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PLANT BREEDING

BY

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Preface

Twenty years ago I wrote my "Handbook of Animal and Plant Breeding" in the Dutch language, and my "Animal Breeding", published in 1939, grew out of the first book.

The publishers have asked me to write a plant-breeding book as a companion volume to "Animal Breeding", with a similar scope and in the same style, and the present work is the result.

As a young geneticist, I started my career as a plant-breeding consultant with the French firm of de Vilmorin Andrieux et Cie. After the first years I became more and more absorbed in matters of theoretical genetics, and during the last decade I have been chiefly concerned with genetics as applied to mankind and to the breeding of domestic animals. I have, however, never quite given up plant-breeding matters, although the only kind of practical plant breeding I have been more directly engaged upon has been the production of sugar-beet seed.

This book is certainly not a textbook on Genetics, nor does it pretend to be an exhaustive treatise of everything pertaining to plant breeding. As far as possible, I have throughout the book avoided the use of technical and scientific terms where plain English would do as well. The book is written in the first place for those who are actively engaged in the amelioration of cultivated plants or in the creation of plant novelties. I have quite an extensive experience of correspondence with plant breeders and amateurs, and I have often co-operated with plant breeders during some generations of their material, discussing the results obtained and helping to decide future breeding policy. This co-operation with so many people has

helped to give me an understanding of a practical plant-breeder's difficulties, and it has afforded me some experience in explaining genetic complexities in simple terms.

Plant breeding—and this is especially true of plant breeding in the larger institutes—is subject to fashions, and I have a notion that the preoccupation with higher mathematics is due to a certain extent to one of those fashions. I am convinced that there is very much more in selection, and even in the comparison of the yield of experimental plots, than in matters which can be approached only by means of slide-rules and mechanical calculators.

Even though the breeding of plants nowadays is chiefly concentrated in the hands of the bigger Institutes and the more important seed firms, there are (as appears from my experience) large numbers of people interested in plant-breeding subjects. Apart from the host of amateur gardeners and lovers of flowers and fruit, there are thousands of amateur plant breeders, lovers of gardening who sow an occasional bed of dahlia seedlings or who raise a few hundred seedling apple-trees or seedling roses.

Since I started as a plant breeder I have become greatly interested in some tropical plant-breeding problems, and as my animal-breeding book seems to have penetrated to all parts of the world, it seems to me that it is necessary to treat of the amelioration of tropical plants as well as of the breeding of plants in our temperate regions. I collected my examples in the five different countries where I have worked.

The Dutch book has often been used as a textbook, and in writing the present volume I have taken this possible use into account.

It is quite impossible to write a book on plant breeding without going into some technical genetical details, and as identical principles and phenomena are met with in both plant and animal breeding, it is unavoidable that some of the first chapters in both books treat of the same matter in much the same way. As far as possible I have tried to avoid duplications, by using different examples to illustrate the principles. My object has been to write a second volume that can stand by itself, and in the meantime to make the whole of the book readable even to those who have read my "Animal Breeding".

A. L. HAGEDOORN

September, 1949

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Introduction

Notwithstanding the fact that exactly the same genetic principles underlie inheritance in animals and in plants, there are certain far-reaching differences between animal breeding and plant breeding. Those differences are due partly to differences in the material, partly to differences in the groups of men concerned in the breeding industry.

In plants we are mostly dealing with large numbers of individuals, and almost exclusively with individual plants, which taken singly will seldom represent a great value. In the second place, in most domestic plants we have a very quick succession of generations. Both reasons help to make it possible to work with a large number of separate breeding problems at the same time, and, for the same reason, plant breeding has always tended to be concentrated in the hands of important seed firms or large plant-breeding institutes.

This means that a seed firm or an institute can afford to appoint a well-trained geneticist to help with the amelioration of a great many different plants. On the other hand, with most animals the material is in the hands of hundreds or thousands of individual owners, who each own a very few of those animals. Those matters must be thought responsible for the circumstance that, both from a purely practical and from a scientific standpoint, plant breeding has for almost half a century been in the lead, as compared with the breeding of domestic animals.

During the latter part of the first ten or fifteen years of this century, as a young geneticist I had the privilege of playing

my part in the revolutionary change of breeding methods in plant breeding. At that time we strove to put the industry upon a firm scientific basis, and to eliminate all practices due to pure conservatism and to fanciful theories about heredity. In animal breeding the same sort of revolution in methods began to take place fifteen years later, and we are still in the midst of it.

In plant-breeding practice we may say without much fear of contradiction that very few points to-day need any important revision, which cannot yet be said of animal breeding. Of course there are always details that have to be worked out, and here and there it will be possible to make important changes in method; but if we experimental geneticists examine plant breeding to-day we meet no cases of downright false standards or of wholly inefficient working methods.

In one point plant breeding differs radically from animal breeding—namely, in the first stages of the cultivation of a new group. Wild plants are taken into cultivation without any special difficulty. In animals domestication implies making a domestic animal out of wild material, in plants even wholly wild-plant material will be taken up into botanical collections without any special difficulty. For one thing, plants do not run or fly away.

On the other hand, plant breeding is not as uniform a subject as animal breeding. It is curious to observe how with almost all animals the same working principles can be applied. We meet with the same difficulties and problems throughout the whole animal kingdom. Almost identical methods of selection are applicable; we must warn against the same dangers of applying false standards in selection.

In plant breeding our methods of improving different kinds, our methods of selection and of purification are absolutely diverse, according to whether we are dealing with self-fertilizing plants, cross-fertilizers or vegetatively propagated material. There is a much greater similarity between the methods used with poultry and rye, than between working methods applicable to rye and wheat! Very often methods used with sugar beets or maize can be transferred to the work with sheep or poultry with but little adaptation, but the breeders of new potatoes are not helped at all by studying those methods.

In animal breeding there is (or should be) no difference between the group of men interested in breeding and the group of the ultimate users of the material. In plant breeding, however, the user of domestic plants buys his seeds or his tubers. He can be a very good grower without bothering his head about selection at all—the seed firms take this responsibility upon themselves entirely. For this reason the professional plant breeders are specialists, and they must be good practical working geneticists. The animal breeder, on the other hand, should know enough of genetics to form an opinion upon methods in use in the breeding of his particular variety. If he leaves those matters to the professional breeders, a state of things comes to pass which may result in a serious economic loss for agriculture.

PART I

MORE THEORETICAL SUBJECTS

Chapter One

Ecological Considerations

Our cultivated plants do not exist in a vacuum. They and the use man makes of them must be considered in relation to the whole of his environment, and the geneticist co-operating with the breeders of animals and plants should always bear in mind that man and the organisms around him affect each other in the most diverse ways. As domestic animals and cultivated plants differ from wild ones in such a way that they are adapted to the use man makes of them, while they are generally dependent upon his care, we can speak of symbiosis, and we can say that a group of men lives in symbiosis with several kinds of cultivated plants and animals, and that the combination constitutes a " symbiosis group ".

This, admittedly, is an over-simplification. But for my present purpose it will help to direct attention to the necessity of adapting the group of plants and animals chosen to the needs of all the members of the symbiosis-group.

The over-population of almost every country on earth, the abuse of natural resources, especially in so-called " new " lands, the dependence of one country upon commerce in what is loosely called " surplus production " in another part of the world, make our problems of agriculture and of feeding and clothing the inhabitants very much more complex than they would be in isolated communities. The Second World War has taught some of the people along the North Sea what systematic colonial exploitation by a callous conquering group

may mean; it has also shown Western Europe in how far it is possible in a few years to adapt food production to greatly reduced imports, by means of quantitative changes in the groups (reduction of poultry and pigs, better methods of ley-farming and pasturing).

The geneticist interested in agriculture and co-operating with breeders of plants and animals in different parts of the world is often struck by the lack of serious attention paid to the choice of breeds and varieties. In the breeding of animals rival breeds have their advocates, who advertise their striking " selling points ", the gallons of milk produced by one breed of cattle, the longevity, the docility or the high fat percentage in the milk of others. Studies in which breeds of dairy cattle are objectively compared as to their adaptation to a country's economy, or even to profitable exploitation by their farmer owners, are almost entirely lacking.

In the breeding of plants, yield per acre seems a useful criterion of quality. We can go a step farther, and consider adaptation to cheap methods of handling and harvesting. From a broad ecological view it does not seem as if the increasing tendency to find or breed crops specially adapted to agricultural methods of efficient mechanization is of great lasting benefit. Not everybody admires the tendency to adopt agricultural methods that make it possible for only a minimum number of men to work on the land, leaving the great majority of the population in the cities free for the manufacture of useful things and superfluous gadgets in periods of " boom ", or to collect a dole in periods of depression.

New plants, very well adapted to mechanical cultivation and harvesting, are of great benefit from the point of view of the tenant farmer interested in cash crops for sale. It is quite possible that our grandchildren, finding our farms worn out by such crops, may curse our generation. " Efficient " methods of agriculture may often fit in very well with wise and conservative use of the land by means of well-chosen rotations and manuring technique, but the rapid skimming of farming land by hard-boiled profiteers, using high-yielding new varieties, is also much facilitated by mechanization.

When, in times of high timber prices, our European forests

are destroyed, it looks a little better if we plant the denuded slopes with Jerusalem artichokes or with potatoes than when we let them grow up in bracken. Replanting with cheap imported and unsuitable seed is still better, but in such long-lived populations only the very best quality should be judged good enough. Here again we must look to the future, and to-day's profits should not weigh too much.

Canutian methods of interference in the interplay of supply and demand by Government " price-fixing " may be as bad in their effects as the crudest results of free individual enterprise. The worst thing that can happen, I think, is a habit of rapidly adjusting every new symptom of lack of balance, the paternal ruler " fixing it with a law ". It is to be hoped that in future politics in matters pertaining to agriculture in all its aspects may be tempered more and more by biological insight. Some little knowledge of genetics and of ecology would be very useful.

Chapter Two

Large-scale and Small-scale Agriculture

No book on plant breeding should avoid treating of some of the economic aspects of plant production. To a great extent the qualities of the plants used in agriculture must be adapted to the type of plant production in which they must be used.

There is an enormous difference between large-scale plant production and agriculture by a multitude of small individual farmers. In various " new " countries we would be apt to think of large-scale farming as a typical example of " big capital enterprise ", and the peanut-scheme or some of the sugar-producing or tobacco-growing companies would come to our mind. The Soviet-Russian *kolghozes*, however, are certainly not examples of the international capitalists investing in farming!

At first sight it might be thought that in so far as the quality of the plants used is concerned, there should be very little difference between a twenty-thousand-acre farm employing a thousand agricultural workers, and a thousand two-acre farms each worked by one man and his family. This, however, is certainly not the case. I want to treat of a few aspects only.

The large farm can be mechanized, and mechanization in agriculture calls for special qualities. Let us take the peanut as an example. If we want to grow peanuts on a very large scale, the plants must be specially adapted to mechanical

handling, and especially to mechanical harvesting. We can only use varieties that give us pods that all ripen at the same time, that firmly adhere to the compactly bunched plant, instead of trailing kinds that ripen their nuts all over the place and during weeks. The first step in large-scale peanut production, just as in all large-scale plant production, is to test a hundred pure-bred lines from all over the world to find the one or two that are perfectly adapted to our special purpose, even if this should take three years.

On the other hand, the natives growing patches of peanuts in all parts of Africa and Southern Asia will grow several hundred different local varieties that must each be adapted to the local system of rotation and to the local climate, rainfall and latitude. The small man growing a few hundredweight of nuts can afford to harvest them by hand, grade them carefully and spread them in his yard to dry in the sun. The quality of his product is mostly far superior to those that the mammoth enterprise can grow.

If we wanted to collect a few million tons of peanut oil in a short time, it might be very much cheaper to build some railroads and subsidiary lorry lines to collect native-grown nuts where they are now produced, and, by creating a market, to treble that output in a year, rather than to start a vast groundnut-producing enterprise.

From the standpoint of a plant breeder, it would be possible eventually to find or to make a few varieties for large-scale planting and to multiply the seed up to the quantity required for vast farming schemes. On the other hand, it has been shown in Java that even the smallest cultivators take up improved heavy-yielding varieties with enormous enthusiasm, so that oil production for export can easily be stimulated in this way.

Even if to-day it does not pay a small grower to bring a load of groundnuts on his head for a week's journey, it might pay him very well indeed to bring them into a locally established buying centre.

A number of erect-growing groundnut varieties exist to-day that in the right soil produce evenly ripening nuts which firmly adhere to the crown—varieties admirably adapted to mechani-

cal cultivating and harvesting for large-scale production, and it would only require some effort to collect a few dozen of them, test them and multiply them.

From the standpoint of world economy, there are many cases in which the production of an agricultural article in short supply could be left with greater safety to a multitude of small producers than to large-scale enterprise, subsidized or not. If a few thousand small producers find it does not pay them to grow a certain product, this matters very little if ten times as many who are more favourably situated continue with it. If, however, a gigantic one-crop enterprise should prove to be a failure (and the dice are loaded against success), this would not only make the white man look silly, but the economic loss to the shareholder or taxpayer would be appreciable, to say nothing about exhausting the soil.

Many instances could be quoted in which large-scale agriculture has been a very great success compared with small-scale enterprise, and in all those cases success was due to sound plant-breeding effort. I am thinking of sugar-cane and of the oil-palm in Sumatra and in the Congo, where the production per tree has been more than trebled in a relatively short time. Such successes are more likely to be met with where the processing of the harvest entails the building of costly factories. Where this is not the case, as with coffee, groundnuts, wheat, cacao, rubber—the small producer can often compete successfully with the large-scale mechanized enterprise.

It is certainly in the interest of the food production of the world that we geneticists pay some attention to the quality of the crops in the hands of the small and very small producers. One of the main points here is not so much high production per unit of area on " average " soil and in an " average " climate. What is required here is adaptation to the very special combination of special soils under special conditions of cultivation, latitude and climate. In every valley there may be only some restricted area where a certain crop comes to perfection. The large-scale enterprise, started as a " wheat factory " or a " peanut factory ", can never produce as good a crop per acre as the sum of the small, specially selected patches of ten thousand small producers. If the small local men lose, it is

more often through lack of education or of good seed than through lack of opportunity.

For a long time plant breeders have known that they could use some of the astounding qualities of locally used varieties to incorporate their drought resistance or disease resistance or other virtue into our widely grown and well-known assortment of cultivated plants. I think it would be very much worth while, from the point of view of world economics, if occasionally we helped to perfect some of the locally grown varieties of the small farmers while we are teaching them rotation and fertilizing.

Chapter Three

Plant Breeding and the Geneticist

To a very great extent the breeder and the geneticist do the same sort of work. Both follow up their material for several generations and keep track of the results. The scientist is out to discover rules and laws, the practical man is chiefly interested in results. They both observe processes of heredity and of variation. In plant breeding the immediate object is improvement, in science this is certainly not the case, yet it very often happens that the findings of the scientist turn out to be of the greatest practical importance for the amelioration of plants. As in any other science, the practical applications can be regarded as a by-product of science, and it is of very great importance that the development of the sciences shall be free from considerations of utility. Nobody can possibly know in advance just in what respect the results of purely scientific investigations may have the effect of facilitating new methods or improvements of existing ones.

There are, however, cases in which it becomes evident that in some field of practical application of science, knowledge is required which our pure science does not happen to supply, and in such cases it may happen that scientific investigations are instigated and directed to those practical considerations.

For this reason very good results, both for agriculture and for science, are sometimes obtained when science and practice in plant breeding are combined to a certain extent. The

best combination is seen in those cases in which one and the same person does some purely theoretical genetical work with plants, and is also engaged in making valuable new kinds of plants. A few outstanding examples are furnished by Nilsson-Ehle, Emerson, Shull and Erwin Baur. In any institute of plant breeding it is an excellent idea to allow the geneticists to work at some purely scientific side-line, apart from their work in improving the plant material with which they are working.

In this respect official plant-breeding institutes are sometimes working at a higher level than business firms.

In plant breeding it is often necessary to do things which can never pay, and always cost money. Among other things, keeping a collection of material for future breeding purposes may become costly, and all the experimental work may be expensive. It is logical that both experimentation and the keeping of large collections should be undertaken by central institutes. It seems illogical to have several more or less completely parallel collections; a large " école " can be kept for the benefit of horticulture or agriculture as a source of material for further breeding work by institutes and private breeders.

Geneticists can do useful work in plant breeding in several different ways. To a certain extent the actual work of improving existing plants, or the creation of novel, more valuable varieties may be done by trained geneticists either in firms or institutes. In the second place, a few geneticists may co-operate with plant breeders as consultants; they may advise and direct the work and give the plant breeders some help in analysing the results of their experiments. Thirdly, we may teach the principles of genetics to private plant breeders or firms.

I have considerable experience as a consultant geneticist in co-operating with plant and animal breeders, and in my opinion a geneticist can work to best advantage in this way. In the first years it is very difficult to analyse the breeder's problems, but after we have done a lot of this work we become experienced; and we see that, after all, the same essential problems are constantly recurring even in the most diverse material; so that it becomes possible to help solve the problems of one breeder with the aid of experience gained in co-operating

with another, who may have been working with different material altogether.

In this respect it is even possible that experience with plants may help to solve an animal-breeder's difficulty, or vice versa. Fundamentally, there is only a limited number of situations and problems, and novel methods and difficulties often turn out to be only very slight variations on very old themes. For different reasons, it is excellent if anyone who engages in the amelioration of one definite group of plants is conversant with the methods used by his colleagues in entirely different material. Theoretically it would be possible for a breeder to be wholly ignorant of genetics, and of the mechanism of heredity or the causes of variation, whereas he would, by dogged selection and by the application of methods, learned by trial and error, make a success of his work—but without any genetic knowledge one is lost if any novel problem arises. Without an insight into dominance relations and complications arising from dominance it is very easy to attempt the impossible. A mistaken idea about the nature of inheritance will constantly produce a confusion between genotype and phænotype, with a corresponding loss of time and energy spent upon trials to attain the impossible. The amateur breeders of roses and potatoes yearly throw away their most promising material for future progress for lack of a few lessons in genetics.

It is true that a great many valuable plant varieties have been made by breeders without any scientific insight. But the waste of time and valuable material must have been appalling.

Chapter Four

Plant Breeding and Animal Breeding

It is certain that the mechanism of inheritance and the principles governing variation and the effects of selection are the same in animals and plants. In both groups thousands of genes are arranged in chromosomes, and the constancy of the inherited make-up results from the faithful duplication of the chromosomal set at every subsequent cell-division.

Throughout this book we shall see how it is often profitable to know both animal-breeding and plant-breeding methods, for there are instances in which we can profitably adapt some method well known in one field to the other. Progeny-testing is an old story in the breeding of cereals, maize and sugar-beets: in animal breeding it is relatively new. Conversely, the method of grading-up, repeated back-crossing to the same species, is a typical animal-breeding method that can be recommended for special cases in plant breeding.

In one respect plant breeding is different from animal breeding—namely, in respect to agriculture. The users of agricultural plants are seldom actively concerned with the amelioration of their crops. They leave this work to specialist firms and plant-breeding institutes, and buy their seed. But the users of animals, with few exceptions (poultrymen), are deeply concerned with questions of heredity and with breeding methods, for they themselves are responsible for the quality of the future generations of their cattle and pigs. The breeding

of animals is spread over a very wide front, and the improvement of agricultural plants is concentrated. The institutes and seed firms responsible for crop improvement can afford to employ trained geneticists to do their work and direct it; the animal breeders must do their own selection—they must be able to choose their methods intelligently.

Apart from the bigger specialists—the important seed houses —there exist a multitude of people interested in plant breeding. In the first place, the farmers using the improved crops are interested in plant-breeding methods. But apart from them there is a large number of amateur plant breeders. Some of the fields of plant breeding are very well adapted to the enterprise of the amateur.

There is the large group of gardeners, growing their roses, dahlias and alpine plants. Novelties in those plants have originated in the gardens of the private plant-lovers more often than in the professional nurseries. To many garden lovers it is vastly more interesting to bring a number of seedlings to maturity in the hope of a good novelty, than to buy their new varieties ready-made. The same is true of bud-sports. Novelties arising as somatic mutations are much more apt to be noticed in private gardens than in the commercial establishments.

The production of good varieties in the more important vegetatively produced plants by means of seed, must remain a lottery in which the prizes are very few. It hardly pays to grow tens of thousands of seedling potatoes or seedling apples to maturity in the hope of finding a really valuable new one. Here the co-operation of hundreds of amateurs brings the solution. In Holland a great many farmers receive potato-seed from the central State Plant Breeding Station every year, and compare the seedlings grown from those seeds. Thus the work is spread, and many more seedlings are compared than would be feasible at one single institute.

The concentration of the selection work with tropical crops in large institutes, has almost destroyed the interest of plantation owners and managers in plant-breeding problems. I am glad to say, however, that this is not entirely so. In a great many places all over the world the scattered sugar estates and coffee-

gardens are still interested in plant breeding. I have met extremely keen estate managers and coffee-plantation owners who made an interesting hobby of experimental work as a relaxation from the recurring routine of the estate.

Plant-breeding methods are much more diverse than animal-breeding methods. There are several reasons for this. Both in animals and plants the users want uniform quality. Where, as in agriculture, groups are used, it is very important that all the members of a group shall react in the same way to the circumstances in which we use them. In animals, and in the majority of plants, this uniformity in the groups can be obtained only by manipulating the genetic constitution, by methods that reduce genetic variability. In plants, however, we have a very great class of the most diverse plants in which genetic purity—homozygosity—is not required, as we can make up groups of commercial size by means of vegetative reproduction.

There is much less variation in animal-breeding methods. In all our agricultural animals there is the complication of having to work with individuals of two sexes: and in practically all animals our main concern is not to produce a few superlatively good individuals (except in racehorses and animals bred for the shows), but to reduce the proportion of individuals of inferior quality. In plant breeding we only know this same problem in one group of plants—the obligatory cross-fertilizers, such as beets and rye. Here the situations are so very similar that the plant breeders can profit from a study of the methods employed by the animal breeders, and vice versa.

Chapter Five

Inheritance and Environment

The qualities of each individual plant are the result of the way in which the plant develops from the minute germ-cell. This germ-cell shows no trace of the final qualities of the adult plant. The first cell divides and divides again, tissues and organs are formed, and the way this development proceeds is influenced by a very great number of substances and forces. We can speak of development factors, and we can always bring those causes—the developmental factors—to two distinct groups. Some of those causes influence growth and development from without, but there are also numerous factors in the development which were present in the fertilized egg-cell—the inherited factors.

It has been shown that these inherited factors are substances which are found in the nucleus of every cell. In the cell-nucleus those inherited substances—the " genes "—are localized on threads—the chromosomes—of which there is a rigidly determined number in every species. The number of genes in a plant species must run well into the thousands or tens of thousands. We must not think of each of them as of a determinant, bringing along some definite single quality, as some of the older geneticists used to think. Rather must we believe that every single quality of a plant is partly determined by a great number of genes, and that one single gene may make its influence felt upon a great many different parts and upon different qualities of the plant. Nowadays we think of these

genes as of chemical substances of a peculiar nature—substances which have the property of synthesizing new molecules of their own kind. Genes grow in quantity, but it is very doubtful whether during this growth they ever change in composition.

The final qualities of a plant are partly due to genes, and partly to all those substances and forces that influence growth and development from without—environmental influences. Everybody knows the enormous effect of temperature, moisture, light and chemical substances upon the growth and the final qualities of a growing plant. One of the greatest difficulties in plant breeding is that it [is so] difficult to decide in how far a certain desirable or undesirable quality of a plant is due to its genes, and in how far to the co-operation of favourable or unfavourable factors in the environment.

The effect of environmental factors can be enormously great for a plant, but it is limited to the individual affected by them. If we grow a plant of wheat in a well-fertilized and well-watered spot as an isolated plant, it may very well develop forty or fifty full ears of grain, whereas an ordinary crowded plant grown from the same quality seed may produce only one or two ears. Yet the seed of both plants, if grown in similar circumstances, gives similar plants with similar fertility. The effects of the environment are not inherited. This is caused by the fact that, after all, heredity and inheritance are matters due to the presence of genes in the cell-nucleus. And whereas the effect of such genes in the nucleus may be felt in the qualities of the cells, the final quality of the plant will not change the genes or set of genes in the nuclei of the germ-cells.

If we want to be very strict, we must say that inheritance is the passing of genes from parent to offspring, or rather from mother-cell to daughter-cell. In every cell-division we are dealing with a process of inheritance. In fact, inheritance as a process depends on, and is nothing else but, this passing of genes from mother-cells to daughter-cells. Anything which affects this transmission of genes from one cell to its daughter-cells affects the process of inheritance: and there is no essential difference between the formation of germ-cells by a plant and other cell-divisions, as far as the genes are concerned.

Anything which disturbs the " normal " distribution of genes over the daughter-cells, either when germ-cells are formed or when body-cells are multiplied, will cause the production of cells with novel sets of genes.

The final qualities of a plant—its " phænotype "—are determined both by heredity and by environment, and by a mere inspection of two plants it is never possible to find out which has the most favourable set of genes—the best " genotype ". If we possess two strains of wheat or two varieties of snapdragon—a tall one and a dwarf strain—it is quite possible that a member of the short kind will grow taller, in very favourable circumstances, than one plant of the tall kind in poor soil. One of the difficulties in plant breeding is directly due to this circumstance. We may not say that tall stature as such is inherited; we must say that some genes are inherited which make a certain plant taller than a differently constituted one, in identical circumstances.

The smallest genetic difference between two plants is a difference in one gene. That is to say, of two plants that otherwise have an identical set of genes, in respect to just one gene one may have more of this gene than the other. The simplest case is that in which one plant has the gene, whereas the other lacks it, but undoubtedly in other cases the difference is caused by the presence of more or fewer molecules of one gene per nucleus.

To illustrate the simplest case of an inherited difference we may take an example in which we are dealing with presence and absence. In the one plant all the cells of the plant, including the germ-cells it produces, contain the gene, but a second plant is lacking it in every cell.

When we cross two such plants, which differ in one gene, we obtain some fertilized egg-cells, and each of those fertilized eggs is made up of two germ-cells—of an ovum and a pollen nucleus, one germ-cell from the mother, the other from the father. In some cases the result is rather striking, and it often happens that a plant which grows from one germ-cell with and one germ-cell without such a gene shows the effect of the gene fully as much as the parent that carried it.

Let us assume that this one parent belonged to a strain of

plants in which every plant always possesses this gene. In this case there are two doses of this gene in every cell-nucleus. This means that in one of the pairs of chromosomes the gene is present at a certain definite spot (locus) in both.

In genetics we are used to denoting genetic differences by letters. If we call the gene in question *A*, one plant may carry it in all cells, and we give it the formula *AA*. In another plant *A* is lacking, and we write this plant's formula *aa*. The hybrid between both plants, which grows from one germ-cell *A* and one *a*, and which for this reason has the constitution *Aa*, often shows the effect of factor *A* as much as do the *AA* plants.

What happens if an *Aa* plant produces germ-cells? Whenever a plant produces germ-cells, those cells are produced by two rapidly succeeding cell-divisions, during one of which the genes do not double in quantity—a so-called reduction-division. If a plant has six pairs of chromosomes, every cell in the whole plant has six pairs, with the exception of the germ-cells, which carry only six single chromosomes: one complete set of single ones instead of two complete sets. In a hybrid plant (*Aa*) all the cells of the tissues and organs are *Aa*, carrying one chromosome with *A* and one without *A* (*a*). But its germ-cells will be of two kinds, 50 per cent. with *A* (*A*) and the other 50 per cent. without (*a*).

A plant hybrid heterozygous in respect to a certain gene will produce as many germ-cells with it as germ-cells without. Or, if the difference is one between more or less, 50 per cent. of the germ-cells will carry the larger, and 50 per cent. will carry the smaller quantity of it.

Sometimes it is possible to demonstrate this difference in germ-cells in a heterozygous plant directly. If we treat some pollen of a rice-plant with iodine, the pollen-grains turn dark blue. If we take pollen of glutinous rice (ketan), the pollen-cells will not stain blue, and if we take some pollen of a hybrid between rice and ketan, and treat it with iodine under the microscope, we find a mixture of equal numbers of dark blue and light brown pollen-grains. (Fig. 1.)

Another very simple example is seen when it is possible to make unfertilized germ-cells of some hybrid plant develop into seeds and plants. When I crossed a white oblong squash

(vegetable marrow), with a round green kind ("Miracle"), I obtained some hybrid plants. Some of those hybrid plants would give fruits full of viable seeds from unfertilized flowers, parthenogenetically, and half of such plants carried white fruits, the other half green. Or, if we looked at the shape of the fruits, we saw that one half of the plants carried oblong fruits, while the other half gave round fruits. (Fig. 2.)

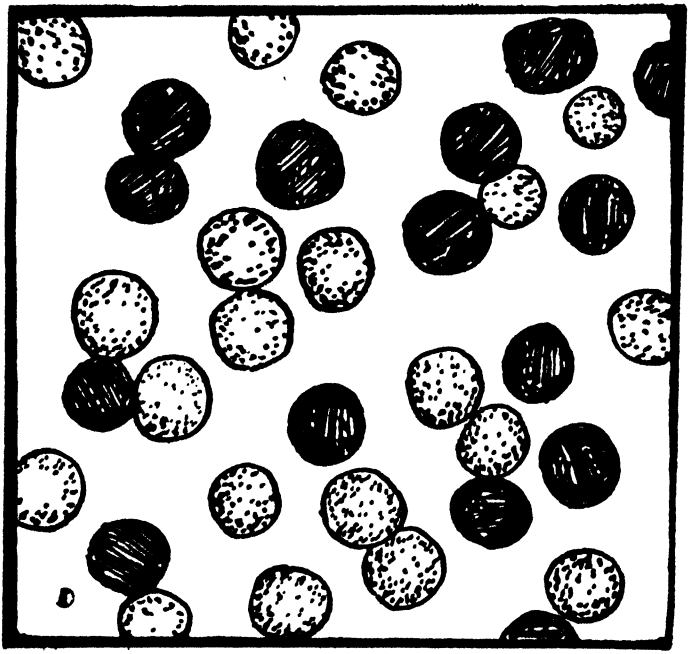


FIG. 1.—Pollen of a hybrid between ordinary rice and glutinous rice (ketan), after treatment with iodine (after Parnell). Rice pollen stains an intense blue, ketan pollen becomes yellowish; the hybrid pollen is of two kinds.

Another way to demonstrate the fact that a plant, heterozygous in respect to a certain gene, produces 50 per cent. of germ-cells with and 50 per cent. without the gene (or with more and less), consists of a back-cross.

Let us suppose that we are crossing a plant with coloured flowers (*AA*) with a plant with white flowers (*aa*) and obtain some heterozygotes (*Aa*) in which the flowers are coloured. Now we can use one of those heterozygous plants either as a pollen-bearer and use this pollen on the flowers of a plant of the white-flowered *aa* strain, or as a female parent, fertilizing

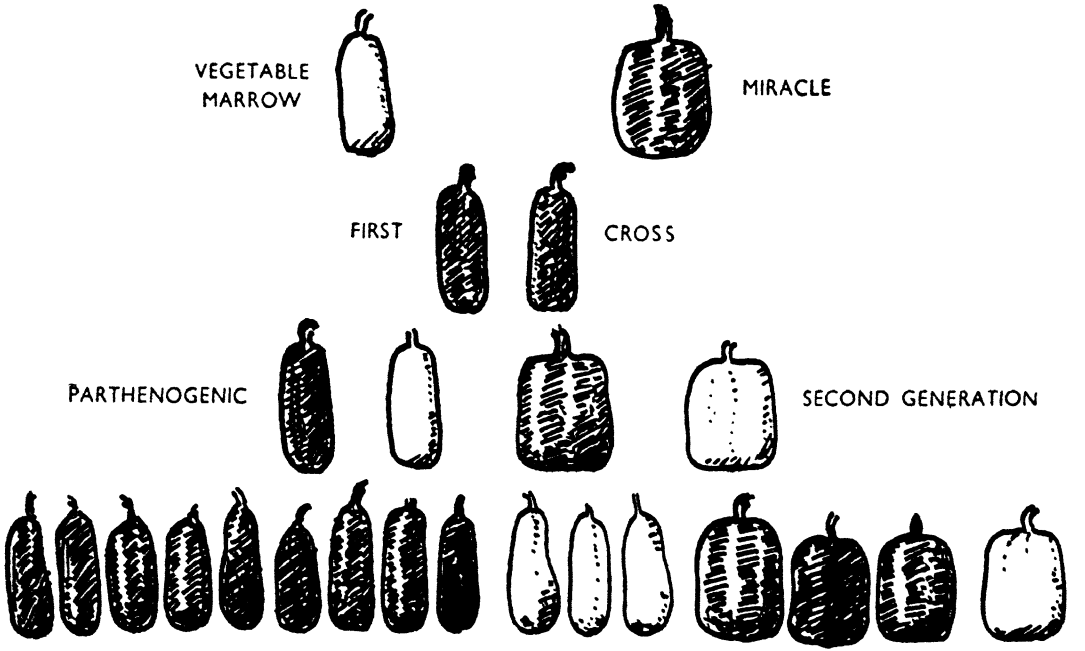


FIG. 2.—When Vegetable Marrow, a squash with narrow white fruit, was crossed with Miracle, with wide green fruit, the hybrid plants had narrow green fruit. Some plants gave good seed from unfertilized flowers, each from an unfertilized egg-cell in a gametic proportion of 1 narrow green, 1 narrow white, 1 wide green and 1 wide white. Other plants did not set parthenogenetic seed. Such plants gave a self-fertilized generation, segregating in a zygotic proportion of 9 narrow green, 3 narrow white, 3 wide green and 1 wide white.

its flowers with pollen of a white-flowered plant. In both cases the *A* germ-cells, even when combined with *a* germ-cells, will produce plants with coloured flowers (*Aa*): but the germ-cells with *a* when combined with germ-cells from pure *aa* plants must necessarily give *aa* offspring, and the result will be again 50 per cent.: 50 per cent.

