA*, *Aa*, and *aa*, of which *AA* and *aa* will breed true. Thus by self-fertilization we can analyse our plant, sort out its genes, and establish true-breeding lines. The breeder, let us say, is growing dwarf beans. In a row of plants is one which, cropping early, commends itself to him as an improvement, so he saves the seed (beans are self-pollinating). In the next generation he finds plants cropping earlier, as early, or later than the parent plant, i.e. the genes controlling early cropping are becoming sorted out. By selecting the earliest (or latest) cropping plants the breeder will be selecting towards pure breeding dominant or recessive types as the case may be (*AA* and *aa*). Thus in one operation he improves the strain in two ways: in earliness of cropping, in uniformity.

In practice, of course, it is rare to find only one pair of genes controlling such a character as earliness of cropping. Usually several genes will have major effects and a number of others minor or modifying effects and all of these genes must be got into the pure-breeding dominant or recessive condition before the maximum improvement is obtained. We say "maximum improvement" since there is a point beyond which selection of the progeny of one plant can result in no further improvement. This is clearly seen if we consider a plant which is hybrid for two pairs of genes, *AaBb*, the dominant genes *A* and *B* both making for *late* cropping. As we saw on p. 65, by selfing this individual we get in the next generation a type *aabb* which will be early cropping since the dominant genes *A* and *B* have been eliminated. The breeder naturally selects this *aabb* type for further selection, but selection can bring about no further improvement since all the progeny of the plant *aabb* will also be *aabb*, i.e. a *pure line* has been established. We can sum this up by saying that selection cannot lead to improvement in a pure line. Thus, valuable as self-fertilization is, in sorting out genes and establishing pure lines, by itself it can only bring about a limited improvement.

The crossing of naturally self-fertilized plants often results in "hybrid vigour," i.e. the progeny grow quicker and are larger than either of the parents. It is probable that breeders generally have not utilized hybrid vigour to the best advantage. It does not follow, of course, that increase in size means increase in the number of flowers and fruits. Nevertheless, there must be many cases where, in some respect, hybrid vigour could be utilized to advantage.

Hybrid vigour is at a maximum in the F_1 generation, hence in plants raised from seed it is necessary to repeat the parental cross for each crop if maximum vigour is required. This is a relatively easy matter if the sexes are borne on different plants, or if the selected parents are self-incompatible. Failing this, the labour of artificial cross-pollination is likely to be unprofitable except where a great many seeds are obtained from each pollination. In plants which can be multiplied asexually the vigour of the F_1 hybrid can be maintained indefinitely by propagation from cuttings, grafting, etc.

Hybrid vigour has been successfully utilized in maize (Fig. 32), *Begonia*, tomato, potato, cucumber, and forest trees.

ii. *Naturally Cross-Fertilized Plants*

In plants which are naturally cross-fertilized, self-fertilization leads to a general decrease in the quality of the strain. Furthermore, abnormalities appear, such as albinotic, chlorotic, and variegated forms; organs are often defective and parts deformed.

The reason for this is as follows. Naturally cross-fertilized plants are bound to be hybrid to a certain extent, that is they carry a number of recessive genes (e.g. *AaBbCcDd*, etc.). Now most recessive genes have an adverse effect upon plant growth, but so long as the related dominant genes are present the harmful effect of the recessive genes is suppressed. Self-fertilization, as we have seen, sorts out the recessive genes and gives forms which are pure-breeding recessives, hence the appearance of abnormal and weak types. By contrast, naturally self-pollinated plants are nearly always found to be pure-breeding (*AABBCC*, etc.), any recessive forms which may occur being quickly eliminated by natural selection.

PURE LINES IN NATURALLY CROSS-POLLINATED PLANTS

Now self-fertilization of a naturally cross-fertilized plant usually results in a general decrease in the vigour of the strain. How then is the breeder to secure the advantages of single plant selection when self-fertilization leads to such undesirable results?

By way of example let us suppose that it is desired to combine largeness of fruit with resistance of the plant to some specific disease, in one true-breeding strain. The method is as follows. Select two plants, each with large

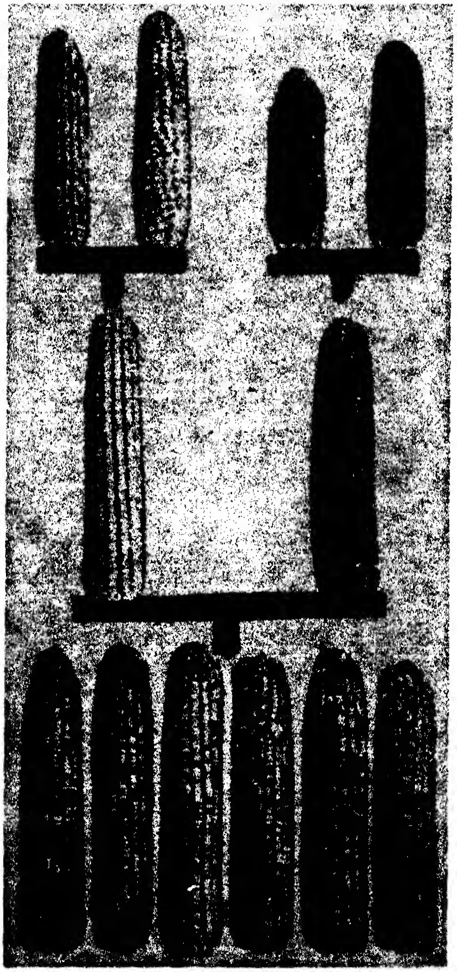


FIG. 32.—The result of bringing together four inbred strains of maize, by three crossings. Note hybrid vigour

From Babcock and Clausen, "Genetics in Relation to Agriculture" fruits and high disease resistance, and self them, keeping the progenies separate. In these progenies there will be a variety of forms, some very weak, some abnormal in one way or another, varying both in fruit size and disease resistance. In each progeny select several seedlings with large fruits and high resistance to disease, *taking care to choose those plants which are the most normal in appearance*, and self these, sowing the seed from different plants separately. One or more of the seedlings should be found to breed true. If none is found, then raise a third generation from selfing those plants in F_2 with large fruits and high resistance to disease—and so on. Usually the true-breeding plants will be noticably weaker than normal. We have now at least two forms breeding true for the desired characters—though both forms may be so lacking in vigour as to be of little value as they stand. But if such true-breeding forms are crossed together, vigour usually returns, giving a strain breeding true for both characters; i.e. vigour returns upon inter-crossing, even after several generations of inbreeding. Thus the weakness incurred by the necessary inbreeding to secure pure lines need be no barrier to success so long as cross-pollination within the strains is practised once the strain is purified.