A complication arises when we interbreed the heterozygous *Aa* plants, or, what amounts to the same thing, when we self-fertilize such an *Aa* plant. In this case both the ovules and the pollen-cells will be of two kinds, *A* and *a*. And now an *A* ovule has equal chances to be combined with either an *A* or an *a* pollen-cell, and the same is true of an *a* ovule. The result will be: 25 per cent. $A + A = AA$, 25 per cent. $A + a = Aa$, 25 per cent. $a + A = Aa$ and 25 per cent. $a + a = aa$. Now, if the *Aa* plants look the same as the *AA* ones, this means that we get a three to one ratio. In this case we say that the quality of the *A* plants is *dominant* over that of the *aa* plants, which quality is called *recessive*.

In many cases dominance is incomplete. It may happen that in a series of *BB*, *Bb* and *bb* plants, the *Bb* plants are somewhat intermediate in character between the *BB* and the *bb* plants. In this case the result in such a self-fertilized set of seeds will be 25 per cent. *BB*, 50 per cent. *Bb* (visibly different) and 25 per cent. *bb*, a ratio of 1 : 2 : 1.

Gregor Mendel first showed the occurrence of this segregation of genes in the process of germ-cell formation of hybrids. In his own experiments with peas, hybrids between tall and short plants were tall, coloured flowers were dominant over white, normal stem over fasciated, and so on, and in every second generation he obtained a three to one ratio of dominants to recessives, with quite large numbers. His experiments and his interpretation furnished us with a key enabling us to understand the process of heredity, and from a full appreciation of his work dates the beginning of genetics as a science.

Many years later, chiefly as the result of the work of Bateson, Morgan and their schools, it was discovered that the genes are localized on the chromosomes, and that each gene keeps its own fixed locus between the others that are present on that same chromosome. The segregation of genes from germ-cells

results from the fact that whereas during growth of the plant every cell keeps its full complement of so many pairs of chromosomes—each pair consisting of two that are on the whole identical—only one chromosome of each pair enters each germ-cell. If in one pair at a given locus in one chromosome we have *A*, and in the other *a*, all the cells of the plants—the "somatic" cells—have the constitution *Aa*, but as only one chromosome of each pair goes into a germ-cell, the germ-cells must in respect of this one gene be of two kinds, as many *A* as *a*.

It was found that at this reduction division this distribution of single chromosomes over the germ-cells happens in such a way that in each case chance determines which member of a pair of chromosomes goes to each cell. For this reason the distribution of one gene (one pair of possibilities, *A* or *a*) happens independently from that of another gene (another pair of possibilities *B* or *b*) insofar as we are dealing with genes located on different pairs of chromosomes. If we are dealing with a plant which is simultaneously heterozygous for *A* and for *B* (a plant with the formula *AaBb*), this plant makes 50 per cent. *A* and 50 per cent. *a* germ-cells, but half of each *group* will be *B*, half *b*.

For this reason such an *AaBb* plant will make four kinds of germ-cells: 25 per cent. *AB*, 25 per cent. *Ab*, 25 per cent. *aB* and 25 per cent. *ab*. And on breeding from such plants, and fertilizing them among themselves or on self-fertilizing them, we obtain a much more complicated picture. As there are now four groups of germ-cells on both sides, the results, as far as the genes and their distribution are concerned, can best be pictured by means of a checkerboard, as follows:

	Germ-cells			
	AB	*Ab*	*aB*	*ab*
AB	*AABB*	*AABb*	*AaBB*	*AaBb*
Ab	*AABb*	*AAbb*	*AaBb*	*Aabb*
aB	*AaBB*	*AaBb*	*aaBB*	*aaBb*
ab	*AaBb*	*Aabb*	*aaBb*	*aabb*

When we have complete dominance in both cases, so that there is no visible difference between *AA* and *Aa* or between *BB* and *Bb* plants, there will be only four groups, according to visible qualities, and the numerical relation between those groups will be (see the checkerboard) 9 *AB* to 3 *Ab* to 3 *aB* to 1 *ab*.

The simplest cases will be those in which we are dealing with two genes which each have a clear-cut (but mutually independent) influence upon the final qualities, such as a colour difference or one of shape or stature. It must be emphatically stated here that in order to study the distribution of genes (segregations) we carefully choose our material in regard to the genes present in it. Of course things are much less clear when two genes both affect the same quality, or if one gene can act only in the presence of a second one. It is not my intention to make a genetics textbook out of this chapter, and the reader interested in these matters is referred to one of the many school books on genetics. We will discuss some cases as we go along, in different chapters where we are dealing with such complications.

When two genes happen to lie in the same chromosome, they are not inherited and distributed independently. In such a case such genes are coupled.

It has been found that there are grades of coupling, close and less close, and it has been proved that the grade of coupling is actually determined by the relative localization of such genes on the chromosome in relation to each other. Morgan has shown that this fact is due to the circumstance that there sometimes happen to be interchanges between two chromosomes of a pair. When the two members of a pair of chromosomes are finally drawn apart in the reduction division, the final single chromosomes may be composed of pieces of both members of the pair. As we can most easily understand this process by picturing the original pair as lying crossed, we speak of the process as of " crossing-over ".

If we look at the diagrams (Figs. 3, 4 and 5, pp. 47–49) we see that the chance of two genes that lie far apart, to become separated and recombined is much greater than in the case of two genes lying close together—in fact, two genes that are located next to each other may nearly always be inherited and distributed as one.

In practical plant breeding we are sometimes concerned with crossing-over and with coupling, if we want to break up certain combinations of qualities. This may make the number of plants we have to grow per generation larger than it would have to be when the genes we were shuffling were located on separate chromosomes. But I must say that whereas a study of coupling has been of the utmost importance for genetics as a science, as practical plant breeders we are very seldom concerned with it—the phenomenon seldom affects our methods of selection. In the chapters on variation and mutation we will have to say something more about crossing-over.

Cross-breeding may easily lead to novel recombinations of genes, and for this reason both to novel recombinations of qualities, *and* to the origin of wholly new qualities.

The size of the cell-nucleus is, to a certain extent at least, determined by the number of chromosomes, and, on the other hand, the size of the nucleus determines the size of the cells.

In plants, more than in animals, it may happen that occasionally a whole nucleus is doubled in content. When a cell normally divides into daughter-cells, the chromosomes are first doubled, and two identical separate nuclei are first formed, after which these draw apart before the cell divides. But something may disarrange this orderly sequence of processes, and after the chromosomes have doubled, this double number of them may stay together in one giant nucleus. Such cells with twice the normal number of chromosomes may be wholly viable and found a long series of cell-generations.

In some groups of cultivated plants such chromosome doubling has been the frequent cause of the origin of novel varieties—many of our cultivated flowers, such as bulbs and dahlias, are tetraploid (we call the original plant with a normal double set of chromosomes diploid), and large flower size is a common result of tetraploidy. Tetraploid plants have germ-cells with twice as many chromosomes as diploids, and for this reason tetraploid races of plants may be wholly stable and true to seed.

If we cross such a tetraploid plant with a diploid, the resulting hybrid will have two sets of chromosomes plus one set. We call it a triploid. Triploids often occur among cultivated

plants—most of our good apples, in fact, are triploids. But it is clear that triploids are unbalanced as far as their chromosomes are concerned, and when a triploid plant produces germ-cells, these are an irregular lot, with some chromosomes single, others double, so that very few of them are able to give rise to viable embryos. In fact, most triploid plants are more or less sterile, and seedlings from triploids are very seldom normal. This is the case with such apples as Belle de Boskoop (Goudreinette), in which only an occasional seedling will give an approximately normal apple-tree.

We can artificially induce chromosome doubling. This to-day is mostly done by an application of a poison, generally colchicine, which seems to paralyse the part of the cell content responsible for the moving apart of the chromosomes preceding cell division. When we induce very rapid growth, as by deep pruning, we may also cause tetraploid tissue to form. In fact, anything that disturbs the normal, exceedingly complex process of cell-division may be the cause of an irregularity of this kind.

In some cultivated plants chromosome sets seem to have doubled repeatedly. Our cultivated sugar-canes have chromosome numbers which are several times larger than those of wild canes, and the same is true of some flowers. In special subsequent chapters we shall have occasion to come back to this subject.

The qualities of a plant are the result of the way this plant grows and develops, and this development and growth are the result of the co-operation of a very great number of developmental factors. Some of these factors are genes, which influence growth-processes from within. But of equal importance are the different substances and forces that influence development from without—the environment in the widest sense.

The yield of a single plant—let us say a wheat-plant—is due to a certain extent to its inherited constitution, but also to the conditions under which the plant developed. If we give the wheat-plant enough room, and furnish it with the right fertilizers, it may continue for a long time to form shoots: it may stool out so much that thirty or forty ears are formed, which each ripen a great many plump seeds. But we have already

shown that the influence of the environment does not affect the inherited quality of the plant. The seeds of this mammoth wheat-plant are in no way superior to seeds grown on plants that in crowded conditions have made only one or two ears. If we start selecting, it is of the utmost importance that we are not misled by the effects of the environment. To a certain extent it is possible in plant breeding to make conditions so uniform that differences between individual plants are certainly due to differences in hereditary make-up, but this is very difficult, and in succeeding chapters we shall discuss methods of finding out which individual plants are best for breeding purposes.

In some cases the influence of the environment, of methods of culture and of differences in soil and watering are exceedingly great. Some of the best examples of this are seen in the cultivation of flowers. In the chrysanthemum we can, starting from identical cuttings, by appropriate methods of pruning and treatment, make either a plant with one single bloom as large as a plate, or a bush full of small flowers, or, again, a trailing cascade. In fruit trees the influence of the standard on which we graft our bud is so great that one tree will make a bush that will start bearing in its third year, whereas another individual in which the graft was taken from the same twig will grow into a large orchard tree which will come into full bearing only after a decade, and will grow into a large tree capable of producing bushels of fruit.

In the growing of sugar-beet seed we often make use of thickly sown, scraggly little beets, that are planted out in spring as seed-bearers, whereas from a sample of the same seed we may produce large, juicy field beets yielding an abundance of sugar.

In plant selection we have the greatest difficulty in accounting for the favourable or unfavourable effects of the environment. Individual excellence is no certain test of quality from a plant-breeder's point of view. What we are continually striving for in plant breeding is adaptation of our plants to their environment. Especially if this environment—this climate or special conditions—is at all peculiar, our plants must be able to produce a good harvest, nevertheless. Adaptation of a

strain of plants to its environment may be a result of natural selection, those individuals or those strains which thrive best in the circumstances having a greater chance of leaving abundant offspring. In other chapters we shall treat of adaptation of plants to infections and to adverse circumstances. Those circumstances may be very severe, as in the case of extremely cold or dry winters, or in the case of desert conditions. Giving our plants the sort of conditions which are most favourable to their growth and development will not help to improve them from a breeder's point of view.

Very often it is quite impossible to find the best individuals for breeding purposes by comparing better and less good individuals. If we want to produce a high-yielding strain, high yield alone is not a very good criterion, because environmental conditions will greatly influence yield. As we shall discuss at length in chapters on selection, individual quality —phænotype—is not a good criterion in selection. Of course, the safest way to find those plants which should be bred from to get better descendants is to defer our decision to the moment when we can judge of the quality of this offspring. If we use such methods we are wholly safe, and we leave nothing to chance. (Fig. 6, p. 61.)

In many cases it helps, in the production of seed or tubers, to use a special environment which has no relation to the conditions under which the plants of the group are expected to grow under commercial methods of production. In the production of sugar-beet seed we may cut up a seed-bearing plant into numerous small pieces, in order to get much more seed than we would normally harvest on one plant. In growing sufficient seed of a wheat variety we may resort to planting out the seedlings from a number of chosen plants and giving them much more space and plant-food than would be economic in a commercial crop. We may protect hybrid plants by spraying them, though we may be endeavouring to produce a variety that will stand infection without any protection, and, in the same spirit, we may grow our hybrid apple-trees in a temperate zone, even if our object is to make apple-trees that will not freeze when planted in a country with very long and severe winters.

One thing we must remember is that the final qualities of individual plants are no criteria by which we can judge those plants as progenitors of commercial generations of their kind. If this were not true, plant breeding would be extremely easy. In reality it is beset with the most diverse difficulties.

Chapter Six

The Nature of the Genes

In plant breeding we are concerned with existing and with novel combinations of genes, and this book would not be complete without a few words on the genes themselves—the ultimate units with which we are dealing in variation and in heredity.

When genetics was a young science most of us considered the genes as the determinants for the " unit-characters ", each gene responsible for a separate quality of an organism. The facts of Mendelian inheritance showed us that there are very small hereditary differences—differences between a contrasting pair of characters. And it seemed obvious to assume that in such a case the genes themselves occur in pairs, one member of the pair causing white flower-colour and one blue colour, one causing waxy endosperm in corn and one horny.

It is very curious that this idea should have taken such a firm grip upon the imagination of the earliest geneticists. If we compare genetics with other sciences—with physics, chemistry, astronomy—we generally see that it is not self-evident to assume that where we see a difference, or where we see two contrasting qualities, two different contrasting *causes* occur.

We speak of hot and cold, of light and dark, of wet and dry. But we do not really think of a separate cause for wetness and a separate one for dryness—a relative presence or absence of water does very well as an explanation—and the same is true in all the other examples. To assume the existence of pairs of

genes in each pair of which the resultant action would be contrasting is an unnecessary complication. The alternative is a much simpler hypothesis which was proposed by Bateson and by myself, and which went under the name of the " presence-and-absence " theory of the gene. We assumed that in a monogenetic difference—the smallest " Mendelizing " difference—we were dealing with the absence or presence of just one gene. At first this hypothesis met with a veritable storm of protests. To some of my colleagues it seemed the height of folly that the absence of anything should ever determine an inheritable quality. On the face of it, this objection seems very strange; for it seems quite logical to speak of silence as determined by a purely negative absence of noise, of dryness determined by the absence of water. But of course the apparent absurdity of thinking of the absence of a gene as causing an inheritable quality grew out of Weismann's conception of determinants, inherited protoplasmic entities that should be each responsible for just one particular property of a living being.

In 1911 I put forward an alternative to this determinant conception of heredity. I proposed the idea, now generally accepted by biologists, that the qualities of an organism develop as a result of growth and development, this development being caused by a co-operation of thousands of factors, some of these factors being environmental, while some others—the genes—influence the course of development from within. If we compare a plant having pale-pink flowers with one having dark-pink ones, we assume that the development which leads to the production of the plant with the pale flowers is due to the co-operation of thousands of causes and substances. But in the other plant one additional substance is present, whose action at the appropriate developmental stage allows a further transformation of the pink colour into a darker one. It is therefore not the absence of this gene which directly causes pink colour; it is the presence of the thousand-and-one genes which both plants have in common. If we knock off a man's hat we may see that he is red-headed. He does not become red-headed as a result of the absence of the hat, but we can see the result of all the other things which cause his hair to be red,

provided we take away that hat. If in the course of this story we substitute an inherited gene which helps to transform red hair into black, the reasoning remains essentially the same.

Very soon after the original presence–absence hypothesis was first published it was found that in its original shape this hypothesis was not adequate to explain all the facts. It was found that very often in inheritance we are not dealing with just *two* contrasting qualities, but with *three or more* alternatives. In snapdragons we have a series of varieties that gradually grade into each other, starting from yellow through different intermediate stages to red. If we call those forms *A*, *B*, *C* and *D*, we find that any pair of them between them show a difference in just one gene. When we mate *A* with *B*, we will get only *A* and *B* plants in following generations; if we combine *B* with *D*, no *A*'s or *C*'s, but only *B*'s and *D*'s will be found in the second generation. The best explanation of such series of multiple alleles is this: that in such cases we are dealing not with the presence and complete absence of one gene, but with different quantities of one and the same gene in the one spot on the chromosome where our gene is located. Instead of the presence–absence hypothesis, we now prefer to speak of a hypothesis about quantitative differences in inheritance. It is highly probable that in certain instances we are really concerned with presence versus complete absence; in other cases, however, intermediate stages may occur in which fewer molecules of the gene are present per cell-nucleus.

This quantitative gene-theory is closely bound up with the hypothesis I proposed in 1911, and which is now generally accepted by geneticists—namely, that the genes are not living protoplasma globules, but that they are non-living chemical substances, that have only this in common: that they are each the ferment for their own synthesis. With Alexander, we may speak of reproductive catalysis. We assume that each molecule of a gene, between every time the cells, in growing tissue, divide, attracts and helps to combine from the ambient building stones just one new molecule that will in every particular be its exact duplicate.

The genes are combined longitudinally in long series—the chromosomes—and it is the chromosomes whose movements

and combinations give rise to the phenomena we notice as Mendelian segregation and redistribution of genes. The number of the chromosomes is highly constant for every plant species; and sometimes, as in wheat and barley, different sections of the group are distinguished by different numbers of chromosomes. In that case the numbers are always multiples

FIG. 3.—Regular disjunction between two daughter chromosomes. Each chromosome is shown as a row of various figures, representing as many genes of different kinds.

of a common basis number, and it is very probable that in such a series the higher chromosome numbers may have originated by reduplication of entire chromosome sets during the course of evolution of the group. In the cells of the plants those chromosomes, made up of genes, occur in pairs. The homologous chromosomes of each pair are not necessarily identical. We know that in a plant heterozygous in respect to one gene, the chromosomes of the corresponding pair are different in that particular spot (" locus "). The two chromosomes of a homologous pair have originally been derived from

the two parents, one from the pollen-cell and one from the ovule. The same is true of all the other pairs. The somatic (body) cells have a double set of chromosomes; the germ-cells have only a single set—one of each kind. In ordinary growing tissue every chromosome doubles its mass (and probably the quantity of every gene present on it) between two cell divisions.

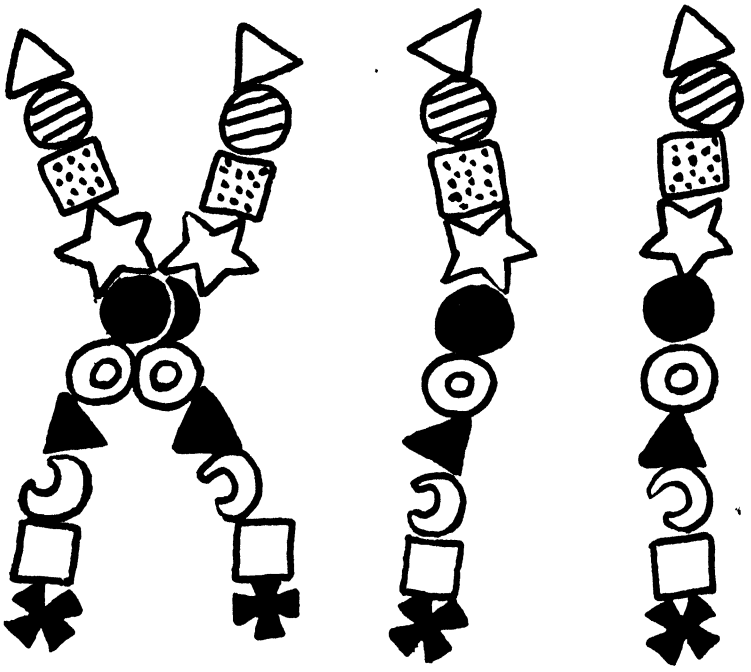


FIG. 4.—Regular crossing-over between two homologous chromosomes. The two new chromosomes each consisting of part of the two original ones are identical, the break occurring on each at exactly the same spot.

And when cell-division commences, the chromosomes are drawn apart to different poles of the cell in such a way that each daughter cell obtains a complete set of chromosomes that is identical with the original set.

The exception is that a " reduction division " occurs when germ-cells are formed. In this case there is a second cell division without a preceding chromosomal doubling. At this reduction division the two chromosomes of a homologous pair become separated one from the other. The result is that in a plant, heterozygous in respect to one gene, *A*, in which all the

somatic cells are *Aa*, the germ-cells will be either *A* or *a*, or, as I would prefer to say, only half the germ-cells contain the full quantity of gene *A*.

As a gene *B*, which is situated in another pair of chromosomes, and for which the plant was also heterozygous, is equally distributed over one half of the germ-cells, those germ-cells will,

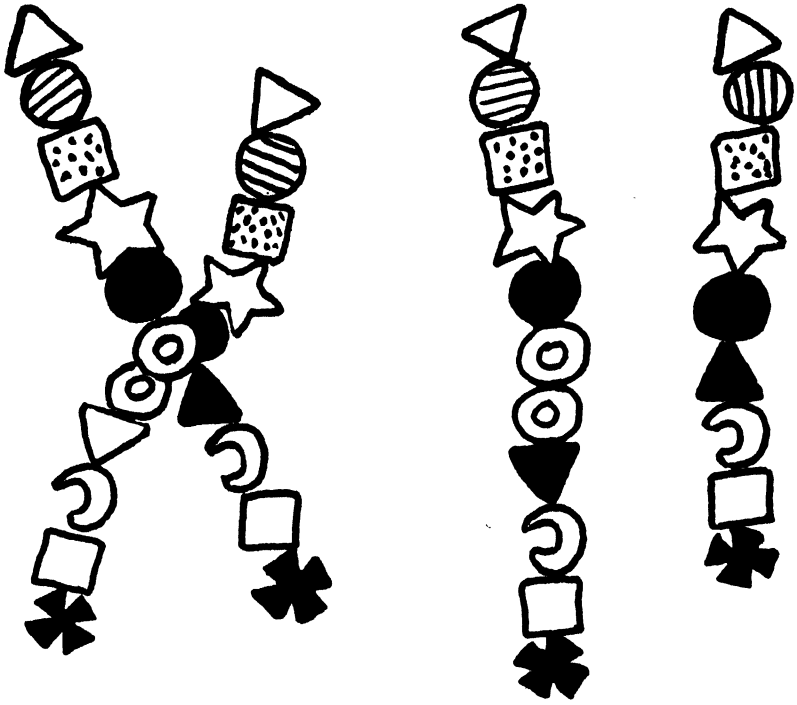


FIG. 5.—Irregular crossing-over. When the break does not happen to occur at exactly the same "locus" in the two original chromosomes, one of the new chromosomes may have one gene in duplicate and the other one may be lacking it. Mutations may arise in this way from small irregularities during crossing-over.

for this reason, be of four kinds: *AB*, *Ab*, *aB* and *ab*. To a certain extent this redistribution of distinct genes over different germ-cells results in a redistribution of the qualities which were shown by the parents of the heterozygous plant. If we cross a plant with *AB* to an *ab* plant, the hybrid will be *AaBb*; and as this hybrid will be making four kinds of germ-cells, there will be all sorts of offspring, with different combinations of the qualities in which the grandparents differed.

We were just speaking of genes located in different chromosomal pairs. But sometimes plants are heterozygous in respect to two genes that happen to be located in the same chromosome. In this case those chromosomes tend to be transmitted as such, in their entirety, so that the distribution of the two genes is not mutually independent. Such genes are " coupled ".

All kinds, all degrees of coupling have been met with, from complete or almost complete coupling to very loose coupling. Morgan proposed a hypothesis which is now very well proven and established—namely, that the degree of coupling is dependent on the greater or lesser degree of contiguity of the genes. Genes that lie close together are closely coupled, those that are far apart must lie farther apart on the same chromosome. The mechanism which is thought to account for coupling is the phenomenon of " crossing-over ". Sometimes chromosomal strands seem to touch at one or more places, and when the strands break apart, the top half of one strand may be attached to the bottom part of the other. A new pair of chromosomal strands originates, but if on both sides of a break there are loci where the strands differ in chromosomal content, those loci are redistributed, so that, as far as the independent inheritance of separate genes is concerned, crossing-over may help to redistribute the genes, even if they are located in the same chromosome.

Chapter Seven

Dominance

A large amount of a certain gene in the nucleus of a plant cell will have a stronger influence than a smaller amount of the same gene; and where we are concerned with a difference due to presence or absence of one given gene, the difference in quality between two plants may be directly due to the presence of the gene in one of them.

In any case of a difference due to one gene, the quality of the heterozygote (*Bb*) may be different from that of the *BB* plants, and roughly intermediate between the corresponding qualities of the *BB* and the *bb* plants, or the *BB* and the *Bb* individuals may be indistinguishable from each other. In this last case we say that the quality of the *BB* and (*Bb*) individuals is *dominant* over the corresponding quality of the *bb* plants. In general, flower-colour is dominant over its absence in white-flowered plants. Hairiness is generally dominant over absence of hairs. But no hard-and-fast rules can be given concerning dominance. In any case, we may never say that one *gene* is dominant over another. Dominance pertains to characters, and dominance is always relative. In fact, dominance is greatly dependent on the hereditary constitution of the plants, so that it is possible that what is dominant in one lot of plants would be recessive in another set. I have been able to prove this experimentally in animals, where it was possible to make albinism dominant, whereas it is generally recessive, while the differentiating gene remained the same, and only the rest of

the genotype was different. So far I can think of no corresponding difference in plants, but no doubt the facts could be shown to be exactly the same in plants as in animals.

To a certain extent we may speak of dominant and recessive virtues in plants, and of dominant and recessive faults. The object of plant breeding is to combine as many virtues as possible in our strains of plants, and to rid the plants of definite faults that make them less useful. In so far as dominance is concerned, we always find that it is easy enough to get the recessive virtues fixed into the material and to get rid of the dominant faults. The difficulty is to get rid of recessive faults, or—what amounts to the same thing—to fix dominant virtues.

If in a certain group of plants some valuable quality is dominant, this means that no difference is discernible between the homozygous and heterozygous plants, between the *AA* and the *Aa*'s. The result is that there are only two groups in this respect: the *A* group and the *aa* group. If we prefer the *a* individuals, selection of the *a*'s and rejection of the *A*'s will have an immediate effect, for the *aa* plants can never again give us *AA* or *Aa* ones. But if we prefer the plants with *A*, selection of the *A*'s and elimination of the *aa*'s will not have speedy or permanent results. *Aa* plants will always reproduce a minority of *aa* plants. To get good and permanent results it is necessary in some way to distinguish the homozygous *AA* plants from the heterozygotes, *Aa*. In plant breeding this can be done much more easily than in animal breeding, where this difficulty is one of the major problems. It can be done by waiting until we have bred from the plants. Some (the *Aa* plants) will produce a minority of recessives (*aa*), whereas between them we shall also find some that breed true for the dominant quality (the *AA* plants). In treating of selection we discuss these methods further.

New dominant qualities are often the result of cross-breeding, but very seldom the result of mutations. One of the most certain ways of producing new valuable kinds of plants is to introduce just one dominant quality by means of a cross. Let us suppose that our problem is to make an otherwise excellent plant resistant to some specific disease. We find some related species that happens to be wholly disease-resistant, but

may be without any other merit. We make a cross, and find that the resultant hybrid plants are fully resistant. Our problem now is to bring this dominant disease-resistance into the old kind of plants. This can be done by back-crosses. The result of a back-cross between our valuable species and the resistant hybrid will almost certainly be that some of the plants obtained will be resistant, even if a great many are more or less susceptible. The next step is to repeat the back-cross, and to repeat this process until we have produced the combination of good resistance and all the valuable qualities of the old variety. This means that all we have to look for during those back-cross generations is to hold fast to the resistance; all the other old and valued qualities will come automatically as a result of the repeated back-cross.

Of course it is understood that the first good plants, that represent the old valuable kind of plants (with resistance added), will still be heterozygous for the gene or genes conferring immunity, and for this reason we must next proceed to produce the required homozygotes by a process of breeding the new plants *inter se*.

It is sometimes important to bear in mind that recessive qualities are always breeding true. If in breeding flowers we want to produce some true-breeding colours, it is good to know that the recessive colours will be the easiest to fix. And in a variable population that is bred from hybrids we know that the recessives are in the minority. For this reason it is easy to remember that those colours and shapes that are found in the minority are easiest to breed true.

Chapter Eight

Virus and Virus Resistance

It occasionally happens that even a scientist dares to prophesy. In fact, science cannot progress without prophecies. Gathering facts is dull work. The important work in science is marshalling the facts, distilling the essence of them and making deductions from those facts. These deductions are called scientific theories, and a scientific theory, like Janus, looks both to the past and to the future. It is both a tool that can be used to understand the facts that have been painstakingly assembled, and it is a prophecy, destined, like every true and useful prophecy, to direct the search for new facts and better applications of our knowledge to practical methods of doing things. The application of science to methods in the interest of humanity should never be left by the scientist to practical workers working by rule of thumb. Yet the paradox exists that practical applications of science should remain a by-product, in the sense that direction of scientific inquiry by the exigencies of life, in peace or war, effectively clips the wings of science and scientists. I could easily quote a dozen instances here.

Two of my prophecies that concern plant pathology and the nature of virus have been justified by subsequent discoveries. They were both made when I was a young geneticist budding out into plant breeding around 1911.

In a little book on the breeding of plants and animals I stated it as my firm conviction that the " degeneration "—the ageing

or " running out "—of vegetatively propagated plants, apples and potatoes, was due to disease, and had nothing to do with the ageing of the clone. In 1911, in my first draft of the " Bio-mechanic Theory of Inheritance " (Autocatalytical substances the determinants for the inheritable characters), I proposed the hypothesis that the genes are not composed of living protoplasm, but that they are chemical substances which have the property of quantitative reproduction, while retaining their qualitative molecular composition (autocatalytic substances). I prophesied that whereas many of such substances were found to be bound up into an organic whole, some of them could exist alone, free, as it were, or in combinations of a few of them, and I gave the filterable viruses as an example of this.

Both theories have by now won general acceptance. Virus infection is a very common cause of " degeneration " in all sorts of plants—in coffee, in cocoa, in the potato, dahlia, beans, cereals, perhaps in all plants; and the chemical, crystalline nature of a virus was first demonstrated by Stanley for the tobacco-mosaic virus, and since then some other kinds of virus have been proved to be of the same nature. A pure virus consisting of just one substance can be diluted, boiled, precipitated, diluted and crystallized again without losing any of its qualities; a minute quantity is infectious and will again overrun the plant or animal in which it finds itself.

One thing about viruses seems remarkable at first sight. We know pathogenic bacteria, and other bacteria which are present everywhere, but which are quite harmless. Why is it that we know only pathogenic sorts of virus?

The answer, of course, is simply that we cannot see a virus in small quantities; we can recognize a virus only in two ways: by its harmful effect or by complicated reactions with the aid of blood from rabbits or similar animals that have been immunized against it. In the latter case we must first know of the existence of a virus, and this means that the substance produces symptoms in a plant or an animal or a human being.

We find every virus present inside living cells, and the growth of the virus (quantitative reproduction) presumably takes place at the expense of the normal constituents of the cells. The virus

is present in the cytoplasm of the cells. What are the normal things present in the cells, outside of the nucleus? A great many substances are present in normal, healthy cells. There are perhaps thousands of different substances; but they have one thing in common: they each have the faculty of growing in quantity while keeping their chemical composition unchanged. In other words, outside the nucleus, inside the cell there must be many substances present that have the same nature as the genes within the nucleus, and the same nature as different viruses.

Some of those substances we can bring from the cells of one species into the cells of another, by substituting the cytoplasm of one for that of the other. By repeated cross-breeding we can make plants that have the nucleus and all the genes of one species of fireweed (Michaelis) while they still show the presence of some of the (normal) substances of the cytoplasm of a second species of the genus.

Now, what is the difference between a virus and one of the normal constituents of the cells? I am convinced this difference is one of degree only. In Japanese hops, for instance, green plants and spotted plants do not differ in the genes; they have the same nucleus. But there is a difference in some cytoplasm constituent. Plants with spotted leaves will have spotted seedlings, always, even if the seedlings had a green-leaved father. And conversely, if we start with a green-leaved plant, we can cross it with pollen from spotted father-plants, and we can even repeat this several times, but no spotted seedlings are ever produced. Between this case and that of an infectious spotting in some plants there is no real difference, and I feel very sure that it would be possible to transmit the spotting of such Japanese hops into normally green plants by grafting or injection.

If we compare " normal " cell constituents with viruses, we not only see cases such as that of the spotted hops or Aucuba, where a cell constituent is passed in the cytoplasm and produces a semi-pathological condition, but there are cases where a virus, that can be recognized by its pathogenic effect, can be present in some plants without any harmful effect at all. This is so when the same substance is a pathogenic virus in one

plant but when it can also be present in another kind of plant without causing any trouble.

This is true of what the potato phyto-pathologists call a " latent virus ". The facts are as follows. We start with two clones of potato, calling them *A* and *B*. No symptoms of virus infection are noticed in either. Now we graft a piece of plant *A* into plants of the *B* clone. As a result, those *B* plants show symptoms of a serious virus infection. This disease can be transmitted from one plant of clone *B* to the other. We are dealing with a virus.

There are two ways of interpreting those facts. The potato pathologist is liable to say that plant *A* is immune to the virus; it carries the virus in a " latent " condition.

But we can also say—and it really amounts to the same thing —that this substance which we call a virus when we see its action in *B* is a normal constituent of the cells of the plants of clone *A*.

Some of the viruses and some of the kinds of infectious spotting in plants can be transmitted by injecting some fresh juice, or by grafting. We must ask ourselves this question: is it possible that what we call viruses in our plants (or animals, or even humans) are substances which are normally present in the cells of healthy living beings?

I would like to answer this question in the affirmative. It seems the most probable hypothesis. It seems reasonable to believe that brand-new viruses may start attacking our plants or ourselves, but that they are new only in so far as they are quite common substances in the wrong place. A few examples will make clear just what I mean by this. Some genes have a decidedly pathogenic effect in individuals with one certain combination of other genes, whereas they do not show such an effect in the species in which they are normally present. I am speaking of such cases as Kosswig's experiments with species crossing in fish (pigment tumours).

I would also like to point to those cases in which an animal species or a plant species, transposed into a new environment, runs riot. The facts relating to the wild rabbit in Australia and to some Opuntias are very good examples. Those species in their original home are certainly not terrible pests; they

fit into the balanced fauna and flora quite normally; they are balanced.

It is quite possible that some of the violent, and some of the variable viruses consist of *combinations* of two or more substances. This possibility might account for the fact that some viruses, like some of the potato viruses or such things as human influenza, occur in grades of severity, changing their effects.

One of my colleagues—Prof. Harland—recently told me of a case in which he had grafted a wild tomato species upon a potato. The combination showed violent symptoms of a virus infection, which rapidly spread to all sorts of plants in the experimental garden, and could be eradicated only by ruthlessly destroying a large area of different kinds of plants. It is quite possible that Harland created a virus by this graft. If this is the explanation, even this case would not need the assumption of a " mutation " !

A healthy plant is one in which the set of genes and the set of cytoplasma " genes " are in complete harmony. The cytoplasm must absorb the material for the synthesis of its own constituents, and it must furnish the material for the simultaneous synthesis of tens of thousands of genes in the nucleus.

If there are any pathogenic bacteria or viruses about, we want our plants to possess a set of genes which will make them resistant. In virus infection this may mean that what we call a virus is already present as a normal and balanced substance in the cell cytoplasm. Or it may mean that it can be taken care of, and will either fail to find the right conditions for its growth or will take its inconspicuous place between the other thousands of substances.

Immunity to virus is almost always dominant, so that we can easily transfer it from one plant to the other by means of cross-breeding. Wild species are often seen to be very good sources of virus resistance, in tomatoes, in beans, in potatoes, raspberries and other plants. Resistance to bacteria or moulds is largely due to genotype constitution, and it can be selected for.

In practice, what we need is a reliable source of infection, to which we can expose the plants. It so happens that we can generally test for immunity when the plants are still young.

In mould and bacterial infections we can test millions of seedlings of grapes, of flax, of wheat or barley, by growing them in crowded flats under conditions favouring the infection. In virus work we have the disadvantage that we can only keep the virus growing in living cells. In laboratory conditions this means that in favourable cases we can keep the virus going on tissue cultures (tomato roots, for instance). In practice, just growing new clones of potatoes or new lines of tobacco or tomatoes between infected plants will give us a sufficient indication of their immunity.

Amateur plant breeders interested in growing potatoes or tomatoes or raspberries from seed should seek co-operation with some central experiment station that specializes in testing plants for virus resistance, after they have themselves given the plants a rough test.

Chapter Nine

Variation Due to Crossing

The relative independence of genes makes it possible that novel combinations occur in material which is heterozygous for several genes. In the example of my squashes, the original two forms used were a plant with oblong white fruits and another with round green-striped fruit. The hybrids between them had oblong green-striped fruits; and in the second generation we obtained not only the original combinations, oblong white and round green, but also the two other, new combinations, long green and short white.

The greater the number of genes for which the original material is impure, the greater the variability in the offspring grown from seeds. As each gene for which a plant is heterozygous makes it produce two kinds of germ-cells, the number of different kinds of germ-cells doubles with every additional gene. If a plant is heterozygous for only six genes, the number of different kinds of germ-cells produced is $2^6 = 64$; and as even closely related subspecies certainly differ in dozens of genes, the variability caused by cross-breeding is enormous. If we cross two different wheats or beans or dahlias, we get hybrids from which we obtain almost as much variability as we need to make hundreds of novel kinds in those groups. To a certain degree this cause of variability—the mating of lines of plants differing in their set of genes—means that we obtain all sorts of novel recombinations of separate qualities. If we cross a bearded, short-strawed, white-seeded winter wheat

with a tall, red-seeded, smooth-awned summer wheat, we can obtain winter wheats in two colours and in two kinds of ears and in all sizes, and summer wheats of similar variety. When W. Orton started to breed his wilt-resistant water-melons by

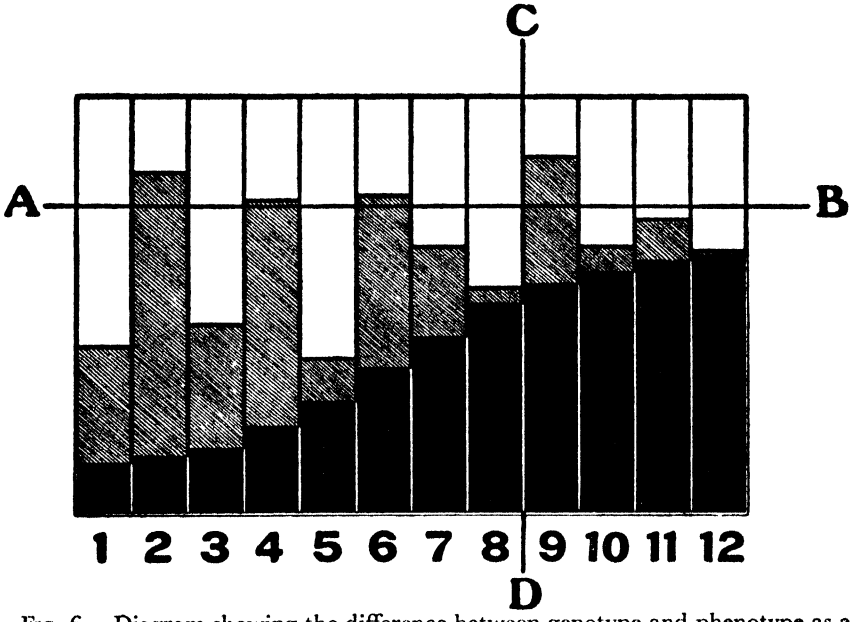


FIG. 6.—Diagram showing the difference between genotype and phenotype as a basis for selection. The height of the black portion of each column (which represents an individual) represents the part played by the inherited make-up in the development of the character appreciated. The cross-hatched portions show the part played by environmental (non-inherited) factors. The total height of each column shows the quality. Twelve individuals are arranged according to their genotype.

When we select the four individuals that show the character (phenotype) in the most perfect way, we select according to the line A-B and the individuals selected are Nos. 2, 4, 6 and 9. When we select according to the best genotype, for instance by means of a progeny test, we select according to the line C-D, and we actually get the four individuals most valuable for building the next generation.

When we select first according to appearance, this group (2, 4, 6, 9) only contains one of the really good breeders. It is safer to select according to genotype from the very beginning.

crossing a green-striped, red-fleshed, wilt-susceptible water-melon with a white-fleshed, oblong, solid, green, wilt-free citron grown for stock-feed, he obtained a multitude of shapes and colours and sizes, and he ultimately succeeded in making a few pink-fleshed, green-striped, succulent, good water-melons that were wholly free of the disease in all climates.

Very often we are able to add some valuable quality that we

find in a related form of small value to some plant that needs improvement. The breeding of disease-resistant plants is full of examples of this kind.

But apart from recombinations of existing qualities, cross-breeding may be the cause of the origin of wholly *new*, and often wholly unexpected, qualities.

In the first place, we can never know beforehand how a number of genes will act when we get them combined. The co-operation of genes *A* and *B* may produce some quality which is produced neither by *A* nor by *B*. A relatively simple example of this is found in relation to so-called complementary factors.

A blue-flowered wild plant species may produce a white variety. In the white plants this colour of the flowers may be due to the fact that one of a series of genes necessary for pigmentation is absent, so that the plants are *a* instead of *A*. But it is possible that we find a second white variety in which not *A*, but some other link in the chain of factors necessary for colour formation is lacking. Such white plants may be white because they are *b* instead of *B*. If now we put *A* and *B* into more complete formulæ for those three kinds of plants, we have *AB* wild, blue-flowered plants, and two white kinds, *AAbb* and *aaBB*. Now, it is evident that crossing *AAbb* with *aaBB* will produce *AaBb* plants which will again have the complete complement of genes necessary for colour formation (and we leave all the other genes necessary out of discussion here). In a case like this two whites crossed will give a blue; and it is clear that such blues, heterozygous for both *A* and *B*, when interbred, will again produce some *AAbb* whites, and also some *aaBB* whites. In actual experiments of this kind with varieties of sweet pea by Bateson, he obtained a ratio of nine coloured to seven whites in the second generation, seven being the sum of three plus three plus one. This means that he obtained the ordinary ratio of nine *AB*, three *Ab*, three *aB* and one *ab*.

When we cross-breed different kinds of beans, we very often obtain plants that show some quality of the wild ancestors—marked, striped seeds, or stringiness, or climbing habit, or bitter taste. In the group of velvet beans (*Stizolobium*), hybrids between very good varieties are often covered all over with a

fuzz of stinging hairs. In fact, cross-breeding will almost always give hybrids showing some dominant qualities, even when the corresponding recessive characters are better appreciated: very often hybrid plants are thrown away for this reason, whereas further breeding from them would have given the plant-breeder what he wanted.

A very peculiar phenomenon seen in cross-breeding is the origin of unexpected new recessive (double-recessive) qualities. A striking example of this can be taken from the work of de Haan in Holland. This geneticist crossed two different sorts of relatively short peas, and obtained a very similar hybrid. But when he obtained a large second generation (mostly called the F_2 generation) from those hybrids, he obtained a minority (one in sixteen) of exceedingly tall plants shooting up for several yards. The explanation was obtained by repeated crosses and back-crosses, and it was as follows: The short-statured peas were different in composition. One was *CCdd*, and the other *ccDD*. Both factor *C* and factor *D* in this case restricted the stature. When he interbred the *CcDd* F_1 plants, he obtained a second generation of nine *CD*, three *Cd*, three *cD* and one *ccdd* plant, the very tall, giant kind!

Examples of double-recessive novelties are often met with in our own cross-breeding work with small animals. When interbreeding subspecies of rats or mice we nearly always get some waltzers in F2, and always in that same proportion of fifteen normals to one waltzer. Even when we mated fitch with ferret, we obtained one-sixteenth of waltzing ferrets in the second generation.

The origin of wholly novel characters in the second generation of a cross is a very frequent phenomenon in plant breeding. In most cases the exact numerical relations are not noted down; but, even so, the explanation must often be the one just given for the giant peas.

If we cross two species of horned poppy—*Argemone platyceras* and *A. mexicana*—the hybrids are somewhat intermediate. The flowers are six-petalled, like those of the parent species; the colour is midway between the white of *platyceras* and the yellow of *mexicana*. But when we raise a second generation from such hybrids we obtain an enormously great variability. Not only

do we obtain yellows and creams and pinks, but we get some salmon-pinks and pale lilac plants. Among the six-petalled plants, some have three long and three short petals. A few plants have some of the anthers transformed into petals; they are double-flowered, others are polycephalic, with anthers changed into stamens. We even find some plants with deeply laciniated flowers; and when we breed on from such novelties we find that most of them come true from seed.

Much less striking than this production of unexpected novelties in the second generation of a cross is what is called transgressive variation. By this we mean the production of some plants that exhibit some quality to a greater extent than the parent forms. Very good examples of this are met with in the breeding of cereals. If we want to obtain extremely winter-resistant wheats or ryes, the best way to proceed is to cross two different good, winter-hardy kinds. If we do this, we may confidently expect the resistance to frost among the second-generation plants to differ considerably, and the quality differs so much that we obtain extreme cases on both sides of the scale: plants that can stand no frost at all, and others that are much more frost-resistant than the material with which we started. Exactly the same is true in regard to such difficult qualities as yield and productivity. This is also true of shape and habit, and of the most diverse qualities, pureness in sugar-beet, earliness in coconut palms.

There is one curious rule that plant breeders should bear in mind. When we hope to obtain a certain quality to an even higher degree than we now have it in the best sorts, we can always try crossing good types. If we do so, it often happens that the first-generation hybrids are disappointing, as they are much less good than the parents crossed. Wheat hybrids may be less resistant to infections or to cold; sugar-beet hybrids may have too much salt in the sap.

If this is true, we must certainly not throw away such disappointing hybrids; on the contrary, we must regard this phenomenon as a good omen! This seems very strange at first sight, but the explanation is simple. When two tall plants crossed produce a hybrid that is less tall, this shows that they differ in genotype—the tallness in one is not due to exactly the

same combination of genes as that in the second breed. In a case like this we seem to be dealing with two separate and distinct genetic causes for tallness, and in so far as this is true, we may hope to get some F2 plants in which both separate causes for tallness are combined. Exactly the same reasoning holds good when we are dealing with disease resistance, with frost resistance and similar useful qualities.

In fact, if we do any cross-breeding in order to obtain some improvement in quality, either by a recombination of visible qualities or in the hope of obtaining transgressive variability, the quality of the F_1 hybrid plants should never be the reason for their rejection. We can never know whether the object we seek is or is not attainable before we have the second generation to judge.

This rule will be repeated several times in this book, for I know that in a very great many cases hybrid plants have been rejected that would probably have given the desired result when bred from. This is especially true when we are breeding plants for adverse conditions, frost resistance, drought resistance or resistance to some prevalent disease. In such cases it is immaterial whether the original hybrids are or are not resistant. If we expose them to the unfavourable conditions and lose them we may never know whether they would have given us what we were breeding for. I remember cross-breeding experiments with apples in Canada that were started to obtain frost-resistant apples for that country. Very frost-resistant Siberian crabs were crossed with ordinary good dessert apples that could not stand the climate. Practically all the hybrid trees were lost during the first winters, and only a very few crab-like trees finally survived. Nowadays we know that this was a costly mistake. The hybrid trees should never have been kept in the country for which new apples were sought—they should have been carefully protected, so that they would have given lots of fruit and seeds to be sown and tested in the North.

Exactly the same thing is true of disease resistance. In the breeding of *Phylloxera*-resistant and mould-resistant grapes, by means of cross-breeding good grapes with resistant but otherwise inferior ones, the mistake is very often made of exposing the first-generation hybrids to the diseases. This should never

be done. It is immaterial if the hybrids themselves are or are not resistant: they are only the parents of a variable F_2 generation in which we hope to find our resistant numbers.

When a new species is imported for the first time, in a plant section in which many cultivated plants or flowers are being bred, this importation is often hailed as an important event by plant breeders who understand their business. Not, in the first place, because the new species may in itself possess very valuable qualities, but simply because it has not been crossed into the present assortment of plants before. A novel species of tulip or gladiolus, or a bean or pea or beet, is sometimes of the very greatest value, as from the hybrids that can be bred from it we may hope to raise an exceedingly variable lot of plants—new material for selection. Frequently quite unexpected novel characters are so obtained. Of course it is true that a novel species may often in itself possess some very valuable quality. A new species of digitalis or gladiolus in which the flowers are placed all round the spike instead of all looking in one direction may be valuable for this. A new species of wheat or bean, or soybean, though its yield be quite small, may give us some valuable drought resistance or frost resistance.

I do not think I can over-emphasize the importance of cross-breeding as a source of wholly novel, unexpected qualities. In the breeding of flowers especially, anything wholly new is valuable as such. The history of the dahlia is very illustrative in this respect. There have been three periods in which masses of new dahlias were obtained by breeders, after the very first importation and on two occasions later when fresh material was imported from Mexico. It can safely be predicted that another importation of either wild or cultivated dahlias from middle America would give our dahlia-breeders new material for the production of further striking novelties.

Chapter Ten

Mutation

The process of inheritance depends on the faithful reproduction of the material of the genes. A plant-cell contains a nucleus with a certain number of chromosomes, and each chromosome contains a great many different genes, of which each one has its own particular composition. Before each cell in growing tissue divides, every gene helps to synthesize a quantity of material that is alike in composition, and alike in quantity to the quantity already present. The constancy in long series of cells and long series of plants depends on the regularity of this exact doubling of every chromosome. When two homologous chromosomes in a cell differ in one or more genes, even this difference is faithfully reproduced in a series of somatic cells, and only when germ-cells are formed do those different chromosomes segregate out during the reduction division.

Most of the diversity of plant groups, and certainly most of the diversity within the descendants of one plant, are due to this segregation and random rearrangement of pre-existing differences, and most of those differences have been due to cross-breeding in the widest sense: to the union of germ-cells that differed in their genetic composition.

Although this faithful duplication of the contents and the arrangements in the cell is the universal rule, exceptions do occur. Occasionally an irregularity occurs in this process of the exact duplication of the nuclear contents, and such irregu-

larities may be of the most diverse kinds. As a general rule, the orderly reduplication of every gene and of every whole chromosome in the cell occurs just before this cell divides. The daughter chromosomes wander to opposite poles of the cell, and a new cell wall is formed between the two nuclei. It may happen that after the duplication of the nuclear contents the double number of chromosomes do not draw apart to the ends of the cells, but that they stay together in one lot. No cell division occurs. Somewhat later the ordinary process of gene duplication and chromosome duplication starts anew. Every chromosome with all its contents is doubled, and the new chromosomes draw apart to the poles of the dividing cell. If all this happens, the whole set of chromosomes has been exactly doubled. Whereas ordinarily the cells have just one double set of chromosomes, in *diploid* plants, the new cells and the tissues of plants derived from it are *tetraploid.* A great many causes have been found for this irregularity: extreme heat, great cold, and especially the action of certain drugs. Colchicine is one of the drugs that has been used extensively in these experiments. In very weak solutions it seems to paralyse the forces that act within the cell and that tend to draw the chromosomes into two daughter nuclei.

Tetraploid plants have larger nuclei than normal diploids, and the cells are larger. Even without actual chromosome counts, tetraploids may be recognized by the size of epidermal cells, especially of the stomata. In horticulture this doubling of the chromosomes may give us plants with larger flowers. There is another result of this chromosome doubling. When we are dealing with species-hybrids, such plants may be wholly infertile, because of the fact that the incongruous set of chromosomes derived from two different sets are not able to act normally at the reduction divisions. If the whole set is doubled, each chromosome now has a partner with which it can conjugate. A good example is that of the modern large-flowered primulas of the obconica group (*Primula arendsii*). They arose as a fertile branch on a sterile species-hybrid (*P. obconica* × *P. malacoïdes*).

Another chromosomal mutation which sometimes occurs is caused by the lagging of one chromosome at the moment of

cell-division. As a result of this lagging one daughter cell has one chromosome too many, the other is lacking one (and generally perishes). Blakeslee has shown a whole series of novelties in *Datura*, each due to the duplication of a different chromosome.

Most mutations, however, are due to much smaller irregularities in the usually equal duplication of the complete set of genes on the chromosomes. In most cases of mutation we are dealing with changes that apparently concern only one single gene.

There are different hypotheses to account for such gene mutations (point mutations). I want to give my own hypothesis first.

When I discussed crossing-over and its effect on coupling, I assumed that in both strands of the chromosome the break occurred at exactly the same spot, so that after this happened the new chromosomes had the same general constitution and the same length as the original strands that entered into the process. But we can easily imagine that once in a while, at crossing-over, the break does not occur at exactly the same spot on both strands. A glance at Fig. 5, p. 49, will show what would be the result of this. We would find that in one chromosome a small part would be duplicated, whereas in the other chromosome a corresponding piece would be lacking.

In fact, in *Drosophila*, where giant chromosomes occur in which we can see the actual loci where the genes are located, we know that often enough small duplications and small deletions *do* occur. For this reason I assume that often enough quite small irregularities in the process of crossing-over may cause a gene (or a few adjacent genes) to drop out somewhere (Serebrowsky).

It is very difficult to distinguish a case of mutation from that of the production of a recessive out of material already heterozygous for a gene. In fact, in some material this is absolutely impossible. In autogamous plants, however, where long lines of generations have remained constant, we may assume homozygosis in respect to most genes, and when a heterozygous plant suddenly occurs in such a line, which will then give us 25 per cent. of recessives, we must assume that a mutation has occurred in that material.

If, as I suppose, mutations are always due to the rearrangement of genes already present in the material, there is no very fundamental difference between mutation and recombination of genes by cross-breeding. Many authors assume that while chromosomal mutations (duplications and deletions of parts of chromosomes) are due to recombination of pre-existing genes and chromosomes, the smallest mutations—point (or gene) mutations—must be due to a change in just one chromosome. They assume that the gene is changed in its chemical composition, whereas I would prefer to assume only a quantitative change (reduplication or partial or complete loss). I do not think there are any real grounds for the alternative hypothesis, and I would like to point out that the evidence for a chemical change in the genes themselves is wholly circumstantial. In another chapter I have more fully discussed this point.

From the cases in which it has been possible to heighten the incidence of mutations, it follows that anything which may disturb the regularity of the process of nuclear and cellular division may also cause a mutation. We can induce mutations by means of heat or cold or by irradiation, by ultra-violet light, Röntgen rays, radium, etc.

From a practical plant-breeding point of view there is very little object in trying to cause mutations, with the exception, perhaps, of the grossest kind, such as duplications of the whole genom in order to induce fertility in sterile hybrids. The variability that is caused by cross-breeding is so enormous that it is almost impossible to exhaust it or fully to explore it.

Chapter Eleven

Somatic Mutations

When we define mutation as an aberration of the usual, normal exact reduplication of every cell when it subdivides, mutation can be very different in degree. We saw that occasionally the whole set of chromosomes is doubled with all the genes, and that smaller and smaller irregularities occur, down to the reduplication or loss (partial loss sometimes) of one gene.

Mutations can occur at any cell-division, and, on paper at least, we can distinguish between germinal mutations which occur at the formation of germ-cells and somatic mutations that occur in tissues of the growing plant. In reality it is very probable that mutations that are first discovered when a plant reproduces from seeds may have happened several cell generations before the germ-cells were formed, and that the entire flower or the entire flowering branch may already have had the novel, mutated germinal constitution.

Both in plants and in animals (and in man) mutations are often met with that give rise to changes in larger or smaller parts of the individual. In birds, aberrantly coloured feathers or parts of feathers are often noted. In plants the occurrence of branches, flowers, or even parts of leaves or parts of flowers is often seen differing in some marked way from the rest of the plant. The most striking cases are those in which a plant suddenly produces an albinistic branch, or a leaf, devoid of chlorophyll, or in which a plant with pale pink flowers suddenly produces one

branch with dark-red flowers. Some plants seem much more liable to produce mutated cells than others, or perhaps we should say that some somatic mutations are exceptionally striking. Everybody has seen such bud-sports in winter-flowering azaleas, or in chrysanthemums. Polyantha roses are generally full of sports—half an hour's search in a rose-grower's nursery will always yield at least half a dozen. Some of these consist of changes in flower colour only, others are concerned with shape or texture of the leaf, while others change the whole habit of the shrub.

In potatoes rose-coloured tubers often mutate to red or to white spots. I have some seedlings of the red-berried elderberry that are full of somatic leaf-shape mutations, that give us branches which are more or less laciniated. The Boston fern has produced a great many bud-sports that have been given varietal names. In the propagation of apple-trees and citrus-trees, especially grape-fruit and oranges, we must carefully select the budwood, to avoid sported branches of inferior quality. The same is true with several roses, but especially in the polyantha group.

From the evidence in animals, and in some plants, it seems as if the plants heterozygous for any gene are often giving bud-sports that lack that gene. In other words, the dropping out of one gene from a pair of similar ones in a homozygote (change from *AA* into *Aa*) will not be as likely to strike the eye as a similar occurrence in a heterozygote (*Aa* into *aa*). In birds investigations of somatic mutations affecting colour have shown that both sorts of somatic mutations—*Aa* into *aa* and *AA* into *Aa*—occur with equal frequency, but that in certain cases the effect of the mutation may be inappreciable. In animals somatic mutations seem to consist in losses of genes, or perhaps sometimes of chromosomes, and it seems probable that the same thing may occur in plants.

If it is true that a plant which produces somatic mutations is generally heterozygous in respect to the gene involved, it would follow that the same plant would very probably produce the same novelties from seed. For this reason I often recommended the sowing of spontaneously produced seed to the nurserymen and amateurs interested in novelties in polyantha

roses. It seems that here at least there is a parallel between somatic mutations and recessive novelties segregating out.

In some plant groups bud-mutations are of some practical importance. A great many novelties in the Indian chrysanthemum have originated as bud-sports. The same is true of lilacs and dahlias. In potatoes some clones have given more than one differently coloured variety.

It is not always easy to make use of a " sport " to originate a new plant. A great deal depends on the exact stage at which the mutation occurs. When on a pink potato we find a large red skin-spot, an eye growing out of that spot will very likely give us a red-tubered variety. In our elders it is easy enough to propagate mutated, laciniated branches by cuttings. It is very much more difficult when the mutation occurs so late in the life of the plant that only a few flowers or sectors of just one flower show the novel characteristic. Sometimes the highest bud, closest to the flower cluster, will show the effect of the mutation in baby-roses, so that this bud, when budded into a suitable standard, will give rise to the new variety. If only one flower or part of one flower is changed, it will not be possible to propagate the changed tissue separately. But even then we may take advantage of the fact that the mutation has probably changed the genotype of that one flower, so that seed obtained from it will reproduce the novelty. Again, we may hope that the plant that did give the somatic mutation will do it again next season, especially when we induce vigorous growth by severe pruning.

Most novelties that arise by vegetative mutation remain very constant. The exceptions to this may be, as I suspect, cases in which instability is the result of the presence of tissues of different genetic composition in periclinal chimeras. Such chimeras are very common in certain ornamental shrubs (elders and privet), and they tend to split up into their component parts occasionally.

It may be possible to induce the formation of " sports ". A good example of this is the treatment of buds by colchicine, which may result in a branch or a sector of a branch with an increased number of chromosomes.

Chapter Twelve

Inbreeding and Outcrossing

Inbreeding is really a method of isolation. This can best be seen in the case of plants in which the biology of the flower enforces the pollination of every flower by pollen of that same flower. In a field of soybeans or peas every plant produces self-fertilized seed, and for this reason the population consists of a multitude of parallel lines, each as much isolated from every other one as if it were being grown on a separate island.

In the chapter on purity I have shown a small diagram from which it can be seen that in respect to any gene for which a plant is heterozygous, self-fertilization will quickly cause the population to consist of a majority of homozygotes of both kinds (*AA* and *aa*) in such a way that the remaining heterozygotes (*Aa*) will get into the minority, so that a periodic reduction of the number of plants per generation will make the recessives disappear. This process of automatic purification is a ratchet mechanism, it works in one way only.

If we want to reduce the genetic variability in a group of plants, every reduction of the number per generation helps. In any group there must always be a number of genes in respect to which all the plants are identical and pure. This block of genes is fixed in the material, until we either import new genes (or new relative absences) by crossing with plants outside the group or until a mutation takes place. In plant-breeding operations within the group this block of common genes must

be accepted as such; as far as variation goes we are not much more concerned with them than so far as they furnish the background upon which other genes (or gene-deficiencies) act.

In any group of plants we want to improve by selection a greater or lesser number of other genes exist in respect to which the group is variable. Some plants in the group may be *AA*, others *aa* or *Aa*, and the same diversity is present in respect to *B* and *C* and *D* and an uncertain number of others. The distribution of the genes over several chromosomes, and the independent distribution of those chromosomes over the germ-cells when these are formed, produce a scattering of such genes (and relative deficiencies). A plant that is simultaneously heterozygous in respect to six genes, will make $2^6 = 64$ different kinds of germ-cells in respect to those genes, whereas in all of them the common block is present. The effect of this is that whereas some plants may be pure in respect to *A* (either *AA* or *aa*), others may be heterozygous (*Aa*). Plants may be homozygous for three or four of the six genes and heterozygous for the rest of them; and if the number of genes concerned is very large—as it probably always is in cross-bred plants—no two of the plants will have the same composition. If we take just one plant out of the number, this plant is almost certain to be homozygous for a number of such genes. This means that in such a plant the block of " stable " genes is proportionately large. I have used the term " potential variability " for the number of genes in respect to which a group of plants or one individual is not pure and homozygous. Using this term we can say that one single plant always has a smaller potential variability than the group from which we take it.

To a smaller extent the same is true of a group of two individuals chosen from among a multitude, and for *any* restricted group. For this reason any group of plants or animals which is somehow isolated from intercrossing with other material, must automatically become purer and purer, unless the group which in any generation has any offspring happens to be completely representative of the population.

This reduction of the potential variability as a result of the chance composition of the group of individuals actually taking part in propagation is a phenomenon which allows of

movement in only one direction. Without cross-breeding (or mutation) the potential variability of a group will always tend to diminish. In fact, I have taken this process as a criterion for the status of a species (or subspecies), saying that we must speak of species when we are dealing with groups of individuals which are so situated (isolation) and so constituted (being variable) that their potential variability tends to diminish, and that they become more and more pure for one set of genes (and for one specific type).

When we are importing a novel plant from some foreign country, it is wise to take a large number of very diverse plants. But if we do this it is also wise to isolate each individual from all the others, because if we do so we are very much less bothered with an excessive variability. If we have several kinds, we may always, when necessary, cross them afterwards.

Any single plant we choose out of a variable lot *must* have a restricted variability. In plant breeding we are generally concerned with two desiderata: with quality plus purity. For this reason a combination of selection and isolation will often bring us excellent results.

Isolation, if repeated through several generations, always spells inbreeding. If we start with an isolated group of four or five excellent plants, we can avoid inbreeding for one generation, by interbreeding those five plants (although it is always possible that they were related to start with). After a few generations—depending on the size of the group—we are constrained to breed related plants together.

If we isolate just one single plant, the only way to proceed is by means of self-fertilization. If our plant was excellent as an individual it may be that it is not only pure in respect to a number of useful genes (and deficiencies) for which the group was variable, but in the variable " lot " of genes it may contain the right material from which to build the ideal plant strain.

It stands to reason that a plant that is heterozygous for a number of genes will make a great many differently composed germ-cells. Let us examine the process of inbreeding in detail in such a case. Let us assume that one plant is still heterozygous for four genes (*Aa*, *Bb*, *Cc*, *Dd*) and homozygous for all the rest. Let us suppose that *A* and *B* in this case are desirable

genes, whereas *C* and *D* happen to be undesirable. The plant makes sixteen different kinds of ovules, and sixteen different kinds of pollen—namely, *ABCD*, *ABCd*, *ABcD*, *AbCD*, *ABcd*, *AbcD*, *abCD*, *AbCd*, *aBcD*, *Abcd*, *aBcd*, *abCd*, *abcD*, *abcd*, *aBCD* and *aBCd*. They can be recombined in $16^2 = 252$ different ways. Of all those possible genetic compositions, only one (*AABBccdd*) is ideal. This means that in such a very simple case we would have to grow a few hundred offspring plants from our one chosen one, and that we would have to inbreed a great number of good ones from among this lot in order to find the ones that are homozygous for both *A* and *B*.

But it is also obvious that in a case where the number of offspring tested was insufficiently large our ideal plant would not happen to be produced. In this case we assumed a number of only four genes; if, however, this number is much larger, the number of plants that has to be grown from inbred seeds must be tremendously large.

It is obvious that selection for the good qualities may help us to find the good plants, and it is also clear that to a certain extent we could save space in our fields by spreading the process of purification over a number of generations. So long as in the hypothetical case a plant is not homozygous in respect to an undesirable gene (*CC* or *DD*), it can still give *ccdd* descendants, and even if the desirable genes *A* and *B* are present only in a heterozygote, *AABb*, *AaBB* or *AaBb*, we may still get our homozygote *AABB* among its descendants. If we can *see* the presence of undesirable genes, we can save a great deal of space by throwing out all the plants showing the action of either *C* or *D*. And conversely, if we can see the presence of *A* and *B*, we need not lose them. The difficulties in such strict inbreeding are due to the fact that we can never know the number of genes concerned. For this reason we can never know how many plants to grow to be on the safe side. Another difficulty may be the result of the fact that we are dealing with desirable and undesirable genes that affect the end results of the development only slightly or in ways which cannot easily be appreciated. Three or four genes may work in the *same* or in *opposite* directions—in fact in many genes this is the rule rather than the exception.

When we are inbreeding just one particularly good plant from a somewhat variable lot we never know for how many genes this plant is heterozygous. But when we start our inbreeding work with plants which are the result of a deliberate cross, it is easy to see that the number of genes concerned is probably colossal. When we cross two species or two rather pure commercial kinds of agricultural plants, we know that in each of those species there is a block of genes for which every plant is homozygous. But when we are crossing two different varieties or species, this block of genes in one group is likely to differ from the block of stable genes in the other group, so that our hybrid is heterozygous in respect to a very large number of additional genes—all the genes which are not common property of the two species crossed.

In order to understand the danger of " inbreeding degeneration " we can use the following simple calculation. Let us suppose that a hybrid plant is heterozygous for a number of desirable genes, and that in the case of each of such genes the corresponding recessive form (*aa*) is somewhat inferior in quality to the *Aa* or *AA* individuals. This means that in respect to gene *A* three-quarters of the next generation will be somewhat superior in quality, and only one in four will be somewhat less good. If we are dealing with a case in which this same thing is true in respect to a second gene, *B*, the result will be that $\frac{3}{4} \times \frac{3}{4}$ will be better than the remaining plants. Now we are dealing with an unknown number of similar cases, but this number may very well be on the large side. If we are dealing with only five genes, $\frac{3}{4} \times \frac{3}{4} \times \frac{3}{4} \times \frac{3}{4} \times \frac{3}{4}$ will be excellent, but this is only $\frac{243}{1024}$ or one-fifth, and for eight genes it is $\frac{6561}{65536}$ or, roughly 10 per cent. of good ones (and the rest inferior).