In the example just mentioned vigour would be maintained by *avoiding* single plant selection and saving the seed from a number of the best plants, i.e. mass selection to take the place of single plant selection. The strain should not, of course, be outcrossed with any other stock.

The same method could be adopted if only one character was concerned, except that at least two true-breeding plants should be isolated and these crossed together finally to restore vigour.

If difficulty should be experienced in maintaining vigour in the strains obtained as above, then instead of saving the mixed seed as suggested the two true-breeding forms could again be crossed together, to give vigorous progeny, as often as it is necessary to secure new vigour.

Self-pollination of naturally cross-pollinated plants is a useful way of eliminating undesirable recessive characters from a strain. Any number of pure lines can be bred, e.g. *A*, *B*, *C*, and *D*, and then, after the weeding out of any undesirable forms in each line, *A* is crossed with *B*, and *C* with *D*, and finally the two hybrids, *AB*, *CD* are crossed together, thus combining in one strain the selected qualities of the four pure lines (Fig. 32).

In selecting for one or two special characters the breeder should not lose sight of such important qualities as robustness and fertility and watch should be kept lest an undesirable character be selected along with a good one, e.g. bolting and early cropping in vegetables.

SMALL IMPROVEMENTS

The selection of new and improved forms from a batch of seedlings is often a matter of some difficulty. In particular there may seem to be few plants as good as the parents; these few, though better in some ways, may be poorer in others. In other words, improvement usually comes only a little at a time, and then only in some of the plant characters. The reasons for this we have already seen. If we cross two plants carrying the genes *AA* and *aa* respectively, then in the second generation there will be three types—*AA*, *Aa*, and *aa*, and the recessive form occurs once in four times. If we cross two plants carrying the genes *AAbb* and *aaBB* respectively, then in the second generation there will be nine types (see p. 65) and the recessive occurs once in 16 times. If three pairs of genes are involved there are 27 types and the recessive occurs once in 64 times; with four pairs of genes there are 81 types and the recessive appears once in 256 times, i.e.

the complexity rapidly increases with every additional pair of genes. Now when the plant breeder crosses two plants, he may actually be dealing with at least half a dozen genes having major effects, in addition to many others having minor effects. Thus the number of possible combinations is very great indeed and among several hundred plants only one or two will come near the particular combination of genes which results in the desired characters. Gene interaction, polyploidy, etc., will further increase this complexity.

Under these conditions the odds are all against the breeder. What can he do to increase his chance of success? In the first place it is probable that one or two characters are the object of the breeder's special attention, although he must also keep his eye on many others which must not be ignored. As a rule these special characters should be given priority in selection, fitting the minor ones in when possible.

Secondly, the fact that improvement often comes a little at a time means that the breeder must know his plants intimately (p. 47) especially the range of variation within the species. *Particularly important is comparison with the parents, since from this will be learnt which characters a plant is most likely to pass on to its immediate offspring*, i.e. which are the dominant characters. Careful note should therefore be made of the different types appearing in the progenies, especially in progenies from selfing.

Thirdly, the numbers of the different types of plant should be counted. While it is true that the practical breeder may rarely come across simple 1 : 1 and 3 : 1 ratios, *on no account should he fail to note the proportions of the different types, since they will point the way to a breeding plan which will yield the desired results.* Thus *A* × *B* may give 20 per cent of plants showing a certain character or combination of characters, whereas *A* × *C* gives 30 per cent. Since parent *A* was used both times such a result can only mean that the potentiality of *C* for passing on the selected character is greater than that of *B*—no matter what the actual appearance of *B* and *C* may be. *C* is therefore to be preferred in breeding and should be used as a parent unless a better type, as judged by its progeny, is found. *The "progeny test" is the only accurate means of deciding the merits of a plant for breeding.* Plants selected as parents should always be chosen on their performance and not merely on their appearance.

FIXING

The fixing of characters so that the strain breeds true in respect of these characters is an essential part of the breeder's work, and *the attainment of uniformity alone is an exceedingly important thing*. Fixing may be regarded as plant improvement applied to the strain rather than to the individual.

The method of fixing a character is as follows. Self the plant showing the desired character. Select *several* of the progeny, self them, *saving and sowing the seed from these plants separately*. If no family from this sowing is found to breed true, the process should be repeated for another generation or longer. *Special note should be made of the segregation obtained when trying to fix characters, since the types and proportion of the progeny will often indicate the quickest way to success.* Much time could be saved in fixing if breeders were aware of the great importance of analysing the desired form into its component characters and noting the separate inheritance of each of them. To take a simple example, it is desired to fix a particular shade of flower-colour, scarlet-crimson. Examination of the whole range of flower-colour within the species shows that colour may be resolved into two components, (1) ground colour ranging from yellow to white, (2) upon which is superimposed a purplish pigment. Purple upon a white ground appears purplish in colour; on a yellow ground it appears scarlet. Scarlet-crimson, therefore, is the colour resulting from the conjunction of a certain intensity of purple with a certain intensity of yellow. In examining the progeny from selfing the scarlet-crimson form, the breeder should make special note of the intensity of (1) the yellow ground, (2) the purple pigment. Do they vary from the parent? In which direction, paler or deeper? Which is dominant, pale or deep intensity? Analysis of this kind demands keen observational powers, but is indispensable for the rapid fixation of characters.

Characters which differ by a single gene, e.g. *A* and *a*, are, other things being equal, quickly fixed. Thus by selfing the hybrid *Aa* we get in the next generation three gene types *AA*, *Aa*, and *aa* in the proportion 1 : 2 : 1. If *A* is completely dominant we cannot tell *AA* from *Aa* forms, therefore if we select a plant showing the dominant character the odds are two to one against it being a true-breeding *AA* type. It is clear, however, that if we save seed

TABLE V

This table shows the number of dominant type F_2 plants which must be self-pollinated in order to stand a 9 : 1, 19 : 1, or 49 : 1 chance of getting at least one true-breeding family in the next generation (i.e. of fixing the strain).

Pairs of genes	*Chances of success*		
	9 : 1	19 : 1	49 : 1
One (*Aa*)	6	8	10
Two (*AaBb*)	20	32	41
Three (*AaBbCc*)	61	79	104

Example: The breeder has crossed two plants *AAbb* and *aaBB* and from selfing the F_1 he has obtained the four classes *AB*, *Ab*, *aB*, *ab*, in the ratio 9 : 3 : 3 : 1. Some of the *AB* class will breed true and others will segregate. How many plants of this class must he self-pollinate in order to stand a 9 : 1 chance of fixing it (i.e. of selecting an *AABB* individual)? Answer: 20.

separately from several dominant forms, then almost certainly one or more of them will be *AA* types and one or more of the families raised from these plants will breed true, i.e. the character *A* will be fixed. But how many plants must we save, in order to be certain of including at least one *AA* type? The answer is given in Table v, for 1, 2, and 3 pairs of genes. By the help of this table we can be practically certain of fixing a character, due to simple gene differences, in two generations.

The greater the number of genes involved in the expression of a character the longer will it take to fix that character, hence this applies in particular to polyploids. At a rough approximation about half of the plants the gardener deals with are polyploids. Polyploids differ from diploids in several ways important to the breeder. For instance, conspicuous mutations are less common in polyploids. When a new character appears in a diploid plant it often appears at a single step, is fixed within two or three generations at the most, and is readily combined with other characters. But in the polyploids a new character nearly always arises as a slight variation and in a "mongrel" condition which must be selected for a number of generations before it is well developed and fixed. The reason is clear. If a plant with four sets of chromosomes carries four dominant genes *PPPP* and one of them mutates to give rise to a *PPPp* plant, then the effect of the one *p* gene may be almost swamped by the effect of the three *P* genes and the mutation if expressed at all will appear as a slight difference only. Further, if the *PPPp* individual is selfed, the next generation would, at the most, only give equal numbers of *PPpp* and *PPPp* forms, so that selection must be carried on until the *pppp* form is obtained and the character fixed.

In illustration of this we may refer to the garden dahlia (eight sets of chromosomes), which, although it has been bred, often very intensively, for over 130 years, has never given at a single step a conspicuous mutation. Improvement and the development of new characters have been little by little. By contrast the Spencer character in sweet pea (two sets of chromosomes) was fixed within two or three years. The breeder should not despise variations just because they are slight, especially if he knows his plant to be a polyploid.

When a character has at last, apparently, been fixed it is advisable to grow a fairly large trial lot to be quite certain that variation is not occurring, especially where purity of strain is an economic consideration, or a matter of repute. It may also be necessary to grow the improved strain for two or three years to be sure that its first promise is maintained.

Not all characters are capable of being fixed. Thus if we have three types, tall (*TT*), intermediate (*Tt*), and dwarf (*tt*) it is futile to attempt to fix the intermediate character since, as we saw in Chapter 4, the hybrid *Tt* forms will always give a proportion of talls (*TT*) and dwarfs (*tt*). Characters which are due to the hybrid nature of the plant cannot be fixed. This is another way of saying that only completely dominant or recessive characters can be fixed.

Under certain conditions this inability of a hybrid to breed true may be turned to advantage. For example, if the hybrid itself is of value but will not breed true, then only the breeder who knows the parents can reproduce this hybrid, i.e. he has the monopoly of the strain. In countries where plant patents do not exist this would be a definite advantage, so long as the labour of making the cross-pollinations giving the hybrid strain were not too great. In plants which are self-sterile this labour is reduced to a minimum, it being only necessary to plant alternating rows of the male and female plants and leave the bees or wind (as the case may be) to perform the necessary cross-pollination. If a large number of seeds per capsule is produced, then it might be worth while emasculating as many flowers as possible and pollinating them artificially.

Another type of plant which cannot be fixed is the *chimaera*. One of the best-known chimaeras is *Cytisus Adami*. This plant is made up of two distinct tissues, an outer layer of purple broom (*Cytisus purpureus*) surrounding an inner core of Laburnum (*Laburnum anagyroides*) just as a glove covers a hand. Laburnum has yellow flowers and the broom purple flowers. *Cytisus Adami* has flowers of a dirty pink colour. If C. *Adami* were fertile, seeds saved from it would never give forms with pink flowers, because pink colour results from the chimerical nature of C. *Adami*. Chimaeras of varying kinds and degrees are not uncommon among cultivated plants and failure to fix characters might on occasion arise from this cause (Fig. 33).

A third obstacle to fixing is the "eversporting" gene. Genes are known which are remarkably unstable, changing (within definite limits) from one condition to another at frequent intervals. The stripes and streaks of some variegated plants afford one example of the work of eversporting genes.

General Improvements

In the remaining pages of this chapter a rapid survey will be made of the kind of improvements which should be sought for by the plant breeder. It is impossible to mention more than a few possible improvements, since what is considered desirable for a species grown, say, for cut flowers, may not be altogether desirable for the same species grown as a bedding plant. Readers who are not familiar with the characters desired in vegetables, flowers, and fruits should consult the literature on special subjects