This means that inbreeding must necessarily often make an inbred generation markedly less good than the preceding one—less well adapted to life. Degeneration by inbreeding is almost unavoidable.

In one of the other chapters I describe a plant-breeding method in self-fertilizing plants in which we produce a hybrid, grow a second generation, and leave the automatic reduction of the potential variability of a great many pure lines wholly to chance. I will come back to this method in a special chapter.

It will suffice to say here that if we are working with relatively restricted numbers, this method is a lottery with very many blanks and very few prizes.

In one actual experiment with garden beans a hybrid plant bred from a bush, speckled bean and a climbing, white-seeded green bean was found to produce more than a pound of dry ripe seeds. Next year we sowed all those seeds—over six hundred—and found that we needed two hundred seeds to produce just one second-generation plant that reached the production of the original hybrid. If we had sown the usual small row of beans we would almost certainly have found nothing but a very mediocre lot.

In plant-breeding work with beans and peas, barley and wheat, most firms work in such a way that they make a great number of crosses each season; they grow a few hybrids, and sow a small handful of second-generation seeds. The result is almost always that only a very few of those cross-breeding experiments ultimately produce anything of commercial value—anything better than the original sorts crossed. I think the preceding explanation will make it clear to most of my readers why this must necessarily be so. The majority of cross-breeding experiments are simply doomed to failure by the fact that, to save space and money, the number of F_2 plants taken is much too small. It would be infinitely better to make fewer crossings, choose the material well, do all we can to make the hybrid plants produce a great number of seeds and to sow an enormously large second generation. A preliminary selection in this second generation will help us to reduce the number of lines, and after this we may very well leave things for a few generations (in a habitually self-fertilized plant).

Blind inbreeding, repeated for a few generations, will almost always make the material degenerate in all sorts of respects. This is especially noticeable in such plants as rye or maize, and the facts have brought some authors to the assumption that " heterosis " in itself—the circumstance that a plant is heterozygous for a great many genes—produces an invigorating effect. It seems probable to me that this hypothesis lacks all foundation; the investigations by East and Jones and the results obtained in genetic and practical investigations tend to disprove

it. In theory it should be possible to produce pure-breeding inbred lines with the same high production and the same qualities as the original hybrids.

Habitually freely crossing plants are especially prone to degenerate as a result of inbreeding. This must be caused by the circumstance that in those plants all individuals are heterozygous for a great many genes, including a great many desirable ones, that tend towards vigour and high productivity in their combinations.

Habitual self-fertilizers, on the contrary, are resistant to the effect of inbreeding—that is to say, our present commercial kinds of barleys, peas, etc., are composed of individuals that are homozygous in respect to all the genes they possess. This means that our present highly yielding varieties have gradually been selected from among an enormous number of inbred lines. It is very striking to observe second and third generations of plants in habitually self-fertilizing plants. Inbreeding degeneration can be observed in this material just as well as in maize or cabbages. Autogamous plants have become inbreeding-resistant as a *result* of inbreeding. It is somewhat hard for plant breeders to grasp, and more so for animal breeders, that the best remedy against the evils of inbreeding is continued inbreeding. But it is nevertheless true.

Chapter Thirteen

Transgressive Variability

As hybrid plants are heterozygous in respect to all the many genes in which the parents crossed differed, their germ-cells are extremely diverse, and if we grow a second inbred generation from such hybrids the variability is enormous. Not only can we expect recombinations of the qualities in which the plants crossed differed, but wholly new characters may be expected to turn up, and existing qualities may be greatly enhanced in some individuals.

When most geneticists thought of the genes as determinants, each for a definite and separate " unit character ", this was rather surprising. But gradually we have learned that the relation between the individual genes and the qualities of the plants is very much more complex. In so far as we can say that a certain character in a family of plants is inherited, we mean that the co-operation of a series of genes starts some development processes that will result in certain qualities.

For a plant to show a certain definite quality, a long chain of processes must first occur, and in that chain a number of genes take their appropriate place. Only if in a group of plants the set of genes of all is essentially equal, a difference in one single gene may give us a case of a clear-cut monofactorial Mendelian segregation. In a cross involving a long list of genes such cases are exceptional.

In some cases genetical difference in the plants crossed involves two or more genes that have their place and function

in a chain of genes determining a chain of reactions and developmental processes. Let us use an example from the inheritance of colour differences. One plant group may have white flowers instead of coloured, because of the ten or fifteen genes that must all co-operate in the development of colour; gene *A* is absent, the plants being *aa*. In another strain the plants may be *AA*, but they are white-flowered because, instead of *BB*, they are *bb*.

When now we cross-breed those two strains—the *AAbb* and the *aaBB*—one of the complete set of genes necessary for the chain of processes resulting in pigmentation is re-established, because both *A* and *B* are now present. In this case the hybrids will bear coloured flowers.

Cases in which first-generation hybrids show a quality that we do not see in the parents, or in which a quality is shown to a much greater degree than in the parent strains crossed, are very frequent. In the experiments of Belling with velvet bean crosses, hybrid plants were sometimes covered with a coat of stinging hairs, such as we meet in wild *Stizolobium* species, but not in cultivated plants of this group. Occasionally crosses between soybean varieties may give us very tall, climbing hybrid plants, and the well-known cases of " hybrid vigour " really belong in this same class.

In certain instances novel qualities are found in hybrids, that can be utilized in fashioning profitable new plant-strains. A greater yield or a better disease resistance may often result from a cross.

Whereas here we have been speaking of novel dominant qualities, there also exist numerous cases in which unexpected and wholly new recessive qualities result from cross-breeding.

When we grow a large F2 generation from some cross between wheats or between maize strains, it often happens that in the F2 generation a small minority of plants are devoid of chlorophyll and die.

The explanation of this unexpected production of recessive novelties is as follows. Let us take an example from Meunissier's *Argemone* experiments. In one species the plants bear single flowers instead of double ones because they carry a gene *A* instead of *a*, and, together with all the other genes in this species,

A helps to make the flowers single instead of double. In the other species the plants are *aa*, but there there is a different gene (*B*) which is responsible for singleness of flowers. The hybrids are all single-flowered, as they carry both *A* and *B* (*AaBb*). If we breed a second generation, most plants will carry either *A* or *B* or both, but as 25 per cent. of the germ-cells will be *ab*, one plant in sixteen will be *aabb*, and will for this reason bear double flowers.

This production of double recessive novelties is not always as clear as in some examples. But those examples (and I have met with very clear-cut ones in animals) explain very well how cross-breeding, even between plant groups which are quite alike in some common quality, will give rise to F2 segregants that show an alternative quality that is new for the group. It is quite possible that, especially in plant groups where chromosome sets have been doubled, we are sometimes dealing with the identical gene, located on different chromosomes, but this is a technical nicety that need not occupy us here.

So much is certain: crossing is a frequent source of the production of characters, qualities, that are wholly new in the group.

Who would have thought that a cross of the inconspicuous *Argemone mexicana* with *A. platyceras* would produce such an enormously great variability, and would be the means of producing just as many striking varieties as exist in *Papaver somniferum*?

The practical use of crossing in the breeding of agricultural plants lies in the possibility of extending the existing range of variability in respect to such qualities as winter hardiness, disease resistance, earliness and yield.

Transgressive variability, variation extending beyond the range of variation in the species crossed, is very common after cross-breeding. But it is obvious that if we are really out to improve some important quality in a group beyond the present range of that quality, we can only hope to do so if we grow quite a large number of plants during two generations. It is necessary that the breeders of vegetatively propagated plants should begin to understand this. Much too often the breeders of potatoes, apples, roses, strawberries, expect to find the results of

their crosses in the first generation, and if there is nothing of great merit in the crossbred group they tend to discard it. They should always, when making a cross, try to grow a large number of second-generation plants from those hybrids. This is especially so when they are trying to find plants that exceed both parents in some important quality—in disease-resistance or yield in potatoes, in productiveness and flavour in strawberries, to name only a few examples.

When we are working with plants that have been crossed and recrossed and variously combined before, our chance of producing something entirely new and of outstanding merit may be small. But when we succeed in finding material to work with that has never been used before, we can always hope that in large sowings, and especially in the second hybrid generation, the desired quality for which we are breeding may be better than the best we know in either parent.

Chapter Fourteen

Purity

Plants are almost always used in groups. It is of great importance that such groups shall be as uniform as possible. When we have a very uniform group of plants that all need the same number of days to mature, there is one most favourable day to sow, and all the plants are ripe for harvesting at the same time, so that methods of mass harvesting can be used. In an uneven field the first plants may have scattered their grain before the majority are ready for harvest, and some of the late-maturing plants in such a field are cut while they are not yet quite ready. When the quality differs from plant to plant it is evident that a great improvement would result from having all the plants of the quality of the very best in that group.

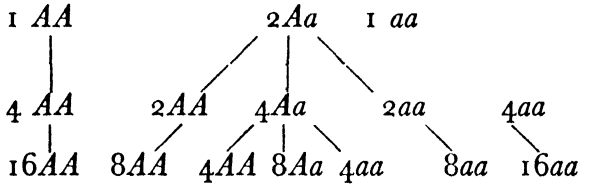
One important object of plant breeding is to produce excellent plants, but immediately after this comes the need for purity *and* uniform good quality.

Many cultivated plants are quite variable. This variation may be of two kinds. We may be dealing with *multiformity*—the existence of plants belonging to different groups in a mixture. In other cases the *variability* may be due to *impurity*—to heterozygosis—to the fact that most plants are impure in respect to many of the important genes that help to give them their quality, and for this reason give a very variable offspring.

In some of our most important cultivated plants—the cereals—we are frequently dealing with strict self-fertilizers.

In such plants as barley or wheat or peas, variation in a field is generally due to the simultaneous presence of a large number of separate lines, each very pure. Land races of wheats are often composed of many different lines, and great progress can frequently be obtained by separating these lines and finding the most profitable. Why do we find such pure and uniform lines in our self-fertilizing plants?

Let us suppose that we have a plant which is heterozygous in respect to a number of inherited factors. To follow what happens it is best to give our attention to only one of them, ignoring the others. We suppose the plant to be heterozygous for a gene *A*, *Aa*. Such a plant will give two kinds of egg-cells and two kinds of sperm, in both 50 per cent. *A* and 50 per cent. *a*. This means that the offspring of this heterozygous plant will be composed of plants which in respect to this one factor fall into three categories, *AA*, *Aa* and *aa* in a certain proportion, in this case one *AA* to two *Aa* to one *aa*. Now, for the sake of a possible calculation we will assume that each plant in every succeeding generation will produce four descendants. The one *AA* plant will produce only homozygous offspring; it will give four *AA*'s. The *aa* plant will also give four *aa*'s. But the two *Aa* plants will again give four *AA*, four *Aa* and two *aa* offspring. If we go on with a few generations we obtain:



This means that the proportion of heterozygous plants (the *Aa*) will get proportionately smaller compared to the homozygotes (the *AA* plus *aa* ones). This proportion declines from generation to generation as 1/1, 1/3, 1/7, 1/15 and so on. In *n* generations it becomes one to 2^n minus one.

Now, it is clear that this is true only so long as every plant has an equal number of offspring. The homozygotes on self-fertilization will give nothing but homozygotes, the heterozygotes (*Aa*) will always produce also some homozygotes. If

for any reason in any generation only a few plants propagate, the chance that the heterozygotes get lost entirely and only homozygotes continue becomes great. This is especially true in later generations, in which the proportion of heterozygotes becomes very small.

What is true in respect to one gene (*A*) is equally true in respect to *B*, *C*, *D* and all the other genes in respect to which heterozygotes occurred in the group. The result is, that if we continue to breed from a group of self-fertilizing plants, even if the material we started with was heterozygous for many genes, after some generations every plant in the group will be homozygous for all the genes it happens to possess. The actual genotype of the plants in the group may differ from plant to plant, but every plant will be homozygous for the genes it has.

It is a fact that even if we start with a cross between two peas or two varieties of wheat or barley, and grow the miscellaneous collection of plants for half a dozen generations, we finally have a collection of the most diverse plants, each one homozygous for its particular genotype. A field of sweet peas or barley or peas will often consist of a great many pure lines. Every plant, when we sow its seeds separately, will produce offspring like itself, and it has often been shown that this is a good method of obtaining excellent results in plant breeding. If we start from a land race of wheat or barley and sow the seeds of a great many plants separately in rows, those rows will look quite uniform, but they will generally be diverse in quality as well as in colour and looks. Many of our commercial sorts of cereals or peas or beans have been originated in this simple fashion.

It stands to reason that we can do better than this, if we deliberately cross two good commercial varieties to produce a very variable and diverse hybrid lot, in order to find favourable combinations of genes amongst them. One method has been worked out in practice by Baur and Nilsson-Ehle. This consists of making hybrids, and of growing the descendants of such hybrids for at least half a dozen generations in a mixture, without any selection at all, waiting for the automatic process of purification which I have just described in detail. After six or seven generations such lots are very heterogeneous, but we can

be sure that almost every plant in the mixture breeds true for its qualities. If we make a number of new crosses every year, and add the hybrid lots to our collection of numbers, every year a few of those numbers will be " ripe " for analysis and selection. In the meantime we save an enormous amount of unnecessary work by leaving all selection till the time when purity will be obtained automatically, as in this way the work left is reduced to a simple comparison of pure lines.

This automatic reduction of the variability by means of self-fertilization is such an excellent method that wherever it is possible to use it we must do so. In certain plants, like wheat, barley or peas, the biology of the flowers almost precludes cross-fertilization in the field, and here we have automatic self-fertilization. In other plants where cross-fertilization is the rule it may be possible to force the plants to self-fertilization by bagging them, or growing them in cages, and whenever this is feasible the work of reducing impurity is greatly facilitated.

Continued self-fertilization in habitually cross-fertilized plants like maize or rye brings its own peculiar difficulties. In those plants heterozygosis for many different genes is the rule. For this reason it is possible that the homozygous gene combinations we obtain by inbreeding are to a great extent unfavourable. It is a fact that continued inbreeding without selection (blind inbreeding) in maize almost always leads to a very great diminution in yield. The same is true of rye and of sugar-beets. In other chapters we will discuss such difficulties and the best ways to overcome them.

Although great purity and uniformity in agricultural plants have their obvious advantages, there may be one drawback to the method of growing just one pure line. This lies in the fact that such a pure line is but little adaptable to changes in conditions of culture and growth. In different climates and with different plants it has often been found that a deliberate mixture of two very slightly different pure lines will produce a better harvest than either of the two lines separately. In France this was extremely striking when we compared the very similar wheats " Bon Fermier " and " Hâtif inversable." These are two semi-winter wheats with very stiff straw and white seeds, that mature in the same number of days. It was found that a mixture of

50 per cent. of each kind would yield something like 10–15 per cent. more grain than neighbouring fields with only " Bon Fermier ", or with " Hâtif inversable " exclusively. The possible explanation of such cases may be that each kind is adapted to slightly different conditions of moisture or of plant food, and that even in a well-tilled field such conditions differ slightly from plant to plant. In so far as this is the case in certain parts of the field, the plants of one kind will be able to profit more than the others, and in other small spots the plants of the second variety will stool out more.

Koch in Buitenzorg, Java, found exactly the same thing in rice, mixtures of certain lines producing more than similar fields of just one pure line in the same season. In plants where yields have been brought up to a high standard of excellence, and where differences between named varieties have become correspondingly insignificant, progress can sometimes still be made by a judicious combination of pure strains.

We must carefully distinguish between uniformity and purity, for the two are not necessarily alike. It is true that a field of plants which are all homozygous in respect to their genes will in good conditions be uniform, but frequently a hybrid lot will present a great uniformity. This is generally the case when two different breeds are crossed. Even if both kinds are rather variable, the lot of the first generation may be strikingly uniform. In later chapters we will come back to this; as the production of first-generation hybrids has been found to be an excellent method in plant breeding. In this chapter it suffices if we point out that great uniformity does not prove genetic purity.

Chapter Fifteen

The Origin of Cultivated Plants

Our cultivated plants are descended from wild ancestors. In plants we can, without much trouble, take any wild plant and grow it in our gardens if we know how to give it what it wants in the way of soil and plant foods. But a wild plant grown in a garden cannot rightly be called a cultivated plant. The only definition which satisfies me is the following. When we have plants whose genotype (inherited constitution) has been so modified that they can be profitably grown, and so that they are adapted to cultivation, we may call them cultivated plants. Wild-plant populations are often variable, so that it is possible by simple selection to find a strain which is better adapted to being grown for profit than the original wild population. If in forestry we import some seed of a non-indigenous tree, some seedlings will thrive much better than others, and even unconscious selection will speedily produce an improved population in the first generation of cultivation—a cultivated plant.

When we grow some plant species in our gardens, selection will soon change the original lot into something better adapted to our special conditions.

Cultivated plants will often be adapted to very special and frequently very trying conditions. I have seen wheat-fields, flooded for several weeks on river-bottom lands, survive this without drowning. Meunissier tried a dozen different kinds of wheats in flower-pots, and found that only this one particular

variety could stand submerging so long. The same is true of desert conditions. Maize can be grown by some American Indian tribes in a country where sufficient moisture to sprout the seeds is only found one to two feet below the surface. The seeds of this corn are buried deeply, and the seedlings are able to reach the surface from this great depth and to grow into mature plants that produce a crop, in spots where it seems a miracle to find any cultivated plants at all.

In most cultivated plants it is relatively easy to recognize the wild-growing species from which they are descended, but this is not true in all cases. One of the most widely grown plants—maize—has no similar wild ancestors, and it is difficult to understand from what ancestors this plant has been originated. Theosinthe and Gamagrass can be crossed with maize and produce fertile hybrids with it, and it seems possible that species crosses in this group have resulted in so much variability that the *first* strains of maize have originated from them.

Practically all wild legumes have bitter seeds, and it is probable that man has utilized chance variants to produce his edible peas and lentils from inedible wild stock. The sweet lupins are recent examples of novel cultivated plants. Tens of thousands of seeds were tested by German and Russian plant breeders in institutes to find the very few sweet individuals from among a host of plants with quite inedible seeds.

Some cultivated plants are of great antiquity. Flax, cotton and maize are extremely old. The presence of highly developed and very rich kinds of sugar-cane in the hands of New Guinea cannibals is a mystery. It seems almost impossible that these men have succeeded in originating those kinds of cane from the wild material of their own cane-brakes; it seems more probable that their species have been imported from some more civilized country, and have only been kept on by the primitive natives.

The long list of useful cultivated plants can still be added to. Many very useful plants are not yet cultivated, or they are being grown without any change from what they were in nature. It certainly pays to give sufficient attention to such plants as derris-root and some of the annual rubber plants.

The same is true of some of the medicinal plants that are now gathered from the wild.

In the case of vegetatively propagated plants it is only necessary to find one excellent, outstanding individual in order to be able to produce clones of greater value than wild material. Recent examples are those of derris and of the blueberries, most of which are still found as outstanding individual plants in wild populations.

In the evolution of all plants—and the same is certainly also true of cultivated plants—isolation is a factor of very great importance. We must always remember that each group of plants has only a limited variability, given by the combination of genes present in it. In many cases one group is more successful than other groups, and the better groups will expand, whereas the less successful groups go to the wall. Crossbreeding as a source of variability will make it possible for new variable groups to come into existence, and, after all, there is more competition between groups than between individuals.

When for any reason a small group of plants is split off from a much larger group, the small group will have a smaller variability than the large one, and evolution is a process of growth and of dying out of groups.

A plant species or a cultivated plant is a group which is so constituted and so situated that its variability (potential variability) tends toward reduction.

Cultivated plants live in symbiosis with man. Both the plants and man profit from the association; the plants are protected and tended, and sometimes they are of such a constitution that they could not survive at all outside of cultivation. This is certainly true of such plants as are not naturally winterhardy. In some cases the capsules of cultivated kinds of plants do not set free their seeds. Some sorts of cultivated poppies or flaxes would certainly not survive one generation of wild life away from human care.

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Both from a scientific and from an agricultural standpoint the question whether cultivated plants are generally monophyletic or polyphyletic, whether a group of varieties originally came from just one wild-living species or from a combination

in identical circumstances. In plant breeding it is sometimes very profitable to use methods of vegetative propagation, sometimes alternately with propagation through germ-cells.

When we study the occurrence of different varieties or clones of cultivated plants we are always struck by the fact that in certain localities an enormous multiformity is seen. We produce such a multiformity of plants artificially when we deliberately collect different kinds from all over the world—the plant collections (*écoles*) of the plant-breeding firms and the institutes. But in other instances we find geographic regions where a great many different kinds of some of the cultivated plants exist together.

In such districts we may find that many rare genes are present that we find nowhere else, and it would be attractive to speculate about the possibility that in those regions we were dealing with the effect of mass-mutations in the sense of de Vries. Vaviloff, who has done more than anyone else to draw attention to the existence of those " gene-centres ", has shown the importance of such centres for the evolution of our cultivated plants, and he is responsible for the hypothesis that the chief centres of the evolution of our cultivated plants are in those localities.

No matter where we look into the assortment of breeds of animals and kinds of plants, we always find a tendency for less important kinds to drop out of the running. The assortment tends to become poorer. On a small scale we can see this process in our own gardens. If we do not from time to time deliberately buy some novel dahlias or perennials or plants for our rock garden, our collection becomes less multiform from year to year. Especially when we are dealing with economically important horticultural and agricultural plants, the less important kinds tend to disappear, and only the better sorts tend to persist in the long run. Why is it that in different localities such a great assortment of breeds happens to co-exist?

The answer to this question is, I think, relatively simple. If we look at a world map for the location of our " gene-centres ", we always find that they are located in the mountains. When we study the agriculture of a well-populated

mountainous district, we generally find that each separate valley is a more or less isolated community. The inhabitants of each valley tend to wear a local variation of the national dress. We find that the dogs, the goats, the chickens, the potatoes, the wheat of one valley differ from those of the next one. Steeper mountain ridges are better barriers than shallow ones, and the more primitive the culture the more isolated these communities are. In a continuous large plain the intercommunication between the townships is much more regular, the markets serve a much larger district, and as far as the animals and cultivated plants are concerned, there is continual competition between varieties and breeds, and this competition tends to make a few fashionable kinds take the upper hand and to cause smaller local breeds to disappear. In the mountains a plant that is grown in a few dozen acres only, or an animal breed of which only a few dozen exist, is not for this reason swamped by greater and more prominent groups.

In each valley there may be considerable variability, and even some multiformity. But in each valley the potential variability in each group must be restricted. Such mountain breeds tend to be somewhat less variable than widely grown valley species: the restricted range makes for a more intensive reduction of the variability—for more inbreeding. Sometimes such mountain breeds of animals or plants happen to be pure in respect to very peculiar characters: many genetic peculiarities must be preserved in a region which consists of a multitude of mutually isolated ranges.

From the standpoint of the evolutionist the study of animals and cultivated plants in such regions as Abyssinia or the Andean valleys, or even nearer home in Switzerland or the French Jura, is very interesting. I doubt whether the presence of such a multitude of rare genes makes it probable that those genes originated where we find them as a result of mass mutation. Among the peculiar qualities of the multitudinous cultivated plants of such mountain regions the plant breeder may find that many are of no special economic value. The isolation from the swamping effect of wider competition may happen to preserve them. Sometimes, however, we may find among such local species qualities that are of great economic interest.

Not only that; it is very probable that among the multitude of cultivated plants surviving in mountain valleys a few happen to fit into a much more extensive system of agriculture elsewhere.

As far as the allogamous plants are concerned, it is possible that in such districts we may meet with populations of rye or maize that are more resistant to inbreeding than the populations commonly used as material for selection work.

Chapter Sixteen

Periclinal Chimeras

If we examine the growing tip in a bud, we see that it is composed of rapidly growing layers of cells, one superimposed upon the other. During the growth of the bud and its differentiation into leaf-buds those layers of cells tend to retain their identity, their mutual independence.

This can be seen whenever the outer cell layers of a plant have a distinct colour. The best-known example of this is that of the well-known albomarginata varieties of many plants. In those plants the leaves have a neat white margin. If we examine cross-cuts of those leaves under the microscope, we see that the outer layer of cells of the plant are lacking in chlorophyll, whereas the more deeply situated cells are normally green. The white margin results from the circumstance that the leaf is thicker in the middle than around the edges, which, being composed of only the outer top and bottom layers, consist of those whitish cells only. In fact, the plant is seen to be composed of a normal green plant in a skin of chlorophyll-deficient cells. In some plant-groups, as in pelargonium and privets, all sorts of different " marginata " varieties are met with—plants in which the two outer cell layers are white, those in which the outer layers alone are green and the rest of the leaf white (in which plants we see a whitish leaf bordered with green).

This independence of the superimposed layers of cells in a plant may sometimes be of a very peculiar kind ; many

instances are known in which those cell layers belong to different plant species. One of the best-known examples of this is *Cytisus adami*. This is an ornamental tree that looks like a flesh-coloured variety of our common garden *Cytisus laburnum*. In fact it is a tree of this species, with the exception that its epiderm belongs to the species *C. purpureum*. We can discover this by sectioning the flowers, but we can also discover this from the circumstance that occasionally something seems to happen to disturb this regular association of the two kinds of cells. Almost any tree of *C. adami* forms very vigorous branches that the colour and markings of the flowers show to be unadulterated *C. laburnum*. Occasionally the epidermal *C. purpureum* layer seems to give rise to a bud, for in a tree of *C. adami* we may find dense globular bunches that are very much like the small shrubs of *C. purpureum*.

Other chimeras of a similar constitution are known. The medlar and the hawthorn are the components of two different combinations, the one having one single layer, and the other having the two outer cell layers of medlar over a hawthorn-tree. It is very probable that many more varieties in ornamental shrubs are in reality of a similar constitution.

Winkler has shown experimentally how such combinations may be formed. When we graft *Solanum nigrum* and tomato one upon the other, and later cut through the stem where the union has taken place, we obtain several adventitious buds. Most of these are buds of *S. nigrum* or of tomato, but it sometimes happens that a bud is formed from tissues at the borderline, and that such a bud will give a shoot that is composed of both species, either laterally joined, so that one side is tomato and the other *S. nigrum*, or in the way we have described, as a plant of tomato with an epiderm of *S. nigrum*, or the reverse.

Many well-known plants, especially among the horticultural ornamentals, have this periclinal composition. We may recognize them by the circumstances that either the inner or the outer form occasionally " breaks out ", as in the white-margined forms of spiræa or of elders. We may also find them because of the fact that in most plants the outer layer of cells does not extend to the root system. In such plants a well-known variety may never come true from root-cuttings. Some

albomarginatum varieties of perennials are in this class. One of the spineless blackberries can be reproduced only by layering branch-tips; the plant produces many shoots from the roots, but those shoots are all thorny.

From the experiments of Winkler and others, it can be seen that it would not be difficult to produce periclinal chimeras (or graft-hybrids as they used to be called) experimentally. It can probably be done in all plants in which we can induce the formation of adventitious buds. I can certainly recommend the experiment to horticulturists and nurserymen who are looking for novelties. Plants in which it would probably work well are poplar, elms, maple, azalea, lilac, begonia, ribes.

It is probable that many more of the horticultural varieties are of this type than we now know. In the lilac it is probable that the varieties with white-margined purple flowers are periclinal chimeras. Those plants have a tendency to " sport ", and to produce flower clusters, or parts of clusters, that either lack the white margin or that are wholly white.

Some of the frequently " sporting " varieties are probably in this class, such as some of our pink azaleas, that are always sporting red flowers and flower segments, and I have a suspicion that some of the ever-sporting dahlias are also in the same class.

Chapter Seventeen

Disease Resistance

In practically all our cultivated plants insect pests and infectious diseases can have such an enormous influence on the yield and quality of the product that the harvest may be almost lost. There are always two fundamentally different ways of fighting disease: we may directly try to destroy the pathogenic agents or to remove the source of infection, or else we may try to breed plants that are so resistant that they will produce a good harvest even in an infected field. In practice both methods will frequently be employed simultaneously.

Very often a newly introduced crop will be quite free of disease for a number of years, and suddenly a disease is brought in and spreads like wildfire. Then, if we visit the country of origin, we shall usually find that the disease is widespread there, but that in certain localities good crops are produced notwithstanding the general infection. It is a common rule that we can usually find disease-resistant stocks in the country of origin of a cultivated plant. We have the example of the walnut and chestnut in Eastern Asia, that of the boll-weevil-resistant cottons in South America, mildew-resistant melons in Persia, and wilt-resistant beets in some localities where beets grow wild. If we are lucky we may hit upon a resistant strain that we can use as it is. But as it is only rarely that an imported plant can be used without any change, the possibility of finding a ready-made profitable resistant one is slight. We

must try to transmit this disease resistance to our plants of high quality. This is generally a cross-breeding job.

With very few exceptions, disease resistance seems to be a dominant quality. In the cases in which this is true much work and space can be saved by one or two back-crosses. It is unnecessary to grow all the second-generation plants required to obtain the rare specimens that reproduce the useful qualities of our valuable line in their entirety, while selecting for good resistance at the same time. We can, by back-crosses to our valuable strain, reduce the potential variability of the hybrid group, so that our work is considerably simplified (see Chapter XXXIV on Back-crosses).

To facilitate the work, artificial infection is generally best. In working with well-defined diseases, such as grape-mildew, curly top in beets or warts in potatoes, it is very satisfactory to have some thoroughly infected fields in which we can test our promising numbers.

Erwin Baur in his Müncheberg plant-breeding station had some special greenhouses in which, by means of steam blown from pipes, he could create ideal conditions for mildew infection of grape seedlings. Tens of thousands of seedlings were artificially infected here, so that almost all of them died. The few that resisted the infection were then planted out to be tested for other commercial qualities. When I saw this work, all the hundreds of thousands of seedlings that year were grown from washed seeds of one well-known wine-grape.

In Holland during recent years all promising potato seedlings have been tested as a matter of routine in a well-infected field by Dr. Oortwyn Botjes. Only if the clones stand this infection and remain free from warts further tests are made with them.

In such matters as resistance of cotton to boll-weevil and resistance of maize to corn-borers the resistance may be due to several different things—to actual inability of the pest to penetrate, or to physiological differences which make the plant early enough or late enough to escape heavy infestation.

Sometimes a whole group of varieties of one plant is found to be insufficiently resistant to a common disease. In such cases, like that of the white dried beans of commerce, the

obvious solution is to reconstruct the varieties from cross-bred material. In beans, *Phaseolus multiflorus* happens to be immune from most bacterial and virus diseases to which garden beans are heir. Hybrids with this species are highly sterile, but sufficient fertility exists to make it possible to use the species hybrids in back-crosses in our search for disease-resistant beans.

What I am going to say now may seem so self-evident as to be superfluous, but I know from experience that my warning is actually necessary. When we do succeed in finding our first plants that happen to be completely resistant to a disease of great economic importance, we may start off from such plants to make new strains in which we shall not be bothered by our previous trouble. But we must *not* lose sight of the fact that our aim should never be disease resistance as such, but better harvests, partly due to resistance. In fact, in the breeding of curly-top-resistant sugar-beets I would certainly not place too much importance upon the presence or absence of disease symptoms in the plants in our experimental plots. In a case like this I would always counsel the breeders to work in a region where the disease gave trouble, but for the rest, to select their family groups simply for yield and sugar percentage, or, simpler yet, for sugar per acre. If they do this, the susceptibility of certain plants to the virus, in so far as it is a factor in lower sugar production, will be adequately taken care of, and by the time we have obtained a sugar-beet with a good yield it will probably be resistant. With the other method we may very well end with families that are completely resistant to curly-top but that are not good enough to be grown for sugar.

Disease resistance of plants against filterable viruses brings us some very peculiar problems of great scientific and practical interest. A virus is not an extremely minute micro-organism. It is a substance that has the property of reproductive catalysis. That is to say, a minute quantity of such a substance—even one molecule—will, if building-stones for its synthesis are present, help to build up another molecule that is in every respect just like itself. In this fashion the substance remains qualitatively stable, while increasing in quantity.

It is probable that the genes in the plant-cell nucleus have an essentially similar nature; and it is very probable that the protoplasm of the cells outside the nucleus contains a great many similar substances—substances therefore that are to all intents and purposes viruses.

Now, a virus by definition is something noxious. There are no non-pathogenic kinds of virus, for the simple reason that we only recognize the presence of a virus by the symptoms its presence in the plant produces.

Cross-breeding experiments of Michaelis and others have shown that in the cytoplasm outside the nucleus substances are present that are partly responsible for the qualities of the plants. Such substances show a purely maternal inheritance. The case of the partially white Japanese hops is a very good example. Here we find that seedlings from a piebald plant are always spotted, no matter how the father was, and, conversely, a solid green mother-plant will never give spotted seedlings, even if the father of those seedlings was spotted with white.

It is evident that from the existence of such visible cytoplasm-constituents to that of a great many others that are not quite so manifest is only a small step. I do believe that there is only a partial and gradual difference between such plasma-constituents as are normally present in the plant-cell and a virus that is not normally present.

There are some facts that throw a curious light on the subject. I am speaking of the case of the so-called " latent viruses ". Sometimes, if we graft a piece of tissue of a potato variety A into the stalk of a variety B, this latter plant may develop symptoms of a virus disease. In fact it will soon be so full of virus that its juice introduced into another susceptible plant will give this new plant the disease. Now, there is more than one way of explaining those facts. A plant pathologist would speak of a virus, and say that plant *X* contained the virus, but that it was immune to it, or else that it carried the virus in a " latent " condition—whatever that might mean.