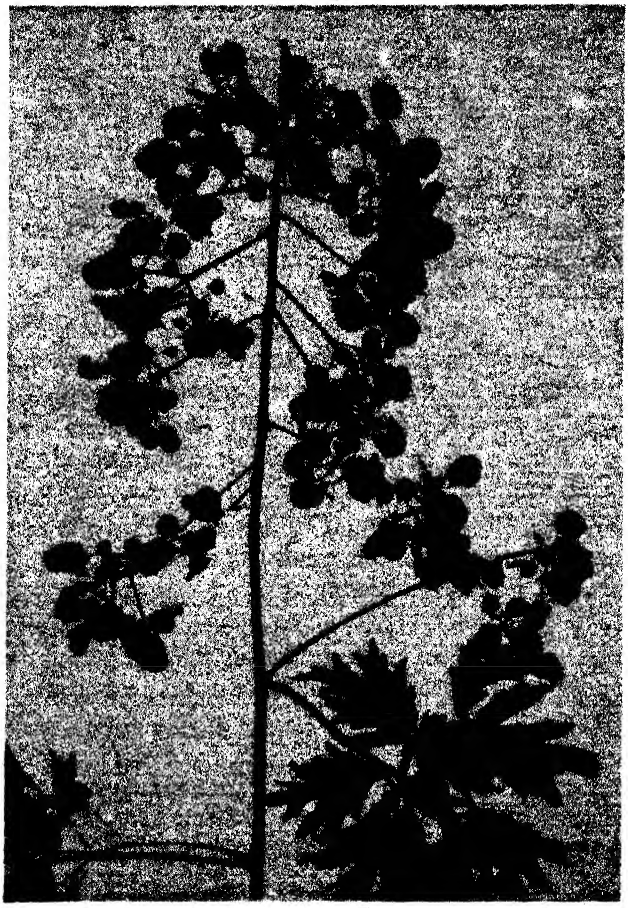


Fig. 33.—A thornless form of the cut-leaf or evergreen blackberry, *Rubus laciniatus*. Thornlessness is a highly desirable character in the blackberry, but the breeder who uses this particular plant for breeding thornless varieties will meet with failure. The thornless variety is a chimaera consisting of an outer layer of cells carrying the thornless gene, surrounding an inner core of cells carrying the gene for thorns. Since the germ-cells arise from the inner tissue they all carry the gene for thorns, therefore all the progeny must be thorny

From Darrow, "Journal of Heredity"

(e.g. salad crops, peas, potatoes, carnations, roses, dahlias, soft fruits, apples, plums, etc., to mention only a few). Points may also be gathered from "Rules for Judging" issued by the Royal Horticultural Society.

Plant Habit

Habit and form are prime considerations and are dealt with below under different headings.

i. *Height.*—The modern quest is more often for dwarfness than tallness. Tall plants are more difficult to accommodate in a small garden or glasshouse than dwarf, since they require more room, shade other plants, and usually need staking. Moreover, the flowers on dwarf plants are often seen to better advantage than in tall plants, owing to the difference in the angle of vision. Taller forms of normally dwarf species may be welcome, however, if only to increase the number of subjects of medium height available for border work.

ii. *Form.*—Shapeliness is almost always to be preferred to a straggly habit, which is usually only tolerated in climbers and basket plants. Form depends mainly upon the number of stems and manner of branching, and may vary considerably though the height remains the same, the "most desirable form" depending mainly upon the mode of flowering and the purpose for which the plant is to be used.

iii. *Density.*—The number of shoots produced, whether main shoots or laterals, greatly affects the form of a plant. Some varieties are naturally thin and of scanty growth, while others are bushy and over-prolific in the production of shoots. Again, the length of the runners in carpet plants (e.g. *Androsace*) will decide whether the carpet is an open or close one.

iv. *Root System.*—Plants which are especially grown for their roots (e.g. carrots, beet, mangolds) have naturally received most attention, as also fruit tree stocks used for budding and grafting. In plants grown for their flowers and foliage little attention has been given to the improvement of the root-system, usually because it is not so important as the aerial parts but sometimes through lack of imagination. To quote one example, most wallflower varieties, though breeding fairly true for flower colour and habit, will be found to vary widely in their root-systems, no selection having been practised in this respect. A good fibrous root-system would be a definite advantage in plants which are normally transplanted. In cases where firmer anchorage is needed for tall subjects, a proportion of "thong" roots would be an advantage. Incidentally the type of root is closely correlated with the plant's resistance or susceptibility to drought—deep-rooting plants surviving dry conditions much better than shallow, or surface-rooting, forms.

v. *Annual, Biennial, and Perennial Habit.*—Although it is customary to divide plants into these three categories, such hard and fast divisions are not always found in nature. For instance, true biennials are by no means common and many plants included as biennials will flower and die within one year under certain conditions of temperature, light, or moisture. Many of the plants which "bolt" come within this category. Again, some plants are strongly perennial, persisting for many years; others weakly perennial, dying out in a few years' time. Annual, biennial, and perennial habits are inherited characters which are susceptible to selection in a number of species. Bolting is a particularly important matter in certain vegetable crops and merits the breeder's close attention.

Constitution

By constitution we mean the resistance of the plant to pests and diseases, frost, drought, and other unfavourable circumstances; and its general robustness. In the last case the breeder usually selects only fairly robust plants, throwing away all weakly individuals. Until recently resistance to pests, diseases, cold, drought, wet, etc., have received little attention from breeders, whose main concern has been the more obvious qualities such as size of leaf, flower, and fruit; in many cases this cannot be helped, since for example the disease-resisting qualities of a plant can only be tested in the presence of that disease, and few people can afford to encourage disease in order to test out the resistance of their plants to it. It is becoming increasingly clear, however, that plants resistant to the common fungal, bacterial, and virus diseases may be, in many cases, the only ones it is profitable or even possible to grow; hence they are bound to be preferred by all sections of the horticultural community. One may cite varieties of roses resistant to mildew and rust, antirrhinums resistant to rust, potatoes to wart disease and scab, apples to red spider, and asparagus to violet root-rot, as examples of what is wanted in this respect. Varieties resistant to virus diseases are especially likely to prove a great boon if they can be found and bred from. Hardiness is another important quality which should not be overlooked, since many an otherwise desirable plant remains unpopular because of its susceptibility to frost and cold. Under the heading of constitution may be included suitability to certain climates, soils, etc.; for example, one variety may be best suited to rich soils and another to poor.

Flowers

The following are some of the improvements commonly sought for in flowers. Increase in size and number; greater variety in form, colour, and colour pattern; better form; purer colour; brighter colour; improved shape of the inflorescence and better spacing of the flowers; earlier flowering; later flowering; longer flowering; freer flowering; simultaneous flowering; longer and stronger flower stems, so that the flowers are borne well above the foliage; better scent.

Another improvement would be the relative absence of fading. Some flowers when newly opened are vividly coloured but fade or change so quickly that the plant seems to carry flowers of two different hues (e.g. the red-brown *Heleniums*; *Pulmonaria officinalis*). In a few species the flower opens white or pale and only develops full colour when mature. Certain species of the daisy family have "eyes" (discs) the colour of which detracts from the colour of the rays, e.g. the yellowish disc in some michaelmas daisies soon turns a brownish colour which makes the flowers look drab, even though the rays are still comparatively fresh and well coloured. There are beautiful flowers which are not so popular as they might be because as soon as the sun goes in they close their petals—a decided disadvantage from the point of view of garden display when we remember the capricious character of the English summer.

The pose of the flower on its stem should also be remembered. For example, many of the Narcissi hang their heads overmuch and, though lovely, are less desirable on this account.

Long and strong stems are wanted for cut flowers, but not so wiry and hard that they do not take up water properly, or so thick as to look cumbersome. The "lasting" quality of the flowers, on the plant or cut, is another highly important character, especially for indoor decoration. Modern rooms and apartments are often hot and dry, conditions which soon cause flowers to wilt unless they are of considerable substance.

Fruits

Apart from obviously desirable qualities such as correct colouring, reasonable size, good shape, good texture, juiciness, good flavour, other points worth watching are: the thickness, toughness, and acidity of the skin, especially in black currants, grapes, and plums; "free" skin and "free" stone in the stone fruits; relative or entire seedlessness in grapes, tomatoes, gooseberries, raspberries, blackberries, and currants; absence of hairs on gooseberry fruits; absence of prickles on blackberry and gooseberry shoots; ease of pulling off the strig or stalk in raspberries and strawberries; the length and thickness of the stalk of individual fruits and fruit clusters.

Vegetables

The breeding of vegetables is very highly specialized, consequently only the most general of suggestions can be made. While the work of the breeder has resulted in great improvements in vegetables, there is still plenty of room for further advance. Thus resistance to the attacks of pests and diseases, and improved quality, are of the greatest importance. Quick maturing forms are valuable, and varieties which can be raised in the winter months are also much wanted. In the root crops, absence of thick adventitious roots, uniformity of colour, shape, and texture (e.g. absence of core in carrots and zoning in beets) and better shape (e.g. stump rooted parsnips) are all to be desired. Among the crops grown for their leaves, improved "hearting" and smaller midribs and veins would be welcome. In lettuce, the hardier sorts are often of poor quality while good quality summer varieties are often of poor constitution and very much inclined to bolt. In peas small seed size, irregularity in the number of seeds per pod and mediocrity in quality are by no means uncommon faults. Lastly, special qualities are required when vegetables (and fruits) are wanted for canning. In this field there is great scope for the breeder, who will find in the publications issued by the Ministry of Agriculture on fruits and vegetables for canning a guide to the desired improvements.

In conclusion there are several points the breeder should never forget. He should be observant. The slightest indication of a new variation may be the starting-point of a distinct success. As a general rule he should cross only the best kinds together. Crossing inferior forms, or a good one with a poor one, in the hope of something good turning up is unscientific, unreasonable, and gambling against heavy odds. The breeder should always aim for purity of strain. A variety which does not breed true is a source of annoyance to the grower or customer and a bad advertisement for the breeder. Finally, the breeder should not think of improvement solely in terms of the current fashion or fancy. Fashions change, and the breeder may be tempted to follow some craze of the moment; but the qualities which the true florist seeks in his flowers are those which the artist seeks in all branches of art—balance between parts and harmony with surroundings. These are the fundamental virtues, and the breeder who trains his eye to this standard is the most likely to enrich our gardens with varieties of lasting value.

CHAPTER 8

RESULTS OF PLANT IMPROVEMENT

EARLY HYBRIDISTS

The practice of plant breeding is as old as civilization itself. Early man was a food-gatherer. He hunted wild animals and gathered fruits and leaves to eat just as he happened to come across them. But as soon as man became more settled in his habits his attention was attracted towards the kinds of plant foods that were most prolific and agreeable to the taste. From these plants he learned to save seeds, and so became a plant producer. Plant breeding therefore began by the *selection* of better kinds of plants.

No real progress could be made, however, until the fact of sex in plants was recognized. The Assyrians and Babylonians knew that there were two kinds of date palm, one bearing fruit (the female) and other sterile (the male), and artificial pollination was practised before 700 B.C. Nevertheless, generally speaking, the fact of sex in other plants seems to have been unrecognized until the eighteenth century, when the experiments of Camerarius (1665–1721), Professor of Natural Philosophy at the University of Tübingen, established the sexuality of plants beyond dispute.

The first record of natural hybridization seems to have been made in 1716 by an American, Cotton Mather, who observed the results of hybridization between different varieties of maize and noted the resemblance of some of the progeny to the male parent.

The earliest recorded artificial hybrid was raised by Thomas Fairchild of London (1717) who crossed the carnation (*D. caryophyllus*) with the sweet william (*D. barbatus*) and raised offspring intermediate in character.

The first systematic investigations on plant hybridization were made by the German, Joseph Kölreuter (1733–1806), in the latter part of the eighteenth century. He demonstrated that species could be crossed artificially and proved that both parents contribute to the offspring. He made numerous crosses in *Nicotiana*, *Verbascum*, *Dianthus*, *Hibiscus*, *Mirabilis, and Leucojum*, and observed the dominance of double flowers over single in *Dianthus*. Kölreuter also drew attention to the importance of insects in pollination, a hitherto quite unrecognized fact. Later Christian Sprengel (1750–1816) discovered the fact that most flowers are naturally cross-pollinated by insects, and from this inferred that the breeding of new forms is going on at all times in the plant world. In spite of the work of Camerarius, Kölreuter, and Sprengel, the belief that species were fixed and unvarying was general among the biologists of the eighteenth century, and only very slowly did the importance of hybridization as a means of plant improvement dawn on the minds of men. Recognition of the orderliness of heredity was even more gradual, and very little progress was made in the science of breeding until 1900.

The discovery of the laws of inheritance was made by the Augustinian monk, Gregor Mendel of Brünn in Moravia (now a part of Czechoslovakia), who published his results in 1866. Mendel worked chiefly with the garden pea. His success was due to the fact that he followed the inheritance of *pairs* of characters and not the characteristics of the plant as a whole. Mendel's paper was completely overlooked until 1900, when it was simultaneously discovered by three European botanists, de Vries, Correns, and Tschermak. It was from this date that the first real progress in the science of plant breeding began.