I prefer to state things in a different way. I would say that the substance transferred from *X* to *Y* must be called a virus when it is present in the cells of *Y*. Its presence disturbs

the health of the plant, its growth in the plant-cells unbalances its processes of life and growth, but I would prefer to say that in the cells of strain *X* the same substance was one of a great many normally present autocatalytical substances, an active participant in the complicated processes of growth and development. In other words, it does not seem to me difficult to assume that the same substance that is a normal constituent, growing and co-operating together with possibly hundreds of other somewhat similar substances in the cells of some plants, may, when brought into the cytoplasm of a different plant where it does not "fit", assume the nature of a pathogen. This hypothesis—that a plant virus is a constituent of plant cytoplasm in the "wrong" environment—would explain a great many apparently unrelated observations. A comparison with another example of a thing in the wrong place will perhaps help to make clear how I picture the virus situation. The fauna and flora of a country may be in a state of equilibrium, and while some of the animal species are quite fertile, they do not tend to swamp everything. The rabbit in England can be used as an example. When it was introduced into Australia, into a set of plants and animals different from the one in which it had its minor niche, it quickly over-ran the place.

Virus resistance is generally dominant. This may mean that in some plants the substance, if it is present in the cells, is either used up in the synthesis of an additional gene, or that it takes its place in the list of the very many cytoplasm-constituents, and plays its minor role in the simultaneous synthesis of all the many substances in the cells.

The search for disease-resistant plants will never end, for as soon as we have an assortment of valuable plants resistant to the common disease of to-day, new bacteria and new viruses will make their appearance.

As a general rule it seems probable that cross-breeding with widely separated species, and especially with wild-growing species, promises most in our search for new, disease-resistant plant strains. In any event, testing new plants for disease resistance is of the very greatest importance. This is especially so in the case of virus troubles, because even if we can combat a fungus or bacterial disease with appropriate sprays, virus

diseases are very little affected by such methods. The testing for disease resistance can generally best be done by growing the numbers to be tested in proximity to diseased plants and on infected fields. Some precautions are indicated to avoid the spreading of such diseases to hitherto healthy stocks.

Chapter Eighteen

Adaptation to Special Conditions

Every plant that grows in a given locality is adapted to the conditions there. This means, among other things, that its growth-processes are geared to the annual cycle of the seasons. Its developmental cycle must be finished between spring and the coming winter. The conditions of temperature, moisture and light must allow it to grow, to flower and to mature. Among those influences the daily rhythm of light and darkness plays a very important role.

The majority of plants have a genotype which allows its growth processes and its development to function in an efficient way only if this succession of light hours and dark hours in the seasons is approximately that of the geographic latitude in which we find them growing. One of the best illustrations is the example of the soybean. If we import soybeans from Manchuria, those beans will grow, flower and ripen their seed in the latitude of England or Holland. But if we try soybeans from the tropics, the plants will grow fairly well, but they will not start flowering till the early frosts begin to kill them. In our latitude the Jerusalem artichoke will start flowering in October, and it will not ripen its seeds. The potatoes, both wild and cultivated, that we import from Southern Mexico will grow, but they will neither flower nor set tubers.

When, however, we shorten the length of our summer days by covering the plants with a dark cover, so that the day is reduced to twelve or fourteen hours, both the tropical soybeans

and the tropical potato behave as they would in their native climate.

In our plant-breeding work we meet this difficulty of the adaptation of certain plants to long days or short days, when we want to use imported varieties in our cross-breeding work. We may want to take advantage of the very high frost resistance or the disease resistance of some of the South American potatoes, but if those potatoes do not flower when our own potatoes are in flower, we cannot very well make use of them for crossing. There are two ways out of this difficulty. Sometimes it is possible to import pollen for our purpose, if the flowering seasons correspond sufficiently. Pollen, if kept dry in well-closed small receptacles, will often stand shipment by air mail over quite long distances. The other way is to give the imported plant an artificially shortened day.

In cross-breeding between long-day and short-day plants we cannot know beforehand how the hybrids will behave. It may be necessary to grow them in some locality that will allow them to flower normally and it is possible that the length of summer day they require is not that of our own summer days. In the ordinary process of plant breeding, individual plants and strains that are not adapted to our own seasonal rhythm will get weeded out automatically.

When we are making a cross between two different plants that are both perfectly well adapted to our own seasons, it frequently happens that in the variability resulting from various recombinations of genes in this material, differences occur in the plant's requirements in respect to length of day. It is a common experience of plant breeders working with beans, with soybeans, and even with such plants as sunflowers and wheat, that in the second generation of a cross a number of plants will only start flowering very late in the season when the days are shortening. Such plants will disappear from our experimental plots. In potatoes we often notice that some seedlings will only start developing tubers excessively late in the season. Again, such plants are automatically discarded. I only draw attention to the phenomenon because I believe that in certain instances such short-day plants, segregating out from crosses between two long-day plants, might be of value

when it is our object to extend the cultivation of some agricultural plant to the tropics. I am fully convinced that one excellent method of finding new kinds of potatoes of good quality for the cooler plateaux in equatorial countries (Rhodesia, New Guinea) will be to raise a lot of seedlings from seed gathered in northern climates adapted to the commercial cultivation of potatoes.

Not all plants are adapted to either a long or a short summer day. In some groups the individual plants adapt themselves to both conditions. It is even possible that in plant groups in which we find both typically long-day and short-day varieties some strains may be more or less indifferent to length of day. I am here thinking especially of the potato.

If it were not for the fact that our commonest varieties of crop plants and vegetables of the northern temperate zone were adapted to our long summer days, it would be possible to do plant-breeding and plant-production work in tropical countries where the price of land under irrigation and the pay for labour would make a larger margin of profit possible. Some of the African and American plateaux within the tropics would seem to have conditions of soil, temperature and labour that are ideal for the establishment of plant-breeding centres. The catch, however, is that the ordinary process of selection of plants from variable generations would not automatically result in valuable strains well adapted to growth in a temperate zone.

Any plant species living on earth is sufficiently well adapted to the conditions under which it lives. This is a platitude, for unless a plant is well enough adapted it dies out. In the tropics, where days and nights are of equal length, the plants that grow there can flower and set seed under those conditions of lighting, but the plants of the high latitudes are equally well adapted to very long days in summer and very short nights. Plants from the high north will not grow, and certainly will not set seeds, in our region. The same is true of plants from the tropics, even in the case of those plants that live in extremely cold and high mountain regions. Wild potatoes from the high Andes will grow very well in our latitudes, but they will seldom produce any tubers, and they will certainly not set

seed. Reducing the length of the day by means of shading will suffice to bring them to maturity.

Plants of the desert will be either protected against excessive water losses by plant habit or by waxy or hairy coverings, or else they will be able to penetrate the water-holding subsoil with very long roots. Some plants will stand conditions of prolonged flooding that drown out all other plants. Some of the best examples of varied adaptation of plants to habitat are found in forestry experience. Wherever we try seed of pines of different origins, it is always found that indigenous seed produces the best trees. This is true in Holland, where seed of Finland, Sweden, Belgium and France gives poor trees that have various defects, and where the best pine seed is native seed. But this very good Dutch seed is inferior in Finland to Finnish seed, and it cannot be profitably grown in the south of France, where local seeds produce the best stand of trees.

One of the most striking examples of adaptation is that of winter hardiness. Our local agricultural plants and the local trees are all adapted to rigorous winters. Some plants escape damage from frost by being annuals and surviving the winter as dry seeds. Very often a large number of annual species is found belonging to the same genus that has many perennial species in temperate climes. Some plants are frost resistant, either because their root system opposes freezing out, or because their plant-juices have a high content of solids.

The best examples of adaptation to special conditions are met with in cases of disease resistance. Where any parasite occurs, the plants that are beset by this parasite are found to be able to survive its attacks. Disease resistance may be due to half a dozen quite different kinds of protection. It sometimes happens that a cultivated plant has been transferred from one continent to another, and that after a lapse of years some mould or virus or parasite starts attacking it. We have gradually learned that the only way out in such event is to send an expedition to the country of origin of our plant in order to find disease-resistant stock for importation and direct use, or for cross-breeding. Very often a newly imported species may seem very well adapted to the conditions of its

new home, and yet we find that after a lapse of years something happens that the importation cannot stand. A very good example is that of the French winter wheats in Holland. Once in a while these are winter killed, whereas they can stand the typical winter well enough.

It is seldom that we can find a sufficiently good climatic adaptation in a group of plants imported from a very different climate, but the adaptation of plants to special conditions is just as much dependent on their set of genes as all other qualities. For this reason it is often quite possible to make a success of importation, provided we do all we can to produce a sufficiently great potential variability in the group.

If we want to adapt such plants as soybeans or maize to English conditions, we shall probably find that none of the American or Manchurian races is satisfactory in the climate. The only chance of success can be obtained by cross-breeding such plants and by hoping that the variability will extend to those physiological properties that make complete adaptation to the new climate possible. Quite often this adaptation to a new climate will be automatically taken care of by a process of unconscious natural selection while we are trying to ameliorate the plant in respect to yield or similar qualities. Some groups will automatically disappear because they ripen too late or stand the climate in spring insufficiently well.

In another chapter I have used the example of frost resistance to illustrate transgressive variability. The only way to produce a sufficiently good winter resistance is by making a group of plants variable by crossing. Even a cross between two different, fairly frost-resistant plants may quite well give us some very highly resistant plants in later generations. In this connection I want to repeat my warning never to submit hybrid plants to the conditions to which we desire our novel kinds to be specially adapted. The quality of the first hybrid generation is wholly immaterial.

PART II

MORE PRACTICAL SUBJECTS

Chapter Nineteen

Selection : A. Natural Selection and Adaptation

Plants and animal species always have such an inherited constitution that they can live in the surroundings in which we find them. If they had not they would not be able to live there. If a plant from overseas penetrates into our fields and forests it may fit and survive, or it may not fit and disappear.

The seeds of wild plants are constantly trying to penetrate into such spots as will not afford them a living. We find Sedum plants growing on the top of walls. This does not mean that the seeds of those plants habitually seek out other walls; it is certain that many more dandelion seeds than Sedum seeds are settling on the wall-copings, but only the species which is adapted will survive in such very special habitats.

Every mature plant produces a multitude of seeds, and it is evident, as Darwin repeatedly pointed out, that any species would choke the earth in a few generations of unchecked propagation. Only very few of those seeds will give plants. In fact, speaking as statisticians, we may say that every plant will produce only one mature descendant. We may take this in a literal way, and presume that every plant will be succeeded by just one single descendant, and that this single daughter-plant will be the very best of many thousands. But we know that although this may be correct as an expression of averages, the biological truth is quite different. In reality extremely

few plants have any offspring at all, and the ones that *do*, have many descendants.

If we observe the flora of any region for a few years, we generally see that for a time certain species will take the upper hand, and that the proportion between several species fluctuates, new species becoming prevalent at other times; and it is becoming more and more evident that our older idea of the struggle for life as an actual competition between individual plants for the available food and light does not give us a complete picture of what actually happens. It is probable that the competition in Nature between plants is a competition of *groups* rather between individuals.

Chance rather than actual competition for space and air plays the most important role in these situations. If we have a garden, we know that from season to season the assortment of plants fluctuates. In a collection of dahlias, some varieties get lost, others are taking the upper hand, and it is not always true that two dahlia-plants of different clones are so close together that one wins and the other withers. All sorts of accidents in the cellar during winter, preferences of our gardener, ease in sprouting, etc., determine what finally happens to our collection.

But so much is evident: if we have a collection of the most diverse plants and seeds, only those species which will stand our treatment or our climate will have a chance to survive.

If we sow the descendants of a hybrid wheat plant or of a pea vine, we shall have an enormously variable collection of plants. If we continue to grow this lot in our fields, mixing the seeds and sowing an approximately equal number every year, we shall obtain a collection of very different lines. But those lines after a few years will at least have this in common—that they all of them are sufficiently well adapted to our climate, our methods of cultivation and harvesting, to live as a cultivated plant in our fields.

Plant breeders can greatly profit by this automatic weeding out of such collections. The method of mixing the seed of the descendants of a cross, and of sowing this mixture for a number of generations—six or seven years in succession—will give us two things: *adaptation* as well as *purity* in the lines

that compose the mixed lot. Adaptation is almost as important as purity. If we started our selection according to yield or to colour or to quality immediately after the cross-bred plants gave us our variable lot, we should do a great deal of unnecessary labour. We should very often choose plants that appeared to be excellent, but which had some innate defect which would cause them to die out in some subsequent year in less fortunate circumstances.

The land races of cereals and legumes that we find in the hands of peasants in some backward countries are almost wholly derived from a continued process of this kind of natural selection. Those groups that have done well in the succession of years have taken the upper hand, for the methods of culture are inextricably mixed with climatic conditions. If the seed is always winnowed, numbers with very light or shrivelled seed will be automatically precluded from further propagation; if wheat is grown as a winter wheat, the summer wheat plants will disappear (or vice versa). Such land races generally consist of mixtures of lines that all have the same requirements and need the same time for ripening. Included in the mixture we always find weeds—plants whose seeds pass the sieves and the processes of preparing the seed, whose time of ripening will be the same as that of the main crop. In fields of winter wheat a certain proportion of rye almost always occurs, and oats are found as weeds in barley-fields.

The best results in plant breeding are almost invariably obtained by a combination of natural selection and artificial selection. In the case of a mixture of hybrid lines, derived from a deliberate cross, natural selection will automatically weed out a large number of inferior lines, after which we can select those lines which promise the most (after isolating the descendants of individual plants). The same is true if we start from peasant mixtures. In peasant wheat and peasant barley, we are dealing with a mixture of lines, and here again we can make a choice after isolating such lines for a group-selection test.

Chapter Twenty

Selection : B. The Material for Selection

Before we knew anything about the nature and action of genes, it was generally understood that organisms were plastic and could be transformed by strict selection. At present we know that this apparent plasticity of living organisms to a great extent really is heterogeneity. Selection enables us to separate those plants with a gene from the other plants without a given gene, and if the material is heterogeneous because of the relative presence or absence of ten different genes, we have a few hundred thousands of different gene combinations to choose from.

That we are dealing with diversity rather than with a change of the components can be beautifully illustrated by selection experiments in pure lines. A pure line, according to Johannsen's definition, is a group of plants grown by self-fertilization from one individual homozygous in respect to all its genes. In our cereals—in oats, barley, wheat—we are practically dealing with such pure lines—lines of plants in which every individual is pure, and homozygous for all the genes it possesses. We are used to success in selection, but selection within such pure lines has no effects whatever.

When Louis de Vilmorin started his collection of cereals in a living museum around 1850, he saved a typical ear of each of the kinds in that collection. One day in 1910 Meunissier rediscovered that collection of named ears in an old cupboard, and we were able to make a comparison between the original

ears and their descendants after half a century of selection. During all this time the most "typical" plant had always been chosen to continue the line. In a variety with long, slender ears the longest ears were chosen, in a line with ramified ears, the most beautifully branched ear, and so on. The result of the comparison was that there was found to be not a particle of difference between the old ears and their descendants of fifty generations later!

A very typical example was that of "Talavera de Bellevue." In this wheat ears are often found that have a supernumerary spikelet somewhere along the ear. Such an irregularity was found in the ear of the old collection, and similar ears are still present in the variety today!

It has been shown repeatedly that selection does not change the action or the nature of the genes themselves; it is active only in discriminating between plants that differ in their genetical make-up, in their genotype.

It is true that in most plant species there is no dearth of variability. Yet we must realize that this variability is always restricted and bounded by the possibilities of the material in hand. If we want tall plants we can succeed in combining into one group all the genes that help to make for tallness and in eliminating all those genes which counteract growth. But this is possible only in respect to those genes for which the material is variable.

If we want to enlarge the size of the seeds in soybeans with the aid of Manchurian kinds, we shall never get so far as when we include some of the Japanese large-seeded horticultural soybeans. If we want resistance for some troublesome infectious disease, it is quite possible that with the material on hand we shall never get anywhere. It may be necessary to send an expedition to the country of origin of our plant group to hunt for new material that will enable us to make progress in breeding for resistance.

As we have seen in other chapters, there are two sources of variability: cross-breeding and mutation. Of the two, cross-breeding can be said to be much more important than mutation. For even if we realize that mutation may give us the novel absence of genes, such as we cannot possibly get rid

of otherwise (because all our plants are always homozygous for them), we cannot possibly *direct* mutation ; we must simply take what it happens to give. On the other hand, it is very difficult to under-estimate the amount of variability which can be due to cross-breeding. As we have already seen, cross-breeding will give us very much more than a mere recombination of pre-existing characters. Very frequently novel combinations of genes will give us wholly novel qualities that were not present in the ancestors of our plant material.

Whenever we want to obtain progress by means of selection, the first step is to have sufficient variability, or, if necessary, to create this variability by means of cross-breeding.

It is simply unbelievable what cross-breeding will often do in the way of creating variability. To any plant-breeder I can recommend trying an occasional species cross, and following it up at least through the second generation and with very large numbers. Such a second generation bred from species hybrids will almost always give us a truly kaleidoscopic collection of different colours and shapes and other qualities. Some of those combinations are certain to be non-viable, we shall almost always find dwarfs and distorted plants. On the other hand, a large F_2 generation bred from species hybrids is certain to give us an abundance of excellent material to work with.

This is one of the reasons for the importation of plant material in the interest of agriculture and horticulture. Almost any species or variety is worth while importing, so long as it has never been imported before ; and this is true of insignificant native potatoes as well as of wild beets, bulbs, trees, legumes, flowers, grain.

Species crosses often give us sterile or partly sterile hybrids, but even where this is so, it is very much worth while to try to obtain some seeds or some viable pollen from such hybrids. Once the initial sterility is conquered, the variability which results from the cross will enable us to make progress, often in unexpected directions. I am here thinking of the species cross between *Phaseolus multiflorus* and our cultivated garden beans. Perhaps it is not superfluous if I repeat here what I

have repeated so often—namely, that the full effect of a cross is never felt until at least a second generation is obtained from it. Uninteresting hybrids should be carefully protected and considered to be of great value as sources of variability in future generations.

Chapter Twenty-one

Selection : C. Vegetatively Propagated Plants

Plants that can easily be propagated in a vegetative way, by budding or by cuttings or dividing, are common. To the plant breeder they offer the enormous advantage of permanence in their qualities. It may be very difficult to find a potato that is good enough to merit being grown commercially, but once the first plant is obtained all we need to do is to propagate it, without any fear of a change in its genetic properties. We need not bother our heads about homozygosity—even a first-generation hybrid that can be propagated vegetatively must retain its qualities for untold years.

Given a mixture of clones (we use this term for the vegetatively propagated descendants of one individual plant) we can disentangle this lot by growing some individuals from each separate plant, and in this way we may find the best clone in the mixture; we can name it and propagate it for sale and for use. Sometimes this is a very good method of obtaining valuable plants. If we are collecting plant material in foreign countries, it always pays well to be on the look-out for tubers and bulbs and cuttings. It is possible that in a mixed field of potatoes one superlatively good clone is hidden in the mixture. Of course we must realize that selection in such material is effective only so long as the material on hand is actually heterogeneous. When we are starting with one pure clone of sugarcane or strawberries or potatoes, one plant in the lot is just

as good as every other, selection of the best individual plants is not likely to be effective. Of course there is one important exception to this rule. Selection within a pure clone may be *very* effective if we are dealing with a number of plants some of which carry some disease—a virus, a mould or a bacillus. In potato selection this is sometimes of the very greatest importance. Another thing to look out for is bud variation. In propagating citrus stock or roses, strawberries or rhubarb, bud sports may have crept in, so that some scions are decidedly inferior to others.

One of the first things to do in the selection of plants in this section is to exhaust the material on hand—to try out a number of pure clones, each started from one individual. Only when this does not give us the required improvement will it be necessary to try producing variability by sowing and cross-breeding. I may add here that there is very little chance of finding new clones in the better-known and highly cultivated potatoes, sugar-canes, etc., as in this material every commercial kind is generally pure, in so far as admixtures of different clones are concerned.

It is very curious that among plant breeders who are developing such plants the opinion seems to be firmly established that cross-breeding is always necessary. Almost all the new roses that are being launched upon the market annually and all the new potato clones are obtained by cross-breeding. I am of the opinion that too much cross-breeding is done in this material. The variability which results from all this cross-breeding is seldom taken advantage of by self-fertilization. The fact that so many novel roses and strawberries, sugar-canes and raspberries are found as chance seedlings should be a warning to us. I am firmly convinced that a plant-breeder who makes a speciality of just sowing large numbers of seeds produced on his plants of good commercial clones will have a better chance of success than the man who is continually cross-breeding his plants. Some of the important qualities sought for are certainly recessive, and sowing self-fertilized seed will give us a very much better chance of producing numerous recessives than will cross-breeding.

If cross-breeding is resorted to it will be very much worth

while to take advantage of newly imported clones from different countries, even when these belong to different species or groups; but in all such cases the material is not fully utilized before a second generation has been raised from such hybrids in large numbers.

Chapter Twenty-two

Selection : D. Autogamous Plants

Self-fertilizing plants are in a section by themselves as far as selection is concerned. The methods of selection in this material differ entirely from what is seen either in vegetatively propagated plants or in allogamous (cross-fertilized) plants.

As I have explained, self-fertilization automatically produces genetic purity in a number of generations. Any old mixture, any land race of such plants as peas, beans or barley generally consists of a mixture of separate pure lines. If such a collection of lines is found, it is a relatively simple matter to separate them, disentangle them and compare them. Sometimes very good commercial varieties have been isolated from such mixtures: all the older famous Swedish wheats and oats in Svalöf were found in this way.

As I have already stated, it is not worth while trying to improve pure lines by selection. Such material is pure and homogeneous; any plant, for purposes of breeding, is as good as the next.

The most promising method is to prepare new collections of self-fertilized lines, as material for selection to act upon, and this can best be done by cross-breeding. In choosing material for cross-breeding work something can be accomplished by selecting a combination of parents in which the weak points of one are balanced by corresponding virtues in the second. If we have an excellent and very productive wheat which is

rather susceptible to a certain rust, we may cross it with another kind which is very resistant to this species of rust, and hope for the best. In any case, the quality of the first-generation hybrids is relatively immaterial. Such hybrids should certainly never be discarded because they disappoint us. On the contrary, they should be well protected and made to produce a very numerous progeny. This progeny must furnish the material for an ultimate selection of new numbers. One very good method is the " Ramsch " method of the Swedish and German plant breeders, in which we leave the progeny of a cross to itself for several generations in a mixture. This has the effect of producing a swarm of different distinct inbred pure lines, after we have left the mixture alone for six or seven generations, so that after this period of time we can proceed to disentangle those lines and choose a few promising ones for further field tests. There are a number of fine points which will be treated of in a special chapter on this subject.

Chapter Twenty-three

Selection : E. Allogamous Plants

The difference between breeding methods in autogamous and in allogamous plants is enormous. Although wheat and rye are so closely related that they hybridize and that the hybrids are at least partially fertile, wheat breeding and rye breeding need wholly different methods.

As in cross-breeding plants, even with the strictest isolation, occasional pollen grains find their way to the stigmata of unrelated plants—almost every plant in those groups is heterozygous for a great many genes. Inbreeding—pollination with the plant's own pollen—almost always produces a very variable progeny.

In some of those plants it is relatively simple to force the plants to self-fertilization. If we do this we transfer the family of plants into the class of self-fertilizers; and so long as we can enforce this artificial self-fertilization we can really use the same methods that are being used in the other group.

Self-fertilization in allogamous plants always gives us a very variable offspring, but the same is true in the case of self-fertilizers after the potential variability has recently been heightened by a cross. When we compare the *average* self-fertilized progeny of a plant of maize or of a beet, this average quality is generally very much below that of the parent plant. But again, this same thing is true for self-fertilizing plants of the other group when the variability has recently been heightened. Of course the difference lies in the fact that in self-

fertilizers the average plant is not heterozygous at all, so that we get the impression that self-fertilization leads to degeneration only in allogamous plants. I treat of the degeneration caused by inbreeding in another chapter.

A great many different methods of plant breeding have been used in this class of plants. A relatively simple, rather rough method is that in which we take only one sex into consideration, leaving everything else to chance. This is the old method of the sugar-beet seedsman.

In using this method we can take advantage of progeny testing by comparing the lots sown from individual mother-plants. The " father " in such a case is the pollen of all the other plants which is flying over the field in clouds. In this method we are really testing those mother-plants for homozygosis, and if we rigidly select those progenies in which no bad recessives (bolters, off-coloured, etc.) occur, our next generation will be improved. This is a method of selection in which we must continually keep on selecting, for only unremitting care will keep the strain up to its previous high level of quality.

In the breeding of cyclamen some seedsmen do exactly the same thing in the male line. Out of every row of plants (grown from one line) they take a very good plant to use as the father of the next generation. Pollen of this one plant is put upon the stigmata of all the flowers of all the plants of this row, and selection is really a comparison of the lots that each have one individual as a father. They have to use this rather unusual system, because each individual plant produces only relatively few seeds.

In the breeding of allogamous plants, vegetative reproduction is sometimes employed. In the first place, this can be done to increase the amount of seed per mother-plant. This is commonly done in the production of sugar-beet seed. The method may also be used when we are making deliberate crosses in the production of commercial seed of such plants. It has been found that very good results can often be obtained by purifying a number of strains by means of continued inbreeding, in order to recross some of those lines in the production of seed for sale. When by actual tests we find that two lines, or even that two individual plants, " nick " (and this means that the

sum of their genes makes a profitable plant), the material will sometimes allow of vegetative reproduction. If this is so we may produce a multitude of cuttings of number 115 and also of number 228, in order to plant them mixed in a seed-producing plot.

The old American " ear-to-row " method of selection in maize is still doing good work. In this method a number of rows of plants are sown, each from one individual ear, and the rest of the ear is saved. When, at harvest, the best rows have become known, the rest of the seed of those individual ears is mixed and sown in order to produce seed for sale to maize-growers.

In the selection of allogamous plants the same is true as in all other classes of plants. In order to get good results the right material must be present in the group. It often happens that we can make further progress only after we have introduced new genes by means of cross-breeding, and in those cases the material in which we find those genes may sometimes appear very unpromising. It has become evident that in the selection of sugar-beet seed valuable genes may be found in mangolds, and possibly in chards. Every cross with such plants gives us so much variability that it seems hopeless to try to obtain better results in this way. In such a case repeated back-crosses to commercially valuable plants may serve to return to the general make-up of the improved type, while retaining the additional gene or genes in the strain.

What is true of genes from other species is also true of absences. If better quality is obtained in the absence of a certain gene, this gene may be present in all our plants, and all our plants may even be pure (homozygous) for it. There is no other way of getting rid of such a gene than cross-breeding with some foreign breed or species from which it is lacking.

Chapter Twenty-four

Pure Line Selection

In autogamous plants like wheat, oats, tobacco, the succession of self-fertilized generations combined with the fact that only a fraction of the descendants of each plant make up the population in the next generation, results in a situation in which every plant in the population is homozygous for all its genes. Even after a rare cross in such material, the descendants of hybrid plants again tend to split up into a multitude of different homozygous lines.

When seedsmen have selected such plant populations according to the quality of individual plants, or even according to competing groups, the population will probably consist of a number of pure lines that look very much alike, but which may still differ among themselves.

In all the autogamous plants very great improvement generally results from the disentangling of the different pure lines that make up the existing mixture. The method is very simple. All we have to do is to grow the descendants of a number of individual plants separately. When we start doing this a comparison of the row plots, each row derived from one mother-plant, will immediately show us if the lot from which we started was or was not heterogeneous. If it was, the lines will show differences, both in appearance and in yield. If they do, it is worth while continuing from a great many good lines, growing the seed on larger and larger fields, Of course we must realize that it is likely that some of the lines will be

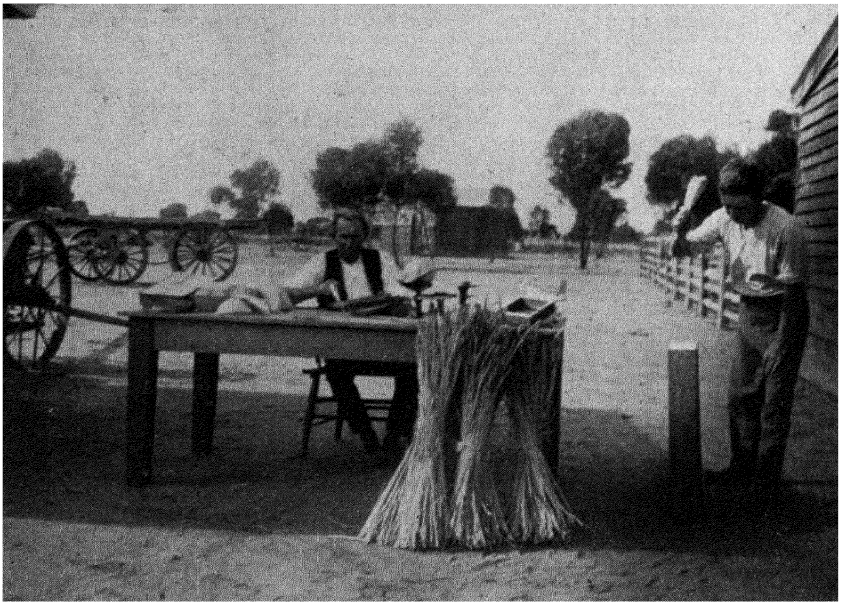
PLATE I

1. Test Rows in the Field being Compared with Standard Rows.

2. Field Rows being Compared.
(Photos: Courtesy of Dr. G. Sutton, Perth, W.A.)

PLATE II

1. WHEAT VARIETY NABAWA IN A FIELD TRIAL, COMPARED WITH SIMILAR WHEAT AT THE CHAPMAN RESEARCH STATION.



2. PROGENY TESTING WHEAT AT MERREDIN RESEARCH STATION, WESTERN AUSTRALIA.

Weighing the yields of the strains and controls.

wholly identical (they may even come from seeds of one plant).

In the first years after the plant-breeding institute at Svalöf was started very great successes were obtained by disentangling prominent pure lines existing in mixtures in established commercial breeds of wheat, barley and oats. In the amelioration of autogamous plants, cereals, tobacco, beans, self-fertilizing grasses, this isolation of the best pure lines is the first step, and very great improvements may result from this work.

The advantage of growing fields of plants that all belong to one and the same line is obvious. Every plant in such a lot reacts in the same way to the same environmental conditions, so that all the plants in a field ripen at the same time. In very good circumstances the best line out of a great number that occurred in a mixture must give a better harvest than the original mixed population.

The technique of the isolation of pure lines is simple enough. We should start with a great many individual plants, sowing a long row of seeds from each plant. This first season it is not possible to judge the value of the separate lines well, as the influence of the adjacent rows is much too great, but it is always possible to weed out a few lines that show definite defects, and in which we find dwarfs or plants that are obviously susceptible to disease. In any event, this first year will show whether or not our original stock of seed *did* consist of a mixture of lines, or whether we were already dealing with a pure line when we started, as is quite possible in modern commercial cereals. When we sow the progeny of our first year's rows during the second year, it is advisable to introduce standard plots for comparison. By comparing the yield of our small experimental plots with that of the adjacent standard plots we can judge their yield much better. As during the first two years all we want is to throw out obviously inferior lines, it should not be necessary to sow our experimental plots and our standards in duplicate. From year to year we now make the plots larger, and, starting with the third year, it is best to repeat the whole series, or have the series in triplicate. From now on it will become obvious whether or not there are lines that warrant the hope that a few of the lines are definitely worth

To enable Farmers to obtain maximum yields from the standard and improved varieties

THE DEPARTMENT OF AGRICULTURE DISTRIBUTES
PURE GRADED PEDIGREE SEED

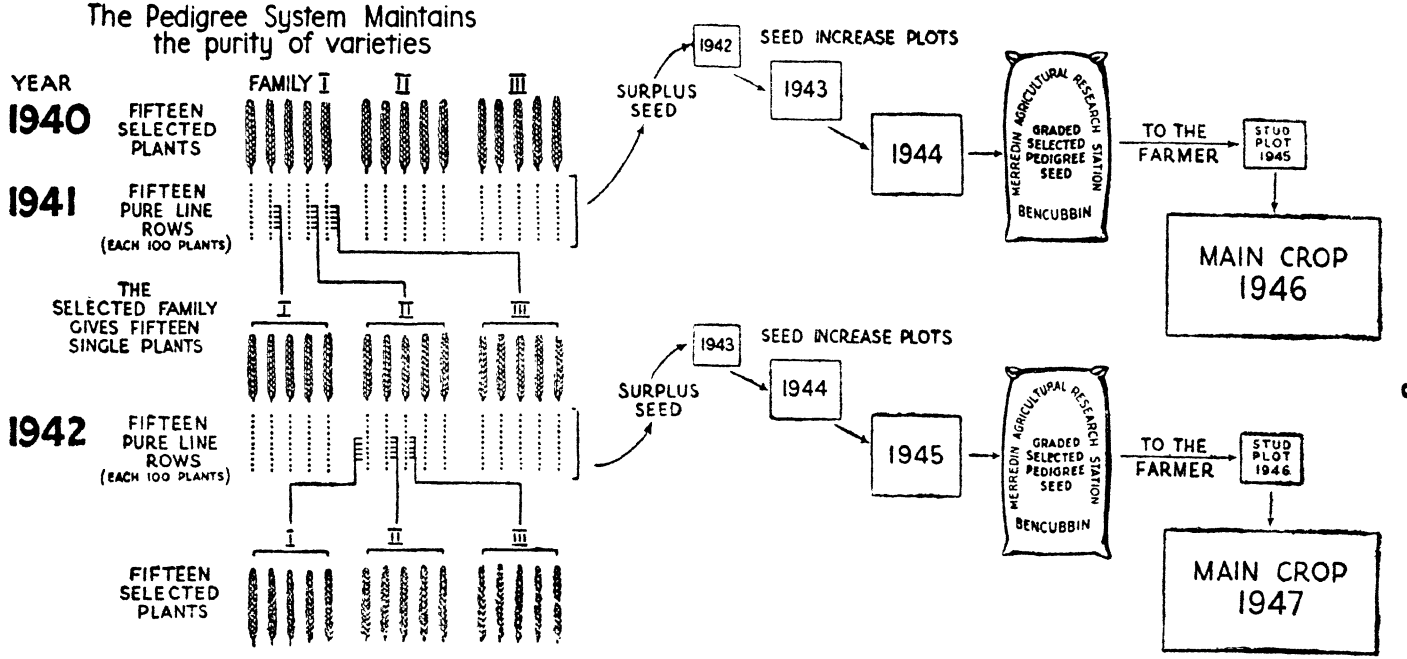


FIG. 7.—Preparing the Dept. of Agric. farm wheat supplies. (Reprinted from *Journ. Dept. Agric. W. Australia*, 1946.)

preserving. Multiplication of the seed up to the point where we can begin selling it will take a few generations, and during those years we have probably seen our lines under all sorts of favourable and unfavourable conditions. If the quality of the product is more regular, but the improvement in yield not too great, it may be best to issue the seed under the old name as an improvement. When, however, the yield is definitely superior—from 5 to 10 per cent. better—it will pay best to give a new name to the line, provided its appearance is distinctive enough to warrant this.