In the meantime the practical plant breeder had not been idle. The English hybridist Thomas Andrew Knight

(1759–1835) "was the first experimenter to apply the science of plant hybridization to plant improvement." Knight held that cross-breeding was the key to the origination of new and improved sorts and he made noteworthy contributions in demonstration of this principle in the apple, cherry, currant, peach, pear, grape, and garden pea. Breeders in nurseries and seed establishments were also beginning to practise hybridization with some effect at the start of the nineteenth century. Thus Dean Herbert produced thirty-five hybrid *Hippeastrums* between 1811 and 1824, and hybridization had begun in *Rhododendron*, *Dahlia*, and *Chrysanthemum* before 1830. By the middle of the nineteenth century hybridization was being widely practised, and many new and improved forms were making their appearance.

THE IMPORTANCE OF PLANT COLLECTION

It should be noted that this breeding work received a tremendous impetus from the introduction of many hundreds of new species in the latter part of the nineteenth century. Plants collected from the four corners of the earth were pouring into the gardens of Europe and providing many new characters for the breeder to utilize. For example, the popularity of the chrysanthemum was greatly increased by the introduction of the Japanese type in 1861. The new character proved highly attractive and cross-hybridization followed by selection of the best of the progeny firmly established the chrysanthemum as a first favourite among flowers for the winter season. In similar fashion the introduction of the cactus dahlia in 1880 revived interest in this genus and led to the production of many new varieties.

Many of our strains of modern garden plants owe their origin to the hybridization of species collected from widely separated habitats. An excellent example of this is seen in the garden strawberry, the parents of which, *Fragaria virginiana* and *F. chiloensis*, come from North and South America respectively. The fruits of *F. virginiana* are of good colour, juicy, and of fine flavour, but they are small in size. On the other hand, the fruits of *F. chiloensis* are large but lack other desirable qualities. Both species were in cultivation in England for about a hundred years before breeders began to raise strawberries from seed. Until that time very little progress was made, but from then onward many new and excellent forms were raised, combining the high quality of *F. virginiana* with the large fruit size of *F. chiloensis.* Thus the development of the garden strawberry was due to (1) the bringing together of species which had previously been isolated geographically, (2) the combining of their respective good qualities by cross-hybridization, and (3) selection of the most desirable progeny. During the early years of the nineteenth century, the strawberry breeders were unconsciously selecting the best forms resulting from natural hybridization of *F. virginiana* × *F. chiloensis* and their derivatives. Later in the century systematic cross-breeding was practised and led to the production of varieties of great merit (e.g. Royal Sovereign).

SELECTION

Not all notable improvements have originated from species-crossing. For example, most of our vegetables and fruit and a number of our flowers were highly developed without the intervention of artificial species-hybridization, indeed, before it was commonly practised. Clearly, then, selection played a very important part in the evolution of these garden plants. This is very evident when we compare, for example, the modern varieties of carrot and cabbage with their wild prototypes still to be found in the English countryside.

It must not be forgotten, however, that many of the improvements apparently due to selection alone have in fact arisen from natural hybridization of species and varieties collected together by the grower.

GENE MUTATION

As we saw in Chapter 5 the ultimate basis of all plant improvement is gene mutation. Two good examples of this are the sweet pea and the chinese primrose (*Primula sinensis*). The sweet pea was introduced into Europe as a wild species in 1699. From the original purple-flowered form have been developed the many hundreds of varieties extant to-day. Crossing with other species of *Lathyrus* has never occurred, each variation from the original species being due to gene mutation. For example, the picotee character appeared in 1860, the cupid form in 1893, and the Spencer type in 1900, and as each mutation appeared the breeder combined it with other forms by hybridizing.

In the case of the chinese primrose, which has never been found wild, seeds were introduced from China about 1821. The first plants had either overlapping or spaced petals and had "pin" or "thrum" eyes, but in other respects they were uniform. The flower colour was magenta. Mutations appeared at intervals and these were selected by breeders who hybridized them with the existing forms. As a result of this selection and hybridization, there are now hundreds of different varieties.

SPECIES-HYBRIDIZATION WITHOUT CHROMOSOME DOUBLING

In contrast to the sweet pea and chinese primrose, in which no interspecific hybridization has occurred, may be mentioned the Cape primrose, *Streptocarpus*. Several species of *Streptocarpus* were in cultivation during the first part of the nineteenth century, all with bluish flowers

Then in 1884 seeds of *S. Dunnii* with brick-red flowers were sent to the Royal Botanic Gardens, Kew, from South Africa. The importance of this new species for hybridizing was at once realized, and crosses were made between it and the best of the bluish-flowered species. From these interspecific crosses the present race of garden hybrids was developed with white, salmon-pink, rose, mauve, magenta, purple and blue flowers. The colours salmon-pink, rose, mauve, and magenta are the result of new combinations of the genes for flower colour found separately in *S. Dunnii* and the bluish-flowered species. *S. Dunnii* has little to recommend it to the breeder.

Nevertheless, it has proved a valuable source of improvement and illustrates how one character alone (i.e. red flower colour) may justify the breeder's selection of a species for hybridizing. The origin of the garden *Streptocarpus* is an example of the production of fertile hybrids from the crossing of species with the same chromosome number but differing in their characters and genes.

Species-Hybridization With Chromosome Doubling

A slightly different example is seen in the origin of the red-flowered race of border delphiniums called, after the raiser, *Delphinium Ruysii*. In a bed of seedlings of the dwarf orange-red flowered species *D. nudicaule*, one plant was found which had every appearance of being a hybrid between *D. nudicaule* and one of the tall, blue-flowered forms of *D. elatum*. The flowers of the hybrid were an unattractive dingy purple. Seeds were saved, and by repeated selection the red flower colour of the weak-growing species *nudicaule* has been combined with the free and sturdy habit of the *elatum* types. A study of the chromosomes showed how this new race had originated. *D. nudicaule* has two sets of chromosomes, *D. elatum* four sets.

Apparently an unreduced ovule of *nudicaule* carrying *two* instead of a single set of chromosomes was fertilized by a normal pollen-grain of *elatum* carrying two sets of chromosomes, giving rise to a moderately fertile hybrid with four sets of chromosomes. If we use letters to indicate the chromosome sets then instead of the cross *nudicaule* (*NN*) × *elatum* (*EEE′E′*) giving a normally expected hybrid with three sets of chromosomes (*NEE′*) in the case of *D. Ruysii* the result was *NNEE′*. *N* chromosomes pair with *N* and *E* with *E′*, thus enabling the germ-cell processes to proceed fairly normally. The raiser of this new race of *Delphinium* had made numerous attempts to cross *nudicaule* with *elatum*, always without success. Apparently seeds with three sets of chromosomes cannot develop, and only when there is a balanced set of chromosomes can a hybrid be raised. The origin of *D. Ruysii* illustrates how the sterility barrier between species with different chromosome numbers may be broken down through doubling of the chromosome number in *one* of the species.