Chapter Twenty-five

Pure Lines *versus* Mixtures

The advantage of pure lines in the autogamous plants over " wild " mixtures is obvious. In a complicated mixture of lines these are bound to vary considerably in quality, so that some are rather inferior, and thus bring down the average yield and the average quality. The plants in a pure line will react in the same way to similar conditions. They will ripen their seeds at the same time; in tobacco it will be possible to divide the harvest into regular times of picking, when on all the plants a sufficient number of leaves are fit to be gathered.

Although this advantage is obvious, it is curious to note that very often a mixture of two different lines, or even of two rather similar commercial wheats, oats or rices, will yield up to 10 per cent. more than an equal amount of seed of either of the two lines unmixed. It is not quite clear to what we must ascribe this phenomenon. The probable explanation is that the two numbers react in a somewhat different way to small differences in the field, so that in the spots favourable to *A* those plants stool out more, while in another spot, where *B* does much better, the plants of *B* will profit most, and will tiller so much that a slightly increased yield results from this.

We must distinguish between deliberate mixtures of two or more lines, or of two rather similar breeds, on the one hand, and original mixtures of many lines, on the other. When a line has been grown commercially for some years, impurities are very liable to appear. Improperly cleaned sowing-

machines, used sacks, scattered seeds being left on the field may all contribute to make the line impure. To a certain extent such admixtures can be guarded against by rogueing.

Even in habitual self-fertilizers occasional hybrids may be produced. To guard against hybridization, it is a good scheme for a seed firm to start every batch of seed to be sold in a given year from one individual plant the necessary number of generations back. The simple precaution of taking three or four

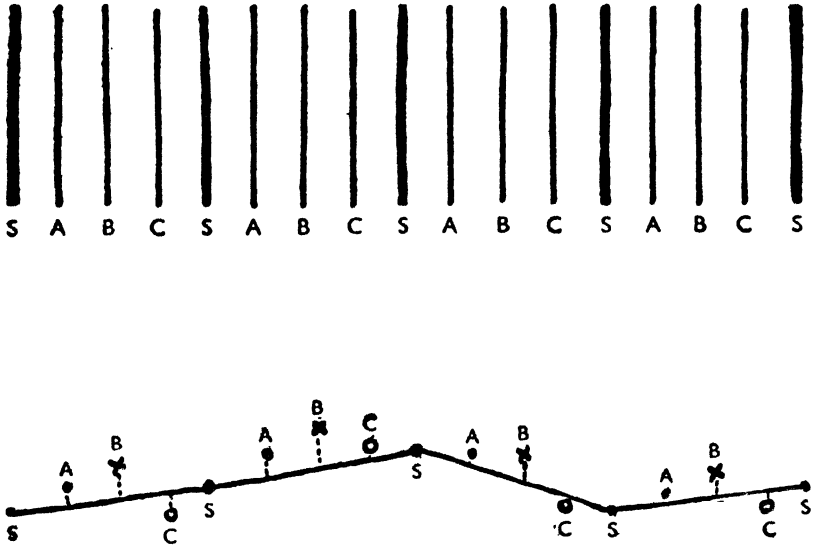


FIG. 8.—Arrangement of three lines A, B, and C, to be tested between standard rows S. The yield of each row can be graphically expressed and compared with that of the standard rows.

one-plant lines will then be ample protection, as we can then eliminate any line that shows evidence of Mendelian segregation.

It is obvious that in wheat, barley and oats so much line selection has been already done that most commercial varieties are pure and promise little for future work of this kind. The exception would be newly imported mixtures from peasant stocks that promised something in the way of exceptional resistance to winter killing or to some disease. For even in a mixture with a moderate average yield the best lines may be rather promising.

In certain cases a mixture of two or three lines may yield

better than either of the lines separately, and it is very much worth while trying out some of those mixtures systematically. Technically the easiest way to arrange the trial plots is to dispense with a standard, but to alternate plots of the two pure lines with plots in which the mixture is grown. In an experiment of this kind, where the samples are small, it is best deliberately to mix two quantities of pure lines *for each separate plot*, and not just to mix a batch to sow in the mixed-line plots, if there will be many duplications in our experiment.

It is known that some seed firms grow several separate lines of one kind and mix them in certain proportions when selling the seed.

In plants in which the unravelling of pure lines is not such a routine procedure as it was in wheat and barley, it is possible even today to obtain very good results by pure-line selection. I am thinking of soybeans, arachis, and some of the autogamous pasture plants.

Chapter Twenty-six

Cross-breeding and Self-fertilization in Vegetatively Reproducing Plants

The majority of named clones of fruit-trees, potatoes, strawberries, have been obtained by cross-breeding. This means that somebody has crossed two different kinds of plants and has found the new valuable clone among the hybrids. When we do this cross-breeding work we almost always obtain an enormously variable group, and this shows that the plants used in the cross were heterozygous for a very large number of genes. This is not surprising if we remember that those parents themselves have also been obtained by cross-breeding.

In work with plants grown from seeds, obtaining a hybrid is regarded as only the first step in our attempts to produce something new and very good. We know that we can never expect to obtain the full assortment of recombinations of the genes that went into the cross before we have seen the second generation, grown from the hybrids. Why is it that the breeders work in such a different way when they are out to improve their roses, apples or poplars?

In some cases this must be due to the fact that it frequently takes a long time for the hybrid plants to come to maturity. Another cause for this difference in method is certainly found in the great variability in the first hybrid generation, due to heterozygosity of the material.

Whatever the reason for the fact, it is easy to see that the plant breeders who are continually making new hybrids, and

then look no farther than the first-generation hybrids, must very often discard hybrid plants that have no value in themselves, but that would be potential parents of excellent new plants of the second generation. Even if many of the valuable qualities in this material are dominant, it stands to reason that some of the most valuable characters in every group are recessive; and we have not a very good chance of obtaining a full sample of the potential variability that results from a certain cross if we look no farther than the first hybrid generation. We might even say, without grossly exaggerating, that most named clones in such plants are the result of a cross that has been made with a definite object which has *not been attained* by the breeder.

When we cross two different plants with the object of combining some good quality of one of them with those of the second plant, our work is only half done when we have obtained the hybrids. To a certain extent we might say that the qualities of the first-generation hybrids are not very important—we must simply regard them as the parents of the variable second generation. Now, in certain groups of plants self-incompatibility is the rule, so that it is impossible to obtain a self-fertilized second generation. In that case we need more than one first-generation hybrid to produce a second generation. But this self-sterility is the exception rather than the rule.

When in plants of this group we sow a great many seeds obtained by self-fertilization, or, by mating together hybrids from the same cross, it is quite possible that we actually realize the hope which set some other breeder working to obtain those hybrids.

Very often we find that some roses, ornamental shrubs or potatoes are setting seed spontaneously. It is frequently asked whether sowing this seed gives the breeder any chance of obtaining something worth while. To answer this question we must remember that sowing seed with the object of obtaining a plant with good qualities—a valuable novelty—is always something of a lottery. It is certainly not true that our chance of drawing a winner is made very much better when the seed sown is obtained by crossing two different sorts, unless again we follow through the cross by growing an extensive second

generation. As breeders generally are not in the habit of doing this, almost all the commercial clones have been obtained as hybrids, so that it will very often be worth our while to follow up their descendents.

If a plant breeder, working with vegetatively reproducing plants, has the habit of sowing only cross-bred seeds, he is certain to ascribe his success to this crossing. But we must realize that in so far as valuable new recessive qualities are concerned, we only find those among the hybrids because both parents were heterozygous. I am absolutely convinced that in groups in which cross-breeding has always been the rule—apples, lilac, roses, potatoes—sowing inbred seeds on an extensive scale is a method very much worth while. In some plants, as in the potato, many valuable clones have been obtained from sowing " spontaneously " formed (and presumably inbred) seeds. The method can be especially recommended in those cases where, for some technical reason, such as minute size of the flowers, difficulties in castration, etc., it is extremely difficult to obtain cross-bred seeds. Sugar-cane is a case in point.

Chapter Twenty-seven

The Use of First-generation Hybrids and Hybrid Vigour

In the autogamous plants where genetic purity, once obtained, is easily conserved, it is worth while concentrating our efforts to produce pure-breeding superior lines. But in other cases this may be so difficult that other working methods are preferable. One of those methods is to produce first-generation hybrids for direct use.

In such plants as maize or beets we often find that groups produced by crossing two distinct lines are superior in some way—for instance in yield—to the lines used in the cross. We must begin by giving an explanation of this phenomenon.

If we could make a complete genetic analysis of a variable family of plants, we should see that in respect to a very large number of genes the group was pure. All the individuals of such a group are alike in respect to a great number of genes, for which every individual is homozygous. On the other hand, there are other genes in regard to which such a line is impure, and when we would inbreed in this line, a number of offspring would be produced, that would differ in those genes from the majority. In a variable lot we should find that to a certain extent plants will differ in the set of genes for which they are either pure or impure. The same is true when we are comparing separate lines.

When we make a cross between two different plants, and especially when we cross two plants of different lines, the result

will be that the group of hybrids will be much more uniform than the descendants of either line. The explanation is very simple. The hybrids will inherit all the genes that are common to both parents. In addition to this, they will inherit all the genes for which only one of the parents was homozygous. If one parent had the composition *AaBB* and the other was *AABb*, the hybrids will all inherit both *A* and *B*. The result will be that the hybrids are more likely to have valuable dominant qualities than inbred offspring of either line.

In the chapters on dominance and on selection we saw that the ordinary selection of the best individual plants will automatically rid the strain of undesirable dominant qualities, when the material is variable in respect to the genes that help to produce such qualities. Where dominance exists, however, and where there is no appreciable difference between homozygous and heterozygous plants (*AA* and *Aa*), individual selection will not quickly bring about purity. In other words, it is likely that good individual plants are still heterozygous for valuable genes, whose presence is desired for good quality.

We can understand why, at least in certain combinations of lines, first-generation hybrid lots of plants are superior in quality to and more uniformly good than, pure-bred lots from the same material. In other words, we could say that the homozygosity of one plant for certain genes will cover up the impurity of another plant in respect to those same genes. We can now understand why hybrid lots are frequently better than inbred lots, and why we find this superiority of the hybrids especially in certain combinations of individuals and of strains.

The simplest instances are those in which we combine two pure inbred lines, or even two clones, to produce the commercial seed. Some of the azalea specialists have found combinations of species that, when crossed, give hybrid seed from which beautiful large-flowered hybrid plants can be grown. A second example is that of the Japanese hybrid egg-plants, and that of hybrid tomato seed. In Java a few tobacco estates have frequently used hybrid seed produced from a cross between quite different lines. This practice of using first-generation hybrids is commercially possible only if producing such seed is not excessively difficult or expensive. In the cases

enumerated, each fertilization gives us a very large number of seeds.

The best-known example of hybrid seed for the commercial production of first-generation hybrid plants is that of maize. I am devoting special chapters to the case of hybrid maize seed. Here it will suffice to say that it was found with maize that very often the first-generation hybrid plants produced by crossing different breeds gave a very high yield. The same was found true for hybrids between different inbred lines in one variety. Starting from small-scale genetical experiments, a very important hybrid-corn seed industry has grown up, first in the U.S.A. and later in other maize-growing countries.

In some cultivated plants (but not in others) inbreeding will have an adverse effect on vigour; and, conversely, crossing between different lines of plants will often give us remarkably vigorous hybrid offspring. Both from a purely scientific standpoint and from a practical one, this subject is of the greatest interest. The facts have been well known for a long time. Darwin made numerous inbreeding experiments, and found that some plants were much more subject to degeneration as a result of it than others.

Many different theories have been proposed to explain both the degeneration due to inbreeding and the great vigour due to crossing. The pre-Mendelian explanations do not concern us much. One of the chief difficulties in the way of a simple genetic explanation has certainly been the old conception of genes as determinants, each calling forth a special discrete unit character. So long as most geneticists had this conception of genes and of their action, the mere sampling effect of Mendelian segregation of genes and the addition of genes by cross-breeding were thought to be insufficient to account either for the degeneration caused by inbreeding or for the very great special vigour of cross-bred individuals.

I do not think it is necessary to go into the different theories that have been proposed and have then been abandoned. I will confine myself to the hypothesis that, to my mind, best explains all the facts.

If we look for evidence of loss of vigour by inbreeding, we are first struck by the fact that certain classes of plants are appar-

ently exceptions to the general rule. In the habitually self-fertilized plants, such as tobacco, wheat, barley, and garden beans, the strictest kind of inbreeding—self-fertilization—does not lower the vigour or the yield. On the other hand, in all the allogamous plants that have been tried—in beets, in maize, in rye—inbreeding brings along a rapid decline in almost all the desirable qualities; and in the same plants, cross-breeding such deteriorated stocks immediately restores full vigour. Now, if we start cross-breeding in the habitually self-fertilizing plants, we often find that the first-generation hybrids are extremely vigorous and productive, and if this happens we notice a very large general reduction in vigour in subsequent inbred generations. This shows that we must not look for a mysterious special immunity to degeneration in some plants, but that resistance to inbreeding degeneration simply spells homozygosity.

In full accord with this is the circumstance that in animals the facts run wholly parallel to what we find in plants. Those groups in which cross-breeding has been the rule show a decline in quality after inbreeding, and those groups that have been regularly inbred—such as fancy pigeons—are inbreeding-resistant. Again, just as in plants, it has been possible both with chickens and with ducks to produce great purity by a system of inbreeding, while we retain full fertility and vigour as a result of strict selection for those very points.

Of course, the examples of the very fertile and vigorous highly inbred wheats and fowls show that the vigour we see in hybrid stock is not in any way due to the fact that the hybrids are heterozygous in respect to a great many genes, but only to the fact that they possess a favourable combination of genes. In theory (on paper) it might be possible, by careful work, to make a group of plants (or animals) that would be homozygous in respect to that ideal combination of co-operating genes. As a matter of fact, I fully believe that the circumstance that we do not attain this desirable end is most often due to faulty principles of selection. Essential mistakes are frequently made that render it almost impossible to attain the much-desired results. In the chapter on autogamous plants I fully discuss an example of this difficulty.

To understand the nature of inbreeding-degeneration we must remember that dominant good qualities, as far as the effects of selection are concerned, are in a class apart from the recessive virtues. If in a variable group some individuals have some unwanted dominant quality, it is quite simple to eliminate that dominant fault from the material. If we prefer white maize to yellow, it is quite simple to produce a pure-breeding, white-seeded maize. But the reverse—to produce a pure-breeding, yellow-seeded maize from the same material—is much less simple, as some of the yellow-seeded plants chosen may again be heterozygous.

What is true for one monofactorial difference is true for all of them. If we subject a group of plants to individual selection, or even to some sort of selection by means of progeny tests (*e.g.*, ear to row in maize), and we do not have recourse to inbreeding in order to purify the genotype, the result will be that the superior strains of beets or maize we have built up in this way will be chockful of individuals heterozygous for very important genetic factors.

As soon as we start inbreeding, we reduce the potential variability of such material. In every succeeding generation from self-fertilization the number of genes for which the material was still heterozygous is halved. In every generation the plants become purer and purer. Let us take the case of just one gene, *A*. If we inbreed a heterozygote, *Aa*, 25 per cent. of its descendants will be *AA*, 25 per cent. will be *aa* and 50 per cent. will again be heterozygous, *Aa*. Now, if *A* is an important gene, the *AA* and *Aa* individuals will be somewhat better than the *aa*'s. If we were concerned with this gene only, we could, by merely eliminating the *aa* plants, work towards better plants, and the proportion of pure-breeding *AA* plants would improve. But now we must remember that we are concerned with a multitude of genes, for all of which our original material may have been heterozygous. If we were dealing with only three separate genes, *A*, *B* and *C*, we might retain only the 75 per cent. *A* plants (*AA* + *Aa*), and of these only the three-fourth *B* plants (*AB* + *Bb*), and of these only the plants with *C* (again three-fourths). But we must remember that the fraction three-fourth power *n* becomes rapidly smaller

and smaller with an increase of *n* (the number of desirable genes for which the stock is impure). For this reason even strict selection for vigour while inbreeding will not prevent a loss of desirable genes from the material in an inbred series. And, of course, blind inbreeding, without any selection, will very rapidly bring down the proportion of plants with dominant desirable qualities, when the material was heterozygous for many genes that helped to build up those desirable dominants.

The mutual independence of genes scattered over the chromosomes of our plants will make it a matter of chance for which desirable genes each inbred line will become homozygous, and which ones will be dropped from the line. It is certain that if we start a number of parallel inbred lines—let us say in beets or in maize—by starting every generation from just one single plant, those lines will become homozygous each for its own genotype. But the genotype of every line will become different from that of every other line. If we are lucky, and are running a good many lines, we may in the end still possess all the valuable genes that are responsible for the good qualities of superior plants. This does not mean that in one line we may have fixed the plants in respect to one desirable dominant virtue, and that in another we may find another separate good quality. For we must realize that such good qualities do not depend each on a separate gene, but rather on the correct combination of genes. To a certain extent it is possible that we shall find good qualities in some of our lines—disease resistance in one, good quality of the product in another one. But if the foundation stock was highly cross-bred we shall seldom find highly inbred lines of sufficient all-round quality to make it worth while growing them commercially.

What happens when we cross-breed such inbred lines? As a general rule the vigour and all-round quality of hybrids between two such lines are very much better than those of the lines themselves. Sometimes, but not always, such hybrids are as vigorous and as good as the original material before we started our inbreeding.

The genetic explanation of this can only be that this is a result of the genetic *difference* between those lines. I explained the loss of quality by an actual loss of genes partly responsible

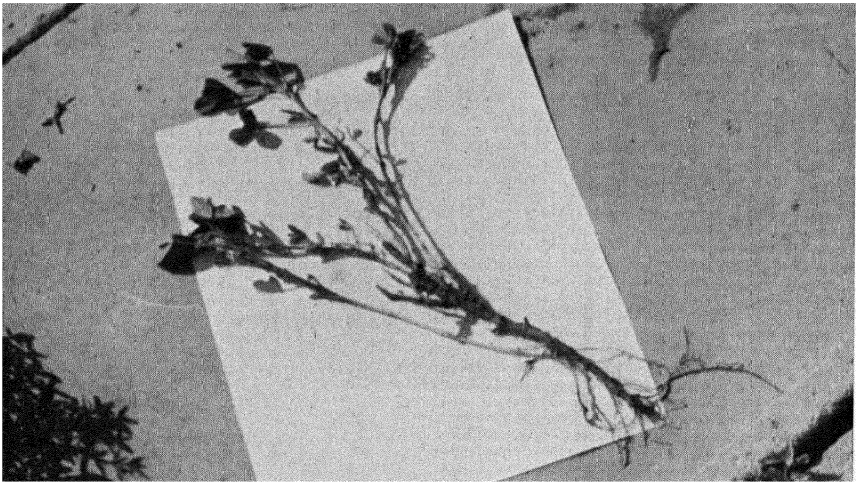
for desirable dominant qualities. Especially in blind inbreeding, chance determines which of such genes will be eliminated in a given line, and which will be consolidated in the line (for which the line would become pure). If we think of the good quality and good vigour of the original strain as partly caused by the right combination of a great many genes, and of the inferior quality of inbred lines as resulting from incomplete sets of such genes, we can see that the hybrids, which inherit a combination of the genes remaining in inbred strain *X* with those for which strain *Y* happens to be homozygous, will be superior to both those strains.

In this superior quality of the hybrid generation between inbred lines we are concerned with the genotype, with the combination of useful genes present in the plants, and our present-day explanation is that it is this good combination of genes only which confers good quality upon those plants, and that the fact that they are heterozygous for many of them does not help. It would be very desirable if we could devise means for making a strain of plants that would be homozygous for all those important genes, and in another chapter we will discuss the possibility of working towards this goal.

PLATE III

1. WHEAT NABAWA, AT ONE TIME THE MOST POPULAR WHEAT IN AUSTRALIA.

2. WHEAT YIELD TRIALS AT WAITE INSTITUTE, ADELAIDE, SOUTH AUSTRALIA.
(Photo: Courtesy of A. T. Pugsley, B.Sc.Agric., M.Sc.)



1. Rhizomatous Alfalfa.
(*Photo: Courtesy of Mr. Geoffrey Sykes.*)

2. Alfalfa Rhizoma.
Note numerous vigorous rhizomes (10 to 18 inches in length) spreading from central crown, and the dense weed-resistant nature of the growth.
(*Photo: Courtesy of Mr. Alan Thompson.*)

Chapter Twenty-eight

Hybrid Maize and Beets. An Example of Utilizing "Hybrid Vigour"

From a small beginning in the experimental plots of the geneticists (G. Shull, East & Jones), the work with hybrid vigour in maize has grown to enormous proportions. The greater part of the corn harvest in the U.S.A. is now produced from hybrid seed, and the yield per acre has been much improved thereby.

In the older well-known maize varieties that formerly were always grown from open fertilized plants the potential variability was very great. Many plants are heterozygous for very many different genes, and the best vigour and the best yield are found in those plants which happen to possess the most complete combination of those genes.

If we start inbreeding in series of lines, so that in every line we take one plant and force it to pollinate itself, we quickly reduce the potential variability in each of those lines. The plants will be homozygous for many genes for which the original mother-plant was still impure, and, on the other hand, we shall lose some of the useful dominant qualities. The general quality and vigour of the inbred lines will decline, especially so if we use blind inbreeding without selection in continuing the lines.

If, after some generations of inbreeding, we now cross those inbred lines, we shall find that, in some combinations more than in others, the resulting hybrids will be of very good quality. We have explained this by the hypothesis that those hybrids again have the full set of valuable genes.

Now, the question may be asked why it should be advantage-

ous to go to all this trouble of purifying those separate lines in order to reconstitute the original set of genes by cross-breeding them. Why should the hybrids between a good combination of those lines be more valuable than plants from the original non-inbred strain? There are at least two reasons for this. In the original lot—in the strain, before it was inbred—the potential variability was very high. A large proportion of the plants—probably all of them—were heterozygous for several of the genes that help to make for quality. The germ-cells produced in the field were of the most diverse kinds, and, as a result, a certain percentage of the plants of the next generation always had undesirable recessive traits. Maize and sugar-beets are full of the most diverse undesirable recessive characters, that crop up in every generation.

The inbred strains may not have a full complement of the desirable genes, but in any case they are homozygous for those they *do* carry. If, for this reason, we are able to find a set of two inbred lines that " click " because together they happen to have a full complement of the desirable genes, the result will be that the hybrids grown from this combination will all carry the whole set of those genes. For this reason the hybrid lot will be much less variable than the original open-fertilized variety. In other words, the method of establishing many different inbred lines is a method of cutting down the heterozygosity in the material. For practical reasons, this reduction of the variability is not attempted in one single series. The breeders know that it would be impracticable with our present methods to produce just one inbred strain, homozygous for all the desirable genes, so they do the work in parallel series, fixing the genotype of several lines by inbreeding, and hoping that after several generations of this they will discover a few inbred lines whose combination will give them the desired hybrid seed that will produce vigorous high-yielding plants.

It is obvious that the quality of such first-generation hybrids depends on the combination of genes present, but that the plants themselves are again heterozygous for all those genes. Those hybrid plants are meant to be harvested for their produce—seed from such hybrid lots would give as variable a supply of plants as the original strain, or almost so. From the

point of view of the seed firms this circumstance is rather happy; the users of the seed are satisfied, but they have to come back next year for a fresh lot of seed.

The fact that most inbred strains of maize and beets are of very low vigour and production makes the production of such hybrid seed expensive. In many maize-strains the cobs are miserable nubbins, the seeds are small and irregular in shape and size, and poorly adapted to the use of sowing by machinery. There are several ways out of this difficulty. Obviously the best way is to produce at least one line that will be a fairly good producer of seed. The methods of blind inbreeding of the first years have been improved, and it is usual nowadays to combine inbreeding with selection. Sometimes this means straight selection in the inbred line, sometimes the selection is used to fit the inbred strain for its ultimate use—cross-breeding. We can do this by testing the pollen of several plants in cross-breeding (top-crossing) tests, and so choose the sub-line which is retaining most of the valuable genes.

Another method which is often used is that of the triple cross, in which the hybrid plants that furnish a lot of good-looking and very even seed are fertilized by pollen of yet a third line, that has been carefully chosen for this very purpose.

If the ultimate product must be very uniform—such as in sweet-corn that is grown for canning, and that must be prepared by machinery—the use of one single cross between two inbred lines is indicated. The use of hybrid plants as parents of the commercial seed gives too variable a crop. In the ordinary use of maize some variability can be permitted, provided the average yield is good.

In certain circumstances inbred strains can be produced that are valuable for " top-crossing ". Such strains must be pure for a great many important genes, and they must be good pollen producers. The usual practice in producing hybrid seed for sale is to grow the mother-plants in a field, and grow the pollen parents throughout that field in every third or fourth row. The mother-plants are then carefully detasselled, and the field produces hybrid seed from these detasselled plants and inbred seed from the pollen-bearers.

Nowadays much of the commercial maize seed is grown by

the system of " double-crosses ". In this system four different inbreds are used, and to grow the commercial seed, hybrids $A \times B$ are crossed with hybrids of two other strains, $C \times D$. This, of course, makes the production of commercial seed much cheaper. It is doubtful if from the standpoint of the seed-user this system is as good as the triple cross. We must realize that the hybrid plants of the first cross are heterozygous in respect to all the genes in which the parents differ. A uniform descendance from such plants can be expected only when the pollen used is from plants homozygous for almost all those genes; and we cannot expect that the pollen of another hybrid is in that condition.

It is certain that even commercial double-cross seed, when well-chosen inbreds are used, gives a better harvest than ordinary mass-selected stock of the same variety. But the results are never as good (and could not be expected to be as good) as those obtained from single-crossed seed.

I am afraid that to a certain extent smart advertising plays a role in this subject of the hybrid-corn seed production. In the catalogues of the seed firms we often see pictures of " typical " ears of inbred strains, of the first hybrids, and of the " double-cross ". In those pictures the ears illustrated not only show the enormous improvement in the first hybrids over the inbred strains, but they always show the largest and finest cob as the result of the double cross. Such pictures must be taken with a grain of salt!

If we look at the production of seed maize from the commercial angle, we must realize that the process of inbreeding those sub-strains costs money. During the first generations many plants have to be enclosed in paper bags, and to be pollinated by hand. But, on the other hand, when the difficult and painstaking labour of purifying and testing the inbreds is done, those inbred strains can be further multiplied, without any manipulation, in fields, sufficiently far removed from other fields of corn. In fact, once we have found the two suitable inbred strains that " click ", or the three necessary for a triple cross, we can reduce our selection to the very minimum, for once such strains are homozygous for the important genes, they remain in that condition, and all we have to do is to make the final cross to produce the seed-crop for sale.

The farmers, especially in the U.S.A., have become " hybrid-corn conscious ". They have experienced on their own farm how much more vigorous are the crops that can be obtained from the hybrid seed. I have no doubt that once the idea of the superiority of cross-bred seed has taken firm root, the name " double-cross " has more advertising value than the facts warrant. The only yield figures I ever saw in which " double-cross " plants gave a (slightly) better harvest than their single-cross parents were taken from a cross-breeding experiment in which four *different varieties* were used.

With beets, especially sugar-beet, the commercial houses use a system of seed production that has great similarities to that of the hybrid maize. They generally use a system of mild inbreeding in isolated lines. Inbreeding is much less easy here, and whole plants must be enclosed in very well-constructed and ventilated cages. Next they try combinations of their selected strains, and finally they grow their commercial seed from a field in which two strains are planted in a mixture. Until recently there has been no unfailing method of producing 100 per cent. hybrid seed, as a certain percentage of the seed must come from self-fertilization or from the intercrossing between different plants of the same line. In practice, however, we find that the vast majority of the beets in a commercial field are first-generation hybrids. If we deliberately cross two strains of beets, in which we can easily recognize the hybrids—by their leaf-colour or by their shape—we find that, with very few exceptions, the field contains only hybrid plants. The cause of this must be sought in the great vigour of the first-generation hybrids. In sowing beets many more seeds are sown than will ultimately grow up into mature beets. Soon after the seedlings are up, the field is thinned, the supernumerary plantlets are hoed out. As this is done by hand, the man who does the thinning always favours the strongest, most vigorous plantlets. Even if we did not consciously select the favourable combinations between lines to be combined for seed-growing (and I suppose all beet-seed firms do this nowadays), the percentage of mature beets that have been grown from cross-fertilized seed is always very high.

Chapter Twenty-nine

Further Improvement in Maize and Beets

In the previous chapter we discussed the theoretical foundation of the work with hybrid maize and beets. We saw that inbreeding will reduce the potential variability of the families subjected to it, that those lines will become homozygous for some of the valuable genes and that they will lose some of the others.

One question that is of the greatest theoretical, but especially practical interest, is what we could do to influence this process of purification in such a way that each line would become pure for the maximum number of useful genes.

For discussing this, we must again look at this process of automatic reduction of the variability during inbreeding. We start with a plant of maize or of sugar-beet that is heterozygous for a great number of valuable genes—genes that we would like to have in every plant. The ordinary selection work ensures that such genes remain present in the stock, even if ordinary mass selection does not quickly ensure purity in respect of those genes.

It does not matter whether we know or whether we do not know all such genes separately in their action upon the end result. But we do know that a plant heterozygous for a gene *A* (*Aa*), on being self-fertilized, will give us 25 per cent. homozygous *AA* plants, 50 per cent *Aa*'s and 25 per cent *aa*'s (which last will tend to be discarded). The chance that we will hit upon a plant homozygous for one of those genes is one

in four; if we are dealing with five genes, we have only one chance in eight hundred of finding a descendant homozygous for all of them—in fact, the chance is one in 4^n (n being the number of genes involved) that we find a plant homozygous for all the genes concerned. In a limited number of inbred plants all we can hope is that we conserve some of those useful genes in the heterozygotes. But from the calculations in another chapter we can see that unless the number of offspring per generation in an inbred line is very large, we may be forced to continue from a plant that lacks one or more of such genes (*aa* or *bb*).

In the work with hybrids between lines we help ourselves by continuing a number of parallel inbred lines, hoping that in the end we shall have two such lines which between them carry the whole series of important genes in homozygous condition.

It is evident that (theoretically) we should be able to produce inbred lines of maize or sugar-beets that were as productive as some of the best strains we now possess, and that would be homozygous and breed true. In fact, if the number of inbred plants from a very good parent plant were only large enough, we should be able to find such a plant homozygous for all those genes for which the mother was still impure, *in the very first generation.* In practice we can never know whether we would have to sow two thousand or twenty thousand plants to find that ideal one. But one thing is certain: that if we sow a few dozen plants from self-fertilized seed we shall undoubtedly have no chance whatever!

The simplest genetic calculations show that in this selection work in such plants as maize and beets the usual number of individual plants grown per generation is far and away too small! Not only should we combine selection with inbreeding, we should see to it that the methods used gave us an adequate chance of finding what we want to select.

Of course a great difficulty lies in the fact that it is practically impossible to appraise the genetic quality of *one* plant by inspecting its individual quality. This difficulty is, of course, greater in beets than in maize. Nevertheless, I think it would pay well to start inbreeding series on a very wide front, sowing all the seeds from an excellent plant, and testing a number of

very excellent daughter-plants by sowing their inbred progeny. The circumstance that inbred series almost always deteriorate rapidly in vigour and yield does not prove a thing, so long as the numbers we work with are so inadequate. A technical difficulty, of course, is that in maize it is not possible to pick out the individually best plants before they have ripened their seeds. When we must pollinate them we do not know their quality. Beets give much less trouble in this respect.

A very great difficulty with which plant breeders have to contend in the allogamous plants, lies in the large number of genes in respect to which our material is variable. Inbreeding will decrease this potential variability, but, as we have already seen, it is extremely difficult to direct the purification in such a way that the inbred lines will be of good commercial value.