Another example of the great importance of chromosome doubling in the origin of cultivated plants is the garden dahlia (*Dahlia variabilis*). With the exception of the garden dahlia, all the species of the genus examined have 32 chromosomes. Further, they may be divided into two groups for flower colour, a group with bluish flowers and another with scarlet flowers. The variation in these species is not great; the bluish species may give ivory-white varieties and the scarlet, yellow varieties. Breeding experiments and examination of the chromosomes show that a bluish-flowered species with 32 chromosomes was crossed (naturally) with a scarlet species, also with 32 chromosomes. If the story had ended there we should have had no garden dahlias, since the hybrid must have been highly sterile. Chromosome doubling occurred at the same time, however, and gave the fertile garden form, *D. variabilis*, with 64 chromosomes; and because the two parent species were very different in their characters, e.g. flower colour, the garden dahlia shows a wide range of variation owing to the many gene combinations made possible. We do not know exactly how chromosome doubling occurred in *D. variabilis*, whether an unreduced ovule was fertilized by an unreduced pollen-grain or whether a sterile hybrid arose first and chromosome doubling in the body-cells of this hybrid gave fertile flowers (e.g. *Primula kewensis*). In either case the chromosome complements of both parent species were doubled. The origin of the garden dahlia is an example of how the sterility barrier between species with the same chromosome number may be broken down by the doubling of the chromosomes of *both* parental species.

A parallel case to *Dahlia* is found in the cultivated plum (*Prunus domestica*). Investigations at Merton suggested that the sloe (*Prunus spinosa*) with fruits black or green was hybridized naturally with the cherry plum (*P. divaricata*) with red or yellow fruits to give the domestic plum with yellow, red, green, and black fruits. The chromosome numbers of the supposed parents are: sloe 32, cherry-plum 16. The domestic plum has 48 chromosomes. Clearly then if the domestic plum has arisen from sloe × cherry-plum, chromosome doubling must have occurred, since the normal hybrid would be expected to have 24 chromosomes, not 48.

This hypothesis has been strikingly confirmed by workers in Russia, who not only found the two species growing wild side by side, but sterile hybrids also. More important still, crosses were made by these workers between the sloe and the cherry-plum and a number of seedlings raised. All had 24 chromosomes *except one which had 48*. This plant had not fruited, but it typically resembled the domestic plum. Thus it appears that not only has the hypothesis been confirmed but the domestic plum has actually been synthesized artificially as it must once have originated naturally.

Other well-known plants which arose through chromosome doubling associated with species-hybridization are the loganberry, veitchberry, and *Primula kewensis*.

Chromosome doubling within a species or strain, though not so important as in the foregoing cases, has often been of some consequence in the development of cultivated plants, chiefly on account of the increase in size obtained. An example of this in a flower still being developed is *Freesia*. At the beginning of the present century the only freesias in cultivation were the white and yellow forms *F. refracta*, *F. refracta alba*, and *F. Leichtlinii*; then about 1901 a pink-flowered species, *F. Armstrongii*, was introduced into Europe from South Africa. It was hybridized with the existing forms and at once gave coloured progeny. Later certain large-flowered varieties appeared and were the subject of some comment because of their sterility (e.g. *var. Apotheose*). These large-flowered forms have since been proved to be tetraploids with four sets of chromosomes, i.e. chromosome doubling within the strain had occurred, hence fertility was reduced. It is interesting to compare the development of the two strains, the giant with four and the normal with two sets of chromosomes. In the normal strain there are numerous fertile varieties of many colours—white, yellow, orange, mauve, crimson, and blue; the intensity of the colours is quite good and most of the earlier varieties have been superseded by modern kinds. In the giant strain there are about a dozen varieties, all highly sterile or of reduced fertility; the colour range and intensity are comparatively limited and few of the earlier varieties have been superseded.

Apart from a lucky accident by way of mutation the only solution to the problem of improving the flower colour in the giant strain is large-scale hybridizing with the deepest coloured varieties of the normal strain and the raising of large F_2s and F_3s. In any case, progress is likely to be very much slower than in the normal diploid strain.

Enough has been said to show the importance of chromosome doubling in the development of cultivated plants. It is true the breeder has had no control over this phenomenon, but neither has he over gene mutation. Both, however, have provided him with invaluable material for plant improvement.

FLOWER COLOURS

Recent years have seen great progress made in researches on flower colour, and the basis of pigmentation is now known.

All flower pigments may be referred to three primary types, (1) plastid pigments, (2) flavones and flavonols, (3) anthocyanins. The plastid pigments are carried by the microscopic bodies, called plastids, found in the cells of plants. These pigments, which are insoluble in the cell-sap, range in colour from intense yellow through cream to white (colourless). Examples of plastid pigmentation are seen in deep yellow tulips and wallflowers, and in *Narcissus*. The *flavones* and *flavonols* are yellow and ivory-white pigments which are dissolved in the cell-sap. Examples are the deep yellow dahlias and antirrhinums, the pale yellow wallflowers, and the great majority of "white" flowers. The *anthocyanins* comprise the red and blue pigments, and they also are dissolved in the cell-sap.

From mixtures of these three primary types in various proportions a wide range of flower colour results. Thus crimson anthocyanin mixed with yellow flavone gives a scarlet colour, as in *Dahlia*; bluish anthocyanin with yellow flavone gives brown, as in wallflower, and so on, the exact colour and intensity depending upon the amount and proportions of the pigments present. Further variations occur, however, through other agencies. Thus some anthocyanins are naturally bluer than others; acid sap makes anthocyanin redder, while alkaline sap makes it bluer; many ivory-white flavones, though practically colourless themselves, have the property of making anthocyanin bluer, cf. chocolate (no flavone) and purple (with flavone) dahlias.

Combined research work by bio-chemists and scientific plant breeders has linked up the flower colour genes with the pigments they control. Thus in the sweet pea *C* and *R* are genes both of which are necessary for the production of anthocyanin; similarly the genes *K* and *M* are both necessary for the production of flavone; *Co* suppresses flavone production partially in the wings and entirely in the standard; *Dw* suppresses anthocyanin formation in the wings; *D* makes the anthocyanin redder; *E* produces one kind of anthocyanin, *Sm* another and redder form. In *Dahlia* *I* produces ivory and *Y* yellow flavone; *A* produces pale anthocyanin and *B* deep. There are also two genes which inhibit the production of ivory and yellow flavone respectively. The effect of these inhibitors is to give colours ranging almost continuously from white through cream to deep yellow. It has also been found that the flavones and anthocyanins are produced from a substance or source which is limited in amount, so that if much anthocyanin is formed the amount of flavone is reduced, and vice versa. If, as mentioned above, the flavone concerned has a blueing effect on the anthocyanin, then reduction in flavone not only increases the intensity of the anthocyanin but makes it redder. In ways such as this the range of flower colour is greatly extended and innumerable hues, shades, and intensities are made possible. Thus the great variety of flower colours (and patterns) in *Dahlia* arises from the action and interaction of six pairs of genes only.

As a result of the investigations on flower colour it is becoming possible for the breeder to select and mix his flower colours by crossing, with as certain a result as when the artist mixes his paints.

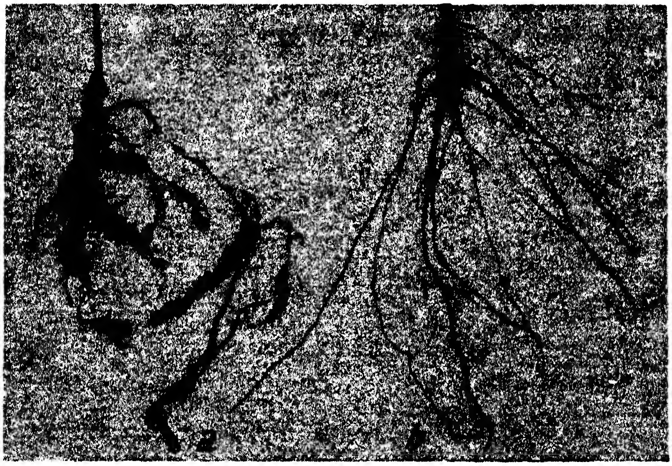
RESISTANCE TO PESTS AND DISEASES

The breeding of strains resistant to pests and diseases is fast becoming an urgent necessity. Success has already been achieved in certain crops. It is clear, for instance, that there is no adequate control for wart disease (*Synchitrium endobioticum*) in potatoes except to grow immune varieties, and the introduction of these in recent years is a notable example of the possibility of breeding high-quality strains which are disease-resistant.

A survey of the many investigations in progress shows that varieties may nearly always be found which are resistant in some degree to diseases caused by fungi, bacteria, nematodes (Fig. 34), viruses, food deficiencies, climatic conditions; etc.—and that this resistance is inherited. Resistance to insect pests is also known.

The apple affords a good example of the occurrence and breeding of resistant forms. Root-stocks have been raised which resist the attacks of woolly aphis, and forms immune to red spider and apple scab (*Venturia inaequalis*) are under investigation. Species resistant to low temperature have been bred with established varieties in order to get new kinds suitable for growing in northern latitudes. Varieties are known which resist injuries from spraying with the standard insecticides and fungicides, and there are other forms which resist leaf scorch caused by potash deficiency in the soil.

A few examples of the many pests and diseases against whose attacks resistant varieties are being bred are: leaf mould (*Cladosporium fulvum*), wilt (*Fusarium*), and curly top or yellows (*virus*) in tomato; frost, blackleg (*Bacillus* *phytophthorus*), blight (*Phytophthora infestans*), and viruses in potato; thrips in onion; finger and toe (*Plasmodiophora brassicae*) in turnip; rust (*Uromyces Fabae*) in bean; nematodes in peas, and rust (*Puccinia antirrhini*) in *Antirrhinum*. The importance of breeding resistant varieties will be apparent from the formidable nature of the above short list of pests and diseases.



IG. 34.—Roots of plants of the kidney or snap bean, *Phaseolus vulgaris*, grown in a bed of soil infested with nematodes. (*a*) Susceptible. (*b*) Resistant

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Space will permit only of the barest mention of the very notable improvements made during this century in many plants; for example, *Narcissus*, *Iris*, Lupin, *Delphinium*, *Gladiolus*, Sweet Pea, Aster, and Carnation. Great as these advances have been, it is a far cry to the day when each variety of flower, fruit, or vegetable in our gardens shall exhibit not merely one or two desirable qualities but combine excellence of habit and constitution with complete adaptation to the soil and climate of the locality. This is not impossible. It is, however, contingent upon two things: first the collecting together of the wealth of plant material not yet drawn upon; secondly the exploration of individual plants for the genes they carry. It will then be the work of the breeder who knows his science as well as he does his plants to add gene to gene by hybridization and selection and thus synthesize the perfect type.

BOOKS DEALING WITH PLANT BREEDING

PUNNETT, R. C. *Mendelism*. 7th ed. 1927. Macmillan, London, pp. 236. 8s. 6d.

A concise account of the Mendelian and chromosome theories of heredity with examples from plants and animals.

SINNOTT, E. W., and DUNN, L. C. *Principles of Genetics*. 2nd ed. 1932. McGraw-Hill, New York and London, pp. 441. 21s.

A comprehensive book for the student.

DARLINGTON, C. D. *Chromosomes and Plant Breeding*. 1932. Macmillan, London, pp. 112. 7s. 6d.

A popular introduction to the rôle of chromosomes in inheritance.

CRANE, M. B., and LAWRENCE, W. J. C. *The Genetics of Garden Plants*. 2nd ed. 1939. Macmillan, London, pp. 287. 12s. 6d.

An introduction to genetics and cytology, with special reference to recent work in horticulture.

JOURNAL

The Journal of Heredity. Published monthly by the American Genetic Association, Washington, D.C., U.S.A. (Victor Buildings, 724 Ninth Street, N.W., Washington, D.C.). 3.50 dollars per annum.

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TECHNICAL EQUIVALENTS OF SOME TERMS USED IN THIS BOOK

Gene "houses."—Chromomeres.

Germ-cell.—Gamete.

Hybrid.—Heterozygote; heterozygous.

Related genes.—Allelomorphs.

True breeding.—Homozygous.

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