There is one way out of this difficulty. We know that the inbred lines are highly homozygous. If they are not good enough as they are, we know nevertheless that such lines are homozygous for many valuable genes. I think it is well worth while trying to improve such pure inbred lines, and this is being widely tried in America to-day. We can do this in two ways: by crossing to another line, followed by another series of inbreeding, or by the use of repeated back-crosses. A cross with another suitable line will give us the genes lacking in our inbred lines. But the hybrids will be highly impure, and we must try to reduce this impurity while profiting by the homozygosity of the inbred line. This we can best do by a combination of repeated back-crosses to that line, and selection for vigour and yield.

In the existence of good inbred lines in maize, that can be propagated separately, we have an excellent and sure method of producing first-class commercial seed for sale. In the beets we are far from this. But in the beet there are certain possibilities that should be worth trying out. In the first place, there is *male sterility*. Certain families of beets have been found that have no functioning pollen. This femaleness is inherited in a very peculiar way; it follows purely maternal lines, and it seems to be due to a peculiarity of the cytoplasm (protoplasm outside the nucleus). By cross-breeding it can be brought into any strain of beets. This gives us a possibility

of producing on those plants seed that is guaranteed cross-bred, by having such plants flower in a field with other plants.

The other possibility in beets is the use of vegetative reproduction. Let us suppose that we possess two plants of sugar-beet that happen to fit together so well that the hybrid seeds produced from their combination give us beets of high purity and sugar content and with an excellent yield. Now our difficulty would be to produce two different groups of beets that would have the same constitution as those two individual beets. This would be extremely difficult and tedious work. On the other hand, if we had a very good method of rapid vegetative reproduction, all we would have to do would be to grow tens of thousands of beets of clone *X* and as many of clone *Y*, and then to make them flower in a mixed field in the ordinary way. There exist a few methods of vegetative reproduction in beets. Some of these methods, involving making the beets produce shoots and reproducing new beets from cuttings from those shoots, work fairly well. If the methods can be perfected, they could lead to an avoidance of the very costly methods of selection now in use.

Chapter Thirty

The Choice of Plant-breeding Material

The advantage of having at one's disposal a large collection of plant varieties, both plants of commercial importance and imported plants of no immediate practical importance, is enormous. A difficult question for the plant breeder is always what crosses to make, what plants to combine with the greatest hope of ultimate success. In the breeding of such plants as potatoes, raspberries and roses, certain clones have the reputation of being profitable parents of hybrid lots. To name a few, I could point to the Early Rose potato, the Lloyd George raspberry, the Chilean strawberry.

In some special instances the choice is obvious. When our present assortment of flaxes or potatoes or roses happens to be deficient in some such quality as disease resistance or winter-hardiness, we are on the look-out for plants that will show those desirable qualities to the greatest extent. In other words, we shall, when choosing the parents of our future hybrids, try to find material that promises the possibility of a combination of the very good points of both. This is obvious. I would like to point out that often crosses that seemed very little promising have given excellent results. As we have seen in the chapter on transgressive variability, novel qualities, and novel degrees to which an existing quality can develop, often turn up unexpectedly in cross-bred material. It would seem that here no definite rule could be indicated. All I can say is that it is always worth while trying crosses with new material, with

newly imported species—in fact with material which has not been used previously. This is especially so when, as in horticulture, everybody is on the look-out for something new.

Another rule that could be given would be that when we make very wide crosses we cannot hope to find commercially valuable strains in the second hybrid generation, unless we grow extremely large numbers of plants in that generation. When we make a very wide cross to incorporate some special quality into the existent stocks, the best thing we can do is to use the hybrids in back-cross series. We can then strive to retain just one special quality of the new species and incorporate it into the general set of genes with which we are familiar in our older stock.

In several instances very wide crosses have been successfully used, and sometimes plants have been used in cross-breeding that in themselves showed very little promise. I am thinking of the inedible cattle gourd that Orton crossed with his watermelons, of some of the potato crosses with Andean wild species (Salaman) and of the back-crosses to hybrids with wild cane from which all our modern resistant varieties of sugar-cane have been derived.

It is here—in the choosing of plant material for breeding work—that cytological studies and chromosomal counts are of the greatest practical value.

Chapter Thirty-one

Methods of Evaluation and Comparison

The aim of every plant breeder is to produce a group that will be worth a place in the assortment of cultivated plants. In some cases the new plant will have only ornamental value, in others it will, for any of a dozen reasons, be better adapted to agriculture than other similar ones.

It is easy enough in all classes of plants to produce novelties, to produce variability. The experimental grounds of the plant breeder would soon be cluttered up with novelties if he did not keep on weeding out the comparatively worthless. After producing our novel plants, we must judge them.

Some qualities are much easier to judge than others. It is comparatively easy to weed out a lot of seedling dahlias and to pick out a few that may be worth keeping on for further testing. In the selection of our agricultural plants, in cereals, in beets, in maize, the assortment of valuable kinds is already so great that only relatively few of the newer selections are worth keeping. In the vegetatively propagated plants this work of testing novelties is comparatively easy. In the first place, we are not bothered by considerations of purity—once we have produced a very good specimen, we can just multiply it with all its properties intact. In the second place, we can easily, for purposes of testing and comparison, produce as many individual plants of the novelty as we require.

When the differences are relatively small—as in cereals and beets, where the novel plant produced must compete with

excellent old stock that has been made by a process of selection and comparison during centuries—a correct system of evaluation becomes of very great importance. What we really want to test is the inherited composition of the material. This may be difficult, as the final quality of the plants to a large extent depends on favourable or unfavourable conditions under which they grew up.

It will perhaps be as well to begin with the simplest problems. In the production of novelties in such flowers as roses or dahlias the value of a new variety depends entirely on the appeal it makes to the gardening public. There is here no real, apparent standard of merit that we could express in figures such as in a variety of wheat.

The man who is proud to have found a novel dahlia seedling or a new and strikingly beautiful rose sends it to a show and hopes that it will take the judge's eye and win him the much-prized ribbon or certificate. But of course the insider knows that many highly commended novelties will never be heard of again, or that they will drop out of cultivation in a few years. There is a difference between the fact that the grower can bring half a dozen perfect blooms to the show on time, and the question whether that same rose or chrysanthemum will ever be popular in the gardens, or even be worth while growing for the commercial producer of cut flowers. A dahlia that wins the medal may be a very weak grower, or it may be very susceptible to rain. The strikingly beautiful rose may be very susceptible to mildew, or its flowering season may be extremely short. If we visit the growers of greenhouse roses, or the gardens of the man who produces cut flowers for the market, we find that the number of varieties that have real commercial value—varieties " with bread in them ", as our gardeners express it—is extremely small. We shall probably find only three or four of the relatively older dahlias worth growing for cut flowers, and it is seldom that a novelty is added to that list.

In testing out agricultural plants, both during the process of selection and after they have finally been introduced, many methods are in use. The direct, simple examination of a number of small plots or rows will show us the qualities of

those lots, but this method will only serve to find the groups with definitely inferior quality. It is not good enough to find exceptional merit, as circumstances may have favoured those qualities we appreciate. The only way to avoid reaching the wrong conclusions is to see to it that environmental conditions do not vitiate our results. The best way to do this is to compare the quality of a number of plants with that of other plants that were grown in wholly comparable conditions.

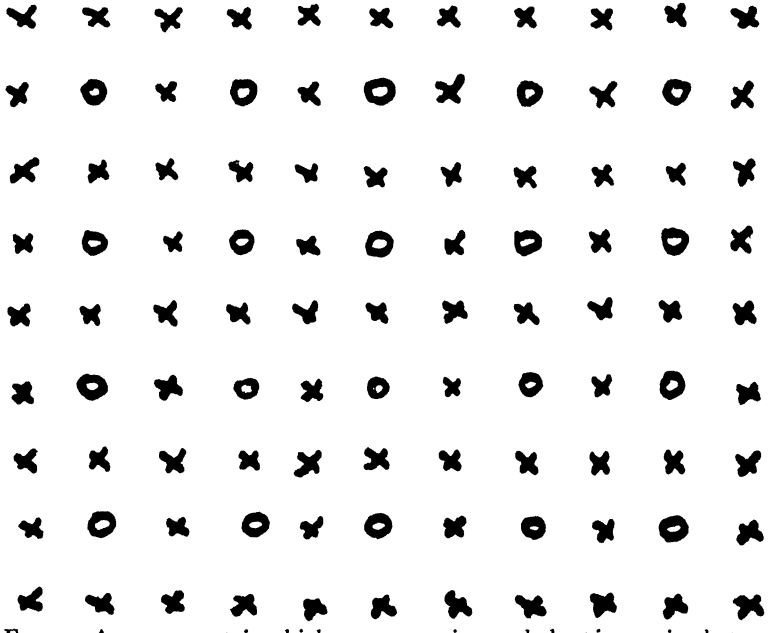


FIG. 9.—Arrangement in which every experimental plant is growing between plants of an older, very pure variety. This arrangement makes the environment for every plant (*e.g.*, in a second generation) as much alike as possible.

One of the best ways to do this is to grow the plots of our plant between similar plots of an older variety, that can be used as a standard of comparison. The choice of this standard is of great importance, and we will revert to this subject when treating of the breeding of special plant groups. As an example we can here take the evaluation of a newly produced (or of an imported) potato clone, or pure line of wheat or barley. In a case like this the standard may be some line or clone that is of commercial importance, against which the tested plant will be called upon to compete.

If there is sufficient material, it is wise to repeat the comparison—that is to say, we should grow the test plot between standard plots in different parts of the field, or preferably in different fields. To equalize accidental conditions in small parts of the field, oblong plots are generally better than square ones. If we are testing a number of experimental lots, we can grow them side by side, and interpolate standard plots to be used for purposes of comparison. In other chapters some of the special points of experimental garden technique are discussed; here it will suffice to say that we must avoid errors due to the influence adjacent plant groups may have one upon the other.

The experimental garden will need an efficient system of book-keeping. We must note down anything of value about the experimental and the standard plots, date of maturity, disease resistance, quality, yield. Now we come to one of the most important problems. How are we going to use those many data? We can calculate average yield for the sum of the plots of one kind, and then compare those figures with the average computed yield of the standard plots or with the average yield of the whole field; and a comparison of the deviation of the yields in the different plots with calculated mean errors will give us valuable data about the question in how far the superiority or inferiority of each separate number is significant as an indication of merit.

It is quite possible that by my training I am conditioned and prejudiced against the use of too much arithmetic in matters of plant breeding. I am fully convinced that in certain circumstances calculations of means and averages and probable errors will help the breeder. On the other hand, no amount of painstaking calculations will help us if the basis upon which those calculations are built is insufficiently good.

I have seen something of the practice of plant breeding in different parts of the world. In some institutes I have seen a multitude of miserably small checkerboard fields being weighed at harvest time to produce the figures for an office staff to juggle with. I have also seen very successful establishments where the field-work was under the supervision of men who were thoroughly conversant with the material, and where

excellent results were obtained with a minimum of calculating machine work.

A method of annotating the results obtained in experimental plots which gives the plant breeder an excellent insight into the merits of his new material is that of graphical registration. This method can be adapted to the most diverse projects; it is very simple, and gives us our results at a glance. The method consists of registering the quality (yield, height, resistance) of each plot, both standard plots and testing plots, on ruled paper. If we do this, the line that can be drawn through the points of the standard plots will probably rise in one part of the field, and descend in some other part of it, and by drawing a line that joins those points we obtain a basis upon which we can found our judgment of the results obtained in the experimental plots. (Fig. 8, p. 133.) If we want to test our experimental material in two or three different qualities, we must construct separate graphs for each of those qualities, or sometimes we can use the same graph, employing different colours for separate qualities (weight, sugar percentage, purity in beets, etc.).

Reading those graphs will now show us the quality of our plant plots, in comparison with the standards, and we can use this relative value as a basis for our selection work. If we compare half a dozen groups in one experiment, and we find that one or two of them will in every duplication remain well below the standard in quality, this may be a very good reason for discarding them. On the other hand, if we find one or two numbers that all through the experiment are well above the standard line in quality, we have a very good reason for preferring them. It may be that in the case of one or two numbers the results are very variable, so that in one part of the field the number is above and in other parts it is below the standard in quality. Then we may well retain this number for another trial in the next season.

The influence of one row of plants on those growing close to it may be considerable, and we must guard against this. If we can grow three rows and use only the middle one for our records, we take a step in the right direction. If we have enough seed to plant six rows, and we examine only the two

middle ones, discarding two rows on each side, this is still better. The greatest difficulty arises in those cases where we are dealing with very few plants of each number; or, worse, where, as in the second generation of a cross, every plant is probably different from every other. It then becomes very important to equalize conditions for each plant as far as this is possible. A very good plan is to grow the plants in rows, and alternate those experimental rows with rows of some pure standard variety. (Fig. 9.) Each plant may then have two diverse neighbours in its own row, but it will touch four other plants that will be of the same kind as four out of six neighbour plants in the case of every other plant in the experiment. As I discuss at greater length in the chapter on breeding grain crops, it is important that during the first one or two generations (counting from the hybrids) we shall grow as many individuals as possible. This means that to save time we must make a preliminary choice out of the many numbers in those early generations, and it is very important that we shall make the cultural conditions as nearly equal as possible for every plant.

This is the place to warn against using apparent correlative qualities in judging the value of our experimental plants. In the breeding of animals even to-day we often see that almost as much attention is paid to correlative qualities as to real merit. Some of this is certainly due to the fact that in some material real merit can only be judged in one of the two sexes. There is no good reason to give any attention to correlative qualities. In so far as a real correlation exists, selection for real quality will automatically bring along the correlative character, and in as far as we are mistaken (and this will nearly always be so) we are simply led astray by paying attention to apparent correlations. In plant-breeding selection according to qualities believed to be indirect indications of good quality used to be very frequently attempted. I am glad to say this has gone out of fashion, and we only meet traces of it in very special fields (sugar-cane, apples). In our selection work we should always consider actual practical merit, and we should carefully study in how far the qualities we can examine, measure and weigh are indications of this real merit.

Chapter Thirty-two

The Importance of Collections

Most plant-breeding institutes own a collection of plants, sometimes consisting of imported and old varieties, sometimes completed with a collection of wild species. Such collections are of the utmost importance to plant breeding. We must remember that by selection we cannot *create* new genes, we cannot even *remove* existing genes that are present in all the plants. For this reason the possibilities for plant-breeding work are restricted to recombinations of the material present in our collection.

The importance of a collection of old varieties is sometimes seen in the historical interest, and occasionally old breeds are retained for sentimental reasons. This is wrong, for at any time somebody responsible for the collection may have other ideas; he may be less of a sentimentalist than his predecessors, or he may think the value of all those old varieties is over-rated now that we have so many superior new ones. The truth is that the collections furnish material for serious future plant-breeding work.

Every new gene added to the complement of genes in our present material doubles the possibilities of recombinations. Every novel (relative) gene-absence does the same. It is sometimes possible to use very important qualities of intrinsically worthless old kinds of plant. I remember a garden pea, called " Acacia". In this pea each leaf consists of an uninterrupted series of pairs of leaflets like a Robinia leaf, tendrils

being wholly absent. The plants therefore cannot attach themselves to supports or neighbouring plants.

One of the difficulties in growing field peas in wet summers in some countries lies in the circumstance that the young plants intertwine themselves into veritable mats before the time for hoeing the weeds is past. To give the plants another cultivation in May would mean tearing apart the tendrils; in most years this would be quite out of the question. For this reason I crossed the " Acacia " variety with a good, green, round field pea, and by selecting among the plants of the third and fourth generation I succeeded in remaking a green field pea with a good yield and a high resistance to mildew, but without tendrils, a plant which could be given a last hoeing fully three weeks after the ordinary peas in neighbouring fields had grown together inextricably. When we want to extend the region in which we can grow some group of plants it is often possible to find plant varieties in an extensive collection which carry qualities that are the very thing we want.

It is uneconomical to duplicate and triplicate such collections; it is much better to have one huge central " école " of cultivated plants than to have a number of incomplete collections in the hands of private plant breeders and plant-breeding firms. Moreover, keeping up such a collection costs money, and for this reason the collection, or some of its less-important-looking species, always runs the risk of being suppressed some day. It is evident that the Government should take over the task of keeping up such plant collections. The American Government has acted upon this idea, and its Plant Importation Bureau has done an enormous amount of very valuable work in this connection.

The keeping of a collection and the importation of foreign plants should go hand in hand. Especially in backward countries a wealth of plants is often present, and we sometimes find a great many curious plants well adapted to special conditions of season and climate. I am thinking of such remarkable plants as the Hopi maize, which comes up from almost two feet underground, the pea that buries its pods like a peanut, and the cauliflower-like sugar-cane of some of the islands around Java. Hull-less oats and hull-less barleys may

be out of fashion in some countries just now, nevertheless they carry extremely valuable characteristics, well worth preserving. Think of the extremely hardy peaches and apricots of the higher Himalayan valleys, of blight-free Chinese chestnuts, of the enormous seedless tangerines from Java.

Keeping a collection is no work for a geneticist; it needs its own specialists with a very special turn of mind—a zest for systematic work and for collecting. Perhaps philatelists might make excellent keepers for such collections! The chief source of plants in such collections must be importations from newly explored countries. Sometimes, however, it might be worth while to add some of the curious plants that turn up in the descendants of hybrids—plants carrying absolutely novel qualities, new for the group. Having an important collection of cultivated plants on hand makes it unnecessary to start hunting for suitable material whenever we want to take the amelioration of some plant group in hand.

Most plant-breeding firms and plant-breeding institutes keep some sort of a collection, mostly of plants that have or that have had some economic significance. I think it is of the utmost importance to centralize this work in every country.

Chapter Thirty-three

Importation

It is obvious that if somewhere in a foreign country some cultivated plant is used that fits better into our conditions than the plants of that same group we already have, importation of that plant is indicated. There are many instances in which a plant variety or a clone that was of commercial importance in one country was found to do equally well in some other country. Some of the popular American apples have lately become very popular in England and Holland, where thousands of trees have been top-grafted with Jonathan and similar apples. Perhaps this success of foreign plants is more frequent in horticulture than in agriculture. The case of the Washington Navel orange is another notable instance—a few specimens imported from Brazil just happened to fit perfectly into Californian citriculture.

Perhaps it happens more frequently that a good ready-made plant is found in an imported *mixture*. Marquis wheat and the Grimm alfalfa are good instances of this.

Whether an imported plant will or will not be a commercial success in any condition depends entirely on the question whether its genotype is adapted to the circumstances. For this reason we cannot be sure that high quality and good yield in one country guarantee the same in a new country. Consequently it may be worth while importing a great many different varieties or clones, to enhance our chance of finding a fitting one.

Plant importation is a very special subject, with a great many aspects. When in a group of plants that have originally been imported we are troubled with insect pests or with infectious diseases, it is always worth while going to the country of origin to study disease resistance and insect resistance in plants of that group. It is quite possible that we have introduced some insect pest, but not the parasite that kept this insect in check. It is also probable that in the country of origin pest-resistant or disease-resistant strains exist that will after importation prove extremely valuable, either as such, or, more probably, as material for cross-breeding with the plants already in our country. It is very likely that we shall find plant material that will not be immediately profitable, but that will give us some quality of which we are in need. I am thinking here of some of the Andean wild-growing or Indian potatoes, in respect to virus resistance and frost resistance.

It is evident that we have the best chance of finding useful plant material if we go to look for it in countries where the general climatic conditions, and especially the latitude (length of the day during the growing season), are like those of our own region. But there are many exceptions to this rule.

Whoever introduces foreign plants takes some risk of importing noxious weeds, insects or plant diseases, and it is important that plant importation should come under strict supervision. The danger is greatest when we are dealing with growing plants; and when we are importing shrubs, tubers or cuttings, it is important to keep those plants in quarantine for some time. Because of this danger, seed should, wherever possible, be imported rather than living, growing plants. There are several instances in which the importation of seeds works much better than one would ordinarily suppose. A good instance is that of citrus fruit. In grape-fruit, oranges and lemons one seed will generally give us more than one seedling. Of these only one is derived from the fertilized egg-cell; all the others are derived from the tissues of the mother-plant, and reproduce this mother-plant's genotype faithfully. If we want to import a collection of grape-fruits or oranges we can safely import fresh seeds, and reproduce our clones from those seeds, instead of risking the importation of budding wood.

Another instance is that of the potato or of the sweet potato. In this group we seldom find valuable plants in seedling lots. Only a very few seedlings will be worth keeping for extensive comparative trials. But it is evident that the chance of finding a seedling of good quality in seed imported from a foreign country is at least as good as that of finding a valuable clone in a collection of many commercially grown clones, that have been imported. If we import seed, we buy many more tickets in this lottery than when we just take clones that have already made their reputation.

If our object is to obtain material with which to improve our present plant assortment in some special quality, it is quite possible that locally grown, non-improved kinds, like peasant wheats or Indian village maize, will be superior for our purpose to well-known named varieties. In some localities those unimproved, locally grown plants may be a source of useful and comparatively rare qualities, that can, by cross-breeding, be incorporated into our own material. Here may be mentioned the extreme adaptation of the maize of the Hopi Indians to desert conditions, of frost resistance in Andean Indian potatoes, of boll-weevil resistance in some South American village cottons.

Frequently, of course, newly imported plant species that in themselves had no special claim on our attention may turn out to be very valuable. The horticulturists welcome every new gladiolus or dahlia, that has not yet been used for cross-breeding, into their collections, for they know by experience that its use may be the starting-point for novel geno-variability.

The U.S.A. Government, with its many professional explorers, its extensive gardens and its Bureau of Plant Importation, gives a shining example to the rest of the world (Fairchild, Meyer).

Systematic plant exploration and importation is the work of the specialist. Very much, however, can be accomplished on a small scale by private plant breeders. We may just buy the commercial varieties that the seed houses list in foreign countries, or when we are on the spot we may collect some seed direct from such villagers as make a habit of using their own seed. A visit to an outlying district on a market day may enable us to collect a great number of samples that will con-

tain many extremely useful things. As will be more fully explained in another chapter, there are some regions that abound in rare and possibly useful plants, and these are found mostly in mountainous districts. The markets in some of these regions will give us an enormous variety of plant material that could be collected from the real sources of origin only with enormous difficulty.

Chapter Thirty-four

Back-crosses

The object in many plant-breeding schemes is to improve one definite quality of a well-known plant. We may want to improve the resistance to a disease, or the quality of the product, or the winter hardiness. When we are dealing with one of the self-fertilizing plants—with wheat or barley or Phaseolus—the inherited composition of our plant is not flexible, the plant generally is completely homozygous. Of course we must never take this for granted, for in the commercial stocks the seed may always consist of a mixture of slightly different pure lines, so that unravelling those lines by one-plant cultures might give us the improvement we are looking for. If this is not so, there is no other way than crossing to improve the genotype.

We must remember that there is no object in cross-breeding to introduce a desirable quality if the two kinds of plants crossed did not differ in more than one gene; and it is probable that the plants crossed differ in several to several dozens of genes. If we proceed by growing the descendants of our hybrid plants and by selecting from among the self-fertilized offspring during several generations, we must realize that the potential variability of this group is very great. The hybrids are heterozygous for all the genes in which the parents crossed differed. It will take a long time to get rid of this genovariability.

In certain cases back-crosses are indicated. When we find

that our first-generation hybrids are definitely superior in the important quality desired, the quickest way of obtaining our object is crossing back to the strain we want to improve. Every succeeding back-cross halves the number of genes for which the hybrid groups are different from the plants we want to ameliorate, so that even one or two back-crosses considerably simplify our breeding problems.

Whether or not this technique of crossing-back materially lightens our work greatly depends on the difficulty of making the actual crosses. Back-crosses are certainly indicated for work with such autogamous plants in which cross-breeding is relatively easy, especially those in which one single cross-fertilized flower will give us a considerable number of seeds. In such plants as the tomato or tobacco, back-crosses would materially help to obtain our object.

In allogamous plants such as beets and maize things are not so simple as in the habitual self-fertilizers. In back-crosses with wheat or tobacco or similar autogamous plants we can be practically sure that every germ-cell from the pure-bred parent has the same composition as every other germ-cell, and this is certainly not true in the habitual cross-fertilizers. For this reason, among others, we cannot proceed in this material with the same precision, nor can we save as much time and space, as in back-crosses with autogamous plants. Yet there are certainly instances in which we can make very good use of back-crosses.

Let us examine the case of the sugar-beet. It is extremely unlikely that the most favourable combination of genes present in the diverse sugar-beets of to-day will give us the maximum yield and quality obtainable. It is almost certain that in other material—in chards, in mangolds, in the wild beet species—genetic qualities are present, which if they could be made available, would help to make further improvement possible. But anyone who has ever worked with wide hybrids in beets knows how hopelessly variable such cross-bred lots are in this material. We cannot help introducing an enormous amount of unwanted geno-variability by such crosses, bringing in genes that must be eliminated again, making the material heterozygous for genes in respect to which the sugar-beet seed selec-

tion has painstakingly built up purity. As material for the ordinary work of beet-seed selection such wide crosses are hopelessly difficult. But surely back-crosses will help us out of this difficulty. I would suggest to the beet-seed specialists that it would be greatly to their advantage to try the following method: Make a few wide crosses, say with mangold or *Beta maritima*, and then proceed by starting a number of parallel back-cross series, breeding back to good commercial stock. In this case I would recommend blind back-crosses. Such back-crosses would soon give them back reasonably good beets. In this material there would in some lines be found one or more whole chromosomes, or parts of chromosome derived from the foreign beet crossed in. After a number of such blind back-crosses the material would be sufficiently like the material they are used to, to begin submitting it to the methods of selection to which they are used.

In maize we are familiar nowadays with the phenomenal success of hybridization. In commercial seed production inbred lines are made, and these are combined for the production of seed corn on the farms. It is the rule that continued inbreeding will bring down the vigour and production of any line to a fixed minimum in half a dozen generations, and it seems evident that this degeneration is due to the dropping out of genes during the process of reduction of the potential variability of such lines. From the fact that some inbred lines are much more vigorous and productive than others it would appear that even in this material it would theoretically be possible to produce reasonably pure and very productive inbred lines.

Professor Harland tells me that in the Indian maize in some of the mountain valleys of Peru, where conditions favour inbreeding, strains are sometimes met with that are highly resistant to the universally unfavourable effects of strict inbreeding.

It would seem that it would be possible to ameliorate highly pure and long inbred lines of maize by the introduction of genes (chromosomes) by cross-breeding, by a process of back-crosses to the pure-bred line, followed by further inbreeding. At some of the American experiment stations this possibility is now being tried out.

The back-cross methods of introducing valuable new genes into old varieties takes advantage of the fact that the established plant is homozygous for a great number of genes, so that by back-crossing to it the material gradually becomes homozygous for all those genes. We have this relative purity of the established variety to fall back upon.

It would seem as if in the breeding of vegetatively propagated plants we would miss this advantage. Yet this is only apparently so. It is true that as a rule the generative descendants of one of these plants are extremely variable. Most vegetatively propagated plants are highly heterozygous, if only because genetic impurity is of no disadvantage in this material, and for this reason is not selected against. But of course even in those plants each one is homozygous for many genes in respect to which a cross-bred seedling is impure. Even in the work of finding new valuable clones of strawberries, manioc, apples, roses or potatoes, it will sometimes be wise to breed back newly made hybrids to older and valuable clones. It appears to me that a great many plants that are now discarded in the breeding work with such plants could very well be utilized in a back-crossing programme. In cross-bred or inbred seedling progeny we always meet with individual plants that are of no real practical value because they do not come up to an all-round standard of utility, but that nevertheless have some particularly outstanding virtue, or even that show a combination of valuable traits. Such plants can be utilized with great advantage in our breeding schemes. In potatoes, strawberries, apples, where we possess a number of valuable commercial clones, our best chance of obtaining something worth while will be to start from one of the best kinds and then try to obtain another very much like it in quality, but superior in some point in which it is weak. If we want to obtain the desired result by cross-breeding, and in the first lot of hybrids obtained we do not find quite what we want, we can start crossing with another commercial clone. But I think our chances of success are much better if we make use of some chance seedling that happens to be strong in the point we want to improve, even if, for any other reason, it would not be of great all-round merit. Such a seedling will be more similar in its geno-

type to the clone to be improved than another clone to be used for crossing, and it will probably give us a better chance of finding what we want, if we use it in a back-cross. The method of crossing back hybrids to one of the parental stocks is used more often in the breeding of animals than in plant breeding, mainly because self-fertilization of hybrids is out of the question in animals, while it is generally quite simple in plant-breeding work. To a certain extent this inbreeding of hybrid plants as a method of producing variable populations for further selection is used much more than we would expect. I sometimes think one of the reasons why so many plant-breeders work in this way is that the experimental geneticists have popularized this method for use in their gene analysis.

In many cases the method of breeding back hybrids to parental stocks during one or several subsequent generations has great advantages over that of inbreeding the first-generation hybrids. In those cases where we are out to produce as much variability as we possibly can, as in the breeding of flowers, inbreeding the hybrids may be the best method. But in many other instances the variability of an inbred second generation is unnecessarily great, so that we must work with enormously large numbers of plants in order to have any chance of finding a suitable combination of genes. In a back-cross generation the geno-variability is much less excessive.

The genetic explanation of what happens in a back-cross is simple enough. A hybrid between two different plants is heterozygous for all the many genes in which the germ-cells differed. This means that such a hybrid is heterozygous in respect to a great many genes for which one of the parents was pure. The hybrid may be *Aa* and the parent *AA*, or the latter may be *aa*. In each case 50 per cent. of the back-cross plants will be homozygous in respect to that gene, and 50 per cent. of them will still be heterozygous, like the hybrid. As this chance is the same in respect to every gene concerned, and while the number of those genes is large, we can say that compared to the parent used in the back-cross, each plant in the next generation is impure only for one half of the number of genes in respect to which its hybrid parent was heterozygous. In other words, by a series of repeated back-crosses we are

halving the number of genes for which the material is heterozygous, in every generation. The plants become more like the parent used in the back-crosses, and after a number of generations there is no difference between the hybrid and the pure-bred stock. During this process it is quite possible to direct and influence what is happening. If the hybrid is in any way superior to one of its parents, it may be tried for retention of this superior quality while getting back the qualities of the pure parent stock. If we do this we can make use of the relative purity and lack of variability of the parent. If we work in this way we need far fewer individuals in every generation than when we are bothered with the excessive variability in interbred hybrid material.

Chapter Thirty-five

Avoiding Castration in Crossing

In some plants emasculation of the flowers presents special difficulties. In the first place, the flowers may be so minute that a binocular microscope is necessary for the work, as in some grasses (finger-grass, sugar-cane). The structure of the flower may make it extremely difficult to take out the anthers without disturbing the style or the ovary, as in some of the legumes. Or we may find that the vast majority of the treated flowers tend to wilt, as in oats.

In many cases it is not really necessary to castrate the flowers from which we want to obtain hybrid seed. In such plants as soybeans or oats it is relatively easy so to choose the combination of varieties crossed that we can recognize the hybrid offspring from plants grown from the pollen of the flower itself. Choosing a father-plant with some clear-cut dominant quality, we need never be in doubt which plants grown from cross-fertilized flowers are hybrids and which are not. But even where no factorial analysis has ever been made, it is almost always possible to recognize hybrids from pure-bred plants if we grow them side by side in one group.

Instead of removing the anthers, we may wash the stigma clean of pollen before applying pollen of the desired father-plant. Oliver has worked out this technique for alfalfa. In some grasses (sorghum) it is possible to make the pollen inactive by treatment of the flower-buds by means of hot water. In certain plants with composite flower-heads some of the florets

are purely female. In zinnia, dahlia, and scabiosa the outside florets are pistillate, whereas the disk florets are complete. In some cases it is possible to cut away the disk florets, leaving the female, marginal florets for cross-breeding purposes.

In the garden bean—Phaseolus—it is sometimes possible to make the style and stigma protrude from the bud, by applying some pressure at the right spot. In those cases the flower's own pollen cannot reach this stigma, so that after pollination all that is necessary is to protect the flower with an appropriate bag.

Chapter Thirty-six

Cross-breeding Technique

There is hardly any plant-breeding project which does not involve cross-breeding. In most cases it is the object to produce variability, in order to obtain the material for selection to work upon. The quickest way to obtain variability is cross-breeding.

I think we should distinguish between the work of the plant breeder and that of the scientific worker. It is true that the great majority of plant-breeding problems are tackled at the larger institutes by genetically trained specialists, and yet the distinction should be made. In scientific experiments only the most painstaking precautions are good enough. We must be absolutely certain about the paternity in our hybrid plants, and for this reason both the collection of the desired pollen and the elimination of the pollen from the mother-plant must be done with the minutest precautions. If our object is a wholly practical one, we may often relax such precautions to a certain extent. For instance, in some plants castration—the elimination of stamens—is not only extremely difficult, but the manipulation brings a risk of seeing the flower wither and die. In such plants (soybeans, oats) castration can often be dispensed with, when we choose the parents in such a way that we can recognize the hybrids from inbred plants.

In every plant-family our first step must be to study the biology of the flower, in so far as this has not been done by others. We must know at what stage of growth of the flower-

bud the anthers dehisce, so as to hit upon the safe time at which we must perform the operation of removing them. We must also know when the stigma is receptive, to find the moment at which to apply the pollen.

In most plants castration and the application of pollen can be done at the same time. This is the case in rice, in most of the cereals, in tobacco, Ipomœa, cocoa, peas, beans and a host of other plants. In some plants with large flowers the stamens are attached to the corolla, and it is possible to cut off the corolla with the stamens in one operation. This can sometimes be done with the fingernail (apple, raspberry, strawberry) or with a scalpel. When a scalpel is used, it is sometimes advantageous to cover the blade almost up to the tip with adhesive tape, to avoid cutting down too deep. Where this is impossible, the stamens have to be extracted one by one. A set of fine pincers with differently curved tips should be in the possession of every worker. Very useful fine instruments can often be made to fit particular occasions. A very fine hook, made out of a bent pin, and mounted into a needle-holder can sometimes be used to great advantage, especially in castrating such minute flowers as in alfalfa or clovers.

For fine work a watch-maker's eyeglass, or even a binocular dissecting glass, may come in useful. On the whole, however, I would counsel dispensing with castration in plants with minute flowers, and to use the method of straight cross-breeding, leaving the finding of hybrids till next season.

In some plants male and female flowers are separate. In such plants no castration is necessary; all we have to do is to protect the flowers from unwanted pollen. In cucurbits, melons, squashes, cucumbers, we found it quite easy to close unopened flower-buds, by means of small pieces of copper, or preferably lead-wire. Of course both male and female buds should be so protected. Lead-wire has the advantage of being very soft, and it can be used many times in one season.

Especially in wind-pollinated plants, care should be taken to protect the pollen used against contamination with unknown pollen. For this purpose the flowers from which pollen must be collected should be bagged. In some plants pollen is so abundant that we can use a separate anther for every flower to

be pollinated, and we can hold this with fine forceps. Where the pollen is dry, it can be shaken out of the anthers into some small receptacle, for which a small gelatine capsule is just the thing. Such capsules can be closed, and the pollen contained in them can often be kept in very good condition for days, if the labelled capsules are kept cool in a well-closed bottle over calcium.

In maize both the male and female inflorescence should be bagged early. When the silks protrude they can be trimmed off short, and the pollen shaken over them from a tassel. If it is wished to obtain a cob full of kernels, it is of some advantage to insert a flowering tassel into the bag that covers the cob, and we can prolong its life and usefulness by standing this tassel in a small bottle of water hooked to the stalk.

In certain plants the operation of castration and fertilization can be performed on cut-off stalks that have been taken into the laboratory. In sugar-cane, in millet and sorghum, and even in wheat and barley, such panicles and ears, when stood in water, will ripen their seeds well, especially if only a few flowers are left on them for this purpose.

Paper bags should be of ample size, and it is necessary to leave them on no longer than is absolutely essential for full protection during the few days in which the stigma is receptive. In certain cases (coffee, cocoa) a finely woven tartan may have advantages over paper; it is softer, and can be arranged around awkwardly placed flowers better than paper. Of course it is useful in certain cases to give the ripening fruit or seeds some protection against loss or damage (stone-fruit, potato, tobacco, Œnothera), and paper bags may be necessary at that stage.

For keeping small quantities of seeds, small paper or preferably cellophane envelopes can be used. Gelatin druggist capsules, however, are preferable. The labels should be enclosed with the seeds.

Chapter Thirty-seven

Labelling, Numbering and Gadgets

Every plant-breeder and every geneticist has his special methods of keeping his records. To be able to do this he must have suitable methods of numbering or labelling his plants or seeds. Every man has his own pet gadgets, and perhaps it is quite unnecessary to enumerate those I have used, or tried, or only seen in use. On the other hand, a few words about such things may save one man some anxiety, or even some awkward mistakes.

Any system of labelling or marking must be legible and indestructible by weather or insects. For merely marking, as an aid to tracing a special plant or part in a field, a coloured thread may be quite sufficient. If such a thread is used in addition to a number or a label, it helps to distinguish that label. Paper labels, even if made from very good parchment paper, tend to become discoloured. To depend on such labels only, let us say in marking pea-pods, is courting trouble, for they closely resemble dried leaves or empty pods. The well-known Vilmorin red woollen thread is of very great value; it may even serve the double purpose of protecting the cross-fertilized ear of wheat or barley and of making it easy to find it again.

To mark seed capsules, fruits and such things, we found that lead-wire was much better than string. We can string a glass or china bead on a small piece of very soft lead-wire, and if we need a few dozen distinguishing marks, combinations of coloured beads will be excellent. We used this method in marking

cross-fertilized squash blossoms and melon blossoms. If we make a loop of sufficient width, we can squeeze one end of this against the fruit-stalk, and it will accompany the fruit until harvesting time, or even beyond.

A very good label that will never lose its legibility is a poultry leg-band with a perforated number. These are made out of thin aluminium, and can be opened and adjusted before closing. Such labels are just the thing to mark plants that must be taken up and wintered in a cellar, like dahlias. Most seedsmen use stout painted stakes for carrying the name and the number of rows and individual plants, the name facing the row it marks. To obviate mistakes it is safer to have duplicate stakes, or to have the name and number of each lot written on a separate stake.

To save time and worry, good use can be made of poultry leg-bands or of the newer coloured plastic numbered wing-shields. These are numbered on both faces, and can be bought in consecutively numbered hundreds or thousands. They can be hung from wire stakes with eyelets, and they accompany such plants as cereals or beans when they are bundled for harvesting.

In some countries one has to guard against theft and mischief. I have known a European blackbird pull out dozens of numbered yellow wooden labels and scatter them all over the place. A system of book-keeping which allows one to find the missing numbers from the book is indispensable if we want to avoid mistakes.

Numerous methods have been invented for protecting flowers and branches against insects or wind-borne pollen. Paper bags come first; they must be strong, rainproof and light. Some cotton-wool may come in very useful in making the connection of bag and stalk pollen-proof. Glassine bags and lengths of seamless sausage casing are being widely used in the United States. They allow one to see the inside of the bag, and so may save much time and error.

In some sympetalic plants flower-buds may be closed hermetically by the application of a length of very soft wire (lead-wire) wrapped round the bud, and used again after fertilization. We have used this method with squashes, melons and Ipomœa.

The American plant-breeding journals and publications

abound with methods for castrating and cross-breeding plants. In a special chapter I have treated of methods to avoid castration. Removing the pollen from the stigmas by washing it off (Oliver) or killing it by heat are methods I have never used myself, but they sound excellent.

Gelatin capsules, made in two pieces, of which one fits over the other, are handy receptacles for keeping very small quantities of seeds or of pollen, for slightly larger quantities sachets for internal use may be used; they are cheap, and can be written upon, but if we close them we can never use them again.

Paper bags must be used a good deal in storing seeds and similar objects (bulbils, bulbs, corms). They can be closed in different ways. The simplest system is the method of the French seed firms, in which each bag is closed by three folds, in such a way that it will never open spontaneously, even if submitted to considerable shaking.

The gadgets used in castration and cross-pollination are very numerous, and must be adapted anew to every new plant. Of course it is necessary to kill adherent pollen with alcohol, and extra scalpels, forceps or scissors are of great help. In working with very minute flowers a good binocular microscope is invaluable. Personally I would avoid castrating minute flowers as much as possible. Everyone doing this sort of work occasionally regrets he was born with only two hands and without a prehensile tail. A ring to which has been soldered a minute cup that holds a small gelatin capsule with pollen, and that can be worn on the index-finger of one hand, is almost as useful. This is another American invention.

Hard seeds can be treated in different ways to make them grow. Some seeds, like those of canna or musa, can be scratched with a file, others may be rubbed on stone. Œnothera seeds can be soaked in water; some seeds will only take up water rapidly when we exhaust the air above the water in which we keep them and then readmit the air.

Seeds of apricots, cherries and plums can be extracted after carefully cracking the stone. The extracted embryos (and the same is true for embryos of apples, pears and citrus) must be protected against bacteria and mould. Thymol solutions, even weak ones, will do this without injuring the seedlings.

Chapter Thirty-eight

Speeding-up Plant-breeding Work

Plant-breeding work involving crosses generally takes a great number of generations before the superior new plant has been obtained. In the routine work of a large plant-breeding station so many breeding projects are under way simultaneously that it matters little how much time elapses between the initial cross and the final purification of a promising commercial variety. Every year there are many projects being started, several are under way, and a few are in their last stages.

It often pays to cut down the time required for work of this kind. One of the most promising means of doing this is to grow more than one generation of plants in one year. This usually means that one of those generations of plants is grown in a season in which the plant is not ordinarily grown, and that for this reason a correct evaluation of the quality of the individual plants is out of the question.

In Europe or in America growing an extra generation on the spot means growing plants in the greenhouse. To grow cereals or beans in winter in greenhouse conditions not only requires heat; we must also have the means of regulating the length of day. The simplest method is to use large electric lights to furnish both the heat and the light, to lengthen the day by those means, and to let the temperature go down during the dark part of the night. Under those conditions cereals and beans will flower and set seed very well in the winter months.

The electricity required per square yard is roughly that used by lamps that require a kilowatt.

It is clear that under such conditions the winter generation will not show the normal qualities of the plants in that group which are grown in summer-time in the field, but there are many cases in which this is not of much importance. If we want to proceed by the method of making some hybrids and then growing a second and third inbred generation from this stock, we can do our crossing in the field, grow our hybrids in the winter, and then grow another crop of second-generation plants in normal field conditions the following summer. When we are using the method of mating back hybrid stock to some pure kind of plants we want to improve it matters but little if we cannot very well select the best plants during some of the generations involved. It is evident that we must grow a generation under normal field conditions whenever we want to make our selections.

In recent years a few seed-firms have hit upon the perfect scheme of growing two generations of annual plants. This does not involve any greenhouse generations. They work in two different localities with very similar climate, but so chosen that one of those localities is situated in the Southern Hemisphere. There are regions of Chili where Californian firms can find conditions of plant-growth that are identical with conditions at home, with the exception that the growing season comes during the Californian winter. In those circumstances it is quite possible to grow two absolutely normal generations during one year. Our present greatly improved methods of communication make such schemes perfectly feasible.

With many tropical plants one generation yearly is grown of plants that need special conditions of either a wet or a dry season. Here it is easy enough to interpolate an additional generation, by looking for a suitable spot, or by providing the necessary irrigation.

Sometimes it takes a very long time to bring the plants to a condition where we can evaluate them. A good example is that of the fruit trees. It takes many years for an apple seedling or a seed-grown cherry to come into bearing. Here we can save a great deal of time by budding or top-grafting

parts of the seedlings upon mature trees in full bearing. By this method we may save more than half the number of years normally required for bringing the seedlings to maturity.

In this connection we might also treat of those cases where certain seeds take a very long time to germinate. Storing the seed in suitable conditions of moisture, and especially of temperature, will speed-up germination in such plants as gooseberries and celery. In stone-fruits it has been found possible to crack open the stone, to extract the kernel and grow the seedlings under aseptic or even under antiseptic conditions (thymol solution).

Chapter Thirty-nine

Shows and Showing

The exhibiting of plants and seed at the shows is a very curious thing. It pays extremely well for a seed-firm to employ some gardeners who know just exactly when and how to get enough plants full of luscious beans or covered with flowers on the exact day for each show. Florists and lovers of gardening see the quality of such plants at the shows, and many people who admire them there try in their turn to win the coveted prizes at their local shows the next year. This show game is certainly very nice and pleasant; it gives the gardeners something to strive after; it may even help to keep some of the lads in the country.

On the other hand, there is very, very little connection between the qualities judged at the shows and actual value of the material shown. I have not only in mind the few selected mangolds, or the mammoth pumpkins, or the bundle of wheat-ears, or even of the maize-ear contests of the American agricultural shows. I hardly think anybody really took them seriously.

All along the line, in horticulture as well as in agriculture, the selected samples shown give no indication of the value of the seed or plant stock the producers have for sale. Of course we can see that those few mangolds have the ideal shape and size, but the seed-firm must give us some guarantee about the percentage of mangolds that will grow to this size and shape from the seed they sell, just as the owner of a prize-winning bull must

give some guarantee of this animal's ability to give profitable daughters, in addition to the blue ribbon awarded to the beautifully coloured and shaped prize-winner. In agriculture this is beginning to be so well realized that the classes for beautiful corn cobs or for the largest mangolds are becoming very rare indeed, even if we still see stock-judging in dairy cows and similar farces. In the horticultural shows much interest is still shown in regard to flowers and vegetables. I must confess that I like to visit a good show, and I hope they will survive for a great many years. It seems evident that when we strive for beauty, beauty contests for roses and begonias, for asparagus and delphiniums and dahlias are indicated. But once more, beauty is only one aspect, even in a rose! Will it flower all summer? Is the splendid new gooseberry mildew-resistant? How will this new dahlia stand up to rain? Will the asparagus pay for the trouble of growing it, with a good harvest during many years?

The show is a shop-window. The seller must show if his competitors show, if only to keep his name before the public. To the public the show is only just a pleasant occasion for a half-day outing. To the buyer the show is much nicer to see than a description in a catalogue. Long lists of novelties are bought at the shows by people with an experimental turn of mind. We see the representatives at the shows kept busy noting down long lists of orders. Showing certainly pays the seller.

A very much more sensible system of showing a great many varieties is that of the demonstration gardens and experimental stations, both stations in which the agricultural authorities try to compare promising new and good old varieties with the aid of objective standards, and such gardens as show-plots arranged by rose-lovers or by societies of growers of gladioli or dahlias. Here the varieties can be judged throughout the growing season in favourable conditions.

PART III

METHODS OF BREEDING AND SELECTION IN SOME SPECIAL GROUPS

The number of plant species now being cultivated by man is really enormous, while only relatively few animal species are kept under domestication. It is possible for the author of a book on animal breeding to take those species almost one by one, and to give the specialist breeders a few hints over and above those which are contained in the general book.

This would be quite out of the question in a book on plant breeding. One way out of the difficulty would be to give one example of each of the three groups—self-fertilized plants, cross-fertilizers and plants that are usually propagated by vegetative means.

I have tried to strike the happy medium between those two extremes, and I have added some special chapters—very short ones mostly—each dealing with some special group of cultivated plants that happen to have something in common, either in the matter of breeding methods recommended, or in the fact that they interest special groups of persons.

While I have tried to make the following chapters as useful as possible without too many repetitions, I realize perfectly well that anyone who would be so ill advised as to try reading them through one by one would find them a hopelessly miscellaneous lot.

Chapter Forty

The Annual Self-fertilizing Crops

I could treat of these plants in two sections—grains and legumes—giving some hints to the breeders of wheat, barley, oats, sorghum, rice, etc., and going into some details about the breeding of beans, soybeans, cow-peas, ground-nuts, peas, etc., separately. But, after all, the self-fertilizing annuals have so much in common from the point of view of plant-breeding methods that I would be repeating myself continually.

Self-fertilization causes isolation. Each plant, as far as reproduction is concerned, is as self-contained and isolated in a crowded field as it would be if grown by itself in a greenhouse in a city. The inbreeding caused by self-fertilization has several results. It makes all heritable variability disappear in every line, it makes every group consist of parallel lines, in which each plant descends from only one parent plant, so that the usual complicated network of ancestry is simplified into a system of isolated parallel lines. Where inherited variability exists, such as happens after a deliberate artificial cross or when accidental cross-fertilization occurs, it will automatically disappear. That is to say, it will disappear in so far as each separate line is concerned, for Mendelian segregation will make the lines, descending from any hybrid heterozygous for a great many genes, diverse in their hereditary make-up.

The result is that a field of self-fertilizing annuals that has not been grown from just one pure line by a plant breeder always consists of a mixture of a number of genetically different

lines. Even if accidental cross-fertilization or irregularities in crossing-over (mutation) are very rare, they do occur, and cause this state of things.

This genetic variability, however, is wholly different from what we find in other plants and animals. We are dealing with mixtures of pure lines, and almost every plant we take from any field is pure, homozygous for all its genes, and will, if its seeds are sown, give a very homogeneous descendance.

From all this it follows that enormous progress can often be made in all self-fertilized plants by simply picking out a great number of promising-looking individual plants and comparing their descendance. Many valuable widely grown wheats, tobaccos, peanuts and beans have been just found. They "just growed", like Topsy.

The first step in plant-breeding in the self-fertilizing plants must always be to look for those ready-made pure lines. The next is to find whether a mixture of two of the very best pure lines can be discovered which will give us still higher production (10 per cent. higher production from a mixture of two strains as compared with that of the best one is quite common).

We have then to produce some more genetic variability by deliberate cross-breeding. This generally means that we try to combine the good qualities of two different strains in one new one.

Here there are two wholly different schools of thought, and two wholly different methods. One of them is to analyse second-generation plants, and to find those individuals that do combine, let us say, the disease resistance of line *A* with the large quantity of big seeds of line *B*. This is a method invented by the experimental geneticists who are trying to combine practical plant breeding with purely scientific gene-analysis. As a theoretical geneticist, interested in genes and their action, I have been guilty of this sort of thing myself. It is great fun playing with a hundred different hybrid lots in one species, growing a few dozen second-generation plants in each lot and tabulating the results. But this is neither sound genetics nor sound plant breeding. We are dealing with so many unanalysed and unanalysable genes which all affect production and quality at the same time, that the chance of

finding something really worth while in a few hundred plants is simply not good enough.

As I explained in the chapter on inbreeding, there is bound to be an enormous "degeneration" due to unfavourable combinations of genes in cross-bred material, especially in self-fertilized plants.

The other method is based upon the realization that hundreds of genes are commonly involved, and upon the fact that purification—reduction of the potential variability—is rapid and automatic in this material. It consists of growing the greatest possible number of seeds from first-generation hybrid plants. We can then proceed in two different ways. One is an analytical method, which means that we are seeking for the very best-looking plants (for instance, by weighing their seeds), and progeny testing those plants by sowing a large number of seeds from each, in order to find the most profitable families. The other method is what Baur and Nilsson-Ehle called a "Ramsch" method. This consists simply of growing the descendance of a hybrid in a vast mixture, refraining from any analysis, and continuing this hybrid lot as a miscellaneous collection for five or six generations, sowing as much of the mixed seed of each harvest as we have room for. If we do this, natural selection will weed out most of the unproductive and undesirable types, such as those plants that ripen after harvesting time, all weaklings and all plants susceptible to diseases and pests. After five or six years that lot will consist of a mixture of pure lines, every line different from every other, with the successful lines represented by more individuals than the unsuccessful ones. After this we will treat the mixture just as if we were dealing with any other mixture, growing separate rows of beds each from one likely-looking plant. This is a very sound method, which saves a great deal of unnecessary labour and time. It is extremely difficult to find just how much better this method is as compared with that of analysis in every generation, starting from the second generation. I am inclined to think that an analytical method could be made to work very well, provided we did all we could to make the number of plants of the second and third generations exceedingly large (in the cereals we can get almost as many

seeds as in tobacco by splitting up the hybrid plant repeatedly before it starts to grow any stalks).

In actual practice there are only a few crosses that really produce anything worth while, and the general practice seems to be to make a great many attempts and grow a large number of first-generation hybrids. This renders it imperative to cut down on the number of plants per experiment. It is a vicious circle. I am convinced this is all very wrong and wasteful. I would rather have one cross every year and work with it, both analytically and by means of a " Ramsch ", doing the final selection after six years for one lot in every season, than waste my time castrating flowers and producing numerous hybrids that would have no really good chance of showing what they could do.

In all the self-fertilizing annuals we must be continually on the look-out for qualities that may be of special merit. I am thinking mostly of adaptations to special conditions. In wheat on irrigated ground, resistance to drowning may be as important as disease resistance or quality of the grain. Conversely, rice could be grown much more extensively if we would take the trouble to do some plant-breeding work on dry-land rices, which abound in the mountain villages of all the tropical Asian islands. In ground-nuts we should look for lines that are specially adapted to mechanical harvesting, as well as for lines adapted to the production of a first-quality product in the hands of tens of thousands of small cultivators. In all the plants of this group it is possible not only to improve the yield and the quality, but also to extend the area in which profitable production is possible. Tobacco, rice, soybeans and cow-peas are just as important in this respect as wheat, barley and oats.

Plant breeding with self-fertilizing plants is comparatively easy. It is even possible for the real amateur plant breeder to do some extremely interesting and useful work with some of the less well-known plants of this group—let us say with beans or cow-peas. Such work needs room, but very little special technical knowledge or talent for higher arithmetic.

I can greatly recommend keeping an eye open for " spontaneous " hybrids. Frequently a few plants will stand out from an otherwise quite even field of barley, beans or sorghum.

Such " high birds "—climbing plants in bush beans, high, semi-awned plants in wheat—are often accidental hybrids. If we sow a few of their seeds, we can see immediately whether they are hybrids or admixtures, for hybrids will have very variable offspring. If then we sow all the seeds from such hybrids, we can start a series of experiments that may easily give us something worth while, even when the father of the hybrid is unknown.

Chapter Forty-one

Herbage Plants

Nobody knows better than I that the division of the material in this part of the book into chapters is no more "systematic" than the well-known classification of hats into black hats, felt hats and Sunday hats. Overlapping between the categories defined is just as conspicuous!

Most cultivated plants are often grown for feeding to animals, even if, as in potatoes and wheat, they are mainly selected with the object of human consumption in view.

The plants specially grown for our domestic animals form a very miscellaneous collection. If we exclude such groups as the cereals (wheat for hay), potatoes and beets, sugar-cane and sorghum, beans and peas and maize and the brassica group, for the reason that they have been written about in other chapters, we are left with what, for want of a better name, we could call "grass."

Most plants for pasture, silage or hay have this in common: the plant-breeders have only comparatively recently become interested in them. It seems that so long as "natural" pastures and meadows are abundant and cheap, very few people are interested in the plants that make up their population. The management and use of grass land by grazing and hay-making, manuring and chalking, drowning and draining, burning and fire-protection, have been developed into a fine art in some countries, while in other districts the destruction of the grass-mat with the soil below it proceeded at great speed

as a result of over-grazing, ploughing, cash-cropping and dry-farming.

Rebuilding grass land by indirect means (Rothamsted) came long before general attention was being paid to the possibility of deliberately constructing pastures and meadows with the aid of selected varieties or clones, single and in mixtures. In a few isolated spots it was only at the beginning of the First World War that plant breeders realized that " grass is a crop ". " Grass-breeding " work started practically simultaneously in America, Denmark, England, Holland, India, Java and New Zealand, to name—in alphabetical order —a few countries prominent in this work The most spectacular results of growing grasses in a rotation of other crops must certainly have been due to the exigencies of " big-business " cattle-raising for European sugar-factory transport in the tropics. Indian, African and native Javanese grasses in pure stands under vegetative propagation can, under fair conditions of agriculture, produce phenomenal yields per unit of area. Under irrigation, a good clone of elephant grass produced for several years nine cuttings of 90 tons each per acre per cutting!

Cultivated grasses and legumes in this class, adapted to a very intensive system of agriculture by means of " soiling ", are in sharp contrast with those on the opposite extreme—the grasses and clovers adapted to extensive systems of cattle-farming in countries where labour is the most expensive item, as in Western Europe, New Zealand and parts of the U.S.A. The most outstanding and deservedly best-known work in this group of plants is associated with the names of Sir George Stapledon and the Aberystwyth group of plant breeders. This is not only due to the application of sensible plant-breeding methods on extensive collections of native and imported varieties of each group taken in hand, for similar work has been going on in dozens of plant-breeding stations and in the hands of many individual breeders all over the world. To a great extent the fame of the British " Stapledon group " is certainly due to the experiments on the *use* of pasture and hay plants in short and long leys. After the " shot-gun " mixtures that tended to be recommended as a result of the

botanist's analysis of good old permanent pasture-lands, the success of simple combinations of one or two selected grass lines with one or two selected clovers has been a revelation! The Second World War has shaken even the most conservative, agriculturally stolid countries into the realization that efficient methods of food production demand serious attention. If this period helped to give us a general interest in better, more efficient animals, and in better, more efficient grass, the world is able to show at least something on the credit side of the balance.

Among the ten possible ways of dividing the collection of herbage plants, there is one that is of great importance for individual plant breeders! Some of the important groups can be propagated vegetatively, and where seeds are sown, some plants are habitual self-fertilizers. The third group, in which cross-fertilization occurs, or where it is the rule, is by far the largest.

When, about twenty years ago, the plant breeders in Holland talked of organizing the grass selection in such a way that each firm would specialize in a separate species, it became very important, for obvious reasons, to know just what grasses were habitual self-fertilizers.

Herbage species, in which vegetative propagation by plant division or cuttings is economically justifiable, are rare, except in the tropics. But both in lawn grasses and in stock-feeding grasses such species do occur. In such plants experimental plots must show the comparative value of several clones, both in a collection of imported and local clones, and among new clones grown from seed. The methods of sugar-cane selection can be copied when we are trying to find the best clones of elephant grass or of Rhodes grass and others of a similar character.

In self-fertilizing groups, what is true of wheat and barley is true for these species. In cross-breeding and in just sowing wild-found seed very large numbers of seedlings and seedling pure lines should be tried. Small numbers make this selection work too much of a gamble.

Vegetative reproduction, even where it is out of the question as a final commercial method, can be of enormous interest when

we want to produce very great numbers of seeds from individual plants. In cereal breeding work it is much easier to split up a hybrid wheat plant into thirty pieces during the winter, than to make the fifty cross-fertilizations that would give us about the same number of hybrid flowering heads, and of course the same is true with other grasses. A row of ten plants of one clone gives us a much better picture of the colour, shape, type and general qualities of a " number " than the one seedling plant.

Vegetative reproduction, as a first step in the breeding of herbage plants would be of great value even if this recognition of the plant's phænotype were its only merit. But of course this is far from true. It is evident that the plants that belong to one clone are still heterozygous for all the genes in respect to which the original plant was. But, after all, this potential variability of such a clone is only a restricted one.

The variability among the seedlings from a plot consisting of alternate rows of two clones of white clover is limited by the fact that the two individual plants from which the clones were started were pure in respect to a number of genes, while they only differed among themselves in, or were heterozygous for, rather a restricted number of genes. Compared with ordinary seed from a multiform population, such seed from one or from two selected individual plants gives us a (relatively) homogeneous crop. This gives the plant breeder the possibility of a process of progeny testing, in which a great many progeny groups are compared with well-known standards in different conditions.

The very first step in selection in all herbage plants must be to analyse the quality of a great many isolated individual plants in native and foreign samples. Variability in wild populations is generally enormous, and valuable types should be found in almost any collected sample. Novel qualities, unexpected in the species, are often enough met. A very good example is that of the " rhizoma " alfalfas that are now being tried in British Columbia, in Arizona and in different continents.

In concluding this chapter I want to add a few words on grass-seed trials, especially on official certification work connected with such trials. The example of the work with hybrid

maize should make it abundantly clear that the quality of the plants grown from first-generation hybrid seed, in grasses or in clovers, should never be taken as an absolute guarantee of the quality of the seed grown from such lots, if two or three generations of propagation must be interposed. Official seed tests should be sampling tests based upon the quality of commercial (farmer's) seeds.

Chapter Forty-two

Sugar-cane, Sorghum, etc.

Sugar-cane is best known as an extreme instance of a crop for big business—a real plantation crop. Curiously enough, the most extremely " highly bred " clones are found in the hands of very small cultivators, and it is highly probable that in spite of the expensive Government- and associations-subsidized experiment-stations, the naked cannibals in the interior of New Guinea have the distinction of having made those clones out of very unpromising wild material.

Without any doubt the origin of sugar-cane is polyphyletic: the variability that gave birth to our present " noble " clones must have been due to good combinations and accumulations of chromosomes from several wild species of tropical and sub-tropical canes. Even to-day those wild plants of the cane-brakes are being used to furnish still more genes; the history of our present sugar-cane clones is a story of repeated crosses with wild species, followed by many back-crosses.

From a cytological standpoint, the case of the sugar-cane is exceptional. We know many other cases in which doubling and repeated doubling of whole sets of chromosomes have probably taken place in the evolution of cultivated plants, but the evidence is mostly circumstantial, the chromosome numbers tend to come in multiples of some basic number, and reduplication of one original set seems the best explanation. Of course the sudden duplication of chromosomes in sterile species hybrids (triticales and primroses), which gave us fertile

strains, makes this explanation of the existence of tetraploid and sextaploid species and varieties extremely probable. In sugar-cane the accumulation of chromosomes has gone to a very great extreme (unless some of the enormous numbers are due to breakage). There is some correspondence between high chromosome counts and size or vigour, and the possibility is not excluded that selection for thicker and thicker canes has had something to do with the very high chromosome counts.

The history of modern sugar-cane is closely bound up with the Dutch sugar production on Java. Two factors have been of very great importance: the fight against virus, and the governmental land policy. To start with this last factor, it must be realized that no Europeans are allowed to buy any land on Java (with the exception of reclaimed swamps). Agricultural land is owned by the Javanese, and may be rented only for half the year—for instance, between two rice harvests for the cultivation of peanuts or maize. Sugar is an exception: land for sugar may be rented for eighteen months, on condition that the same land cannot be rented for another period of the same length. The object, of course, is to protect the natives against their own cupidity and to ensure sufficient harvests for the ever-growing population. This means that sugar-cane must be of a very early maturing kind, and that rattooning is out of the question. The ability to give a second crop from the old roots is of no importance in selection, as it is in countries where the preparation of the ground is expensive and where nobody cares about the pauperization of the inhabitants (which seems to be a " natural " result of sugar-planting almost everywhere).

Early in the history of sugar-cane on Java it was found that the only way to avoid failures and poor harvests was to grow some cane for planting purposes at high altitudes. Special " bibit-gardens " were established, and some specialists made a very good business of selling disease-free cuttings.

As soon as it was realized that the cause of the chief diseases was viruses, virus resistance became one of the many qualities the experiment stations were striving for. It was found that some of the hybrids between two different species of wild canes with good sugar-cane were completely disease resistant. This

cannot be wondered at if we remember that the wild cane-brakes exist in all the hottest and most unfavourable spots.

I do not want to go far into the origin of the latest sugar-cane clones, with their history of professional jealousy between rival experiment stations. The facts are simply these: repeated back-crossing of hybrid canes to productive clones finally gave a number of new canes that were so resistant and so productive that the " bibit-gardens " went out of business. New plantations can now be planted with the tips of the harvested canes. A few clones, especially the P.O.J. (Proefstation Oost Java, geneticist Jeswiet), have been grown all over the world in sugar-producing countries. It so happened that they rattooned well. They have produced many valuable seedlings and hybrids in Indian, American, Queensland and Cuban experiment stations.

Sorghum is an African grain, now grown all over Asia and America for grain, silage and sugar. Special varieties have been selected, mostly from hybrid lots, that are well adapted for the production of syrup. It is only rarely that attempts have been made to select sorghum for crystallizable sugar, but I see no reason why such attempts should not be crowned with success, if it has been possible to eliminate so many impurities from sugar-beets.

Both in Java (Rümke) and in India it was found feasible to cross sugar-cane with entirely different grasses, and in both cases vegetative reproduction of the generic hybrids was secured. It is possible that those are the first steps towards the creation of new sugar-crops that will combine the short life of sorghum, which fits in well with usual systems of rotation, and the high saccharose content of the canes.

Maize should be kept in mind as a potential source of sugar. I know that beet-sugar specialists have tried maize stalks and have found the pressed juice to be a hopeless green pudding. Yet I know of very few plants that are so variable and adaptable as maize, even as regards the chemical constitution of the seeds, and so far the seeds have been given almost all the attention of the breeders. I am not thinking of a double-purpose plant that will give a crop of grain plus some sugar in the stover. The example of flax or of sorghum shows us that

specialization in separate varieties is more likely to succeed. The pressed juice of sugar-corn plants differs very much from starch-corn plant-juice. Some of the South American maizes, with their well-buttressed stalks and swollen internodes, at least point in the direction of possible maizes for the production of stems.

Chapter Forty-three

Flowers and Ornamental Shrubs

Several things combine to make plant-breeding work with flowers a hobby. Perhaps the obvious non-utilitarian preoccupation with sheer beauty attracts the amateurs. It is obvious that even the professional horticulturists who make their living out of producing novelties are real fanciers and seldom give up this pursuit even when they retire from business.

A great many novelties in flowers, in roses, dahlias, chrysanthemums, and even callas and tulips have been produced by non-professionals working in their gardens as a hobby, and it always pays the professional to have an eye open at the horticultural shows, especially at the small local ones.

In the chapter on somatic mutation I have spoken of the circumstance that certain classes of plants are very apt to produce " sports ", and perhaps looking for sports in roses (especially in polyantha roses) is one of the best ways for a real amateur who likes to grow a novelty of really high merit.

If we sow some of the seeds found on our rose-bushes, we are certain to obtain an extremely variable lot of seedlings. But this is a lottery. There is a possibility that we shall find a bush with a combination of genes that will give it all the qualities we are looking for in another ideal rose, but the qualities required are so high, and the chances that every plant grown from those seeds will have some minor disadvantage is so great, that even the amateur had better collect plenty of seeds and sow a few rows of seedlings. On the other hand, the

" sport " will probably differ from the mother-plant in just one striking point, and if this mother-plant belongs to a well-known variety, it will have all those good points of the mother. In roses the best-known " sports " differ in colour, or sometimes in habit. Climbing sports of non-climbing bushes are by no means rare. The fact remains that in the Polyantha group most of the recent new varieties are sports found on other well-known roses.

Exactly the same is true of lilacs and of many ornamental bushes. Fastigiata and pendula forms may arise as seedlings, but most of them have arisen as sports. It is quite possible that in the origin of fastigiate or drooping " mutants ", no difference in the genotype—the set of genes in the cell-nucleus—has taken place at all. We may have been dealing with a change in the disposition and arrangement of the kinds of cells that make up the outer layers of the branches—something that would be comparable to what happens in the formation of periclinal chimeras (see that chapter). Different facts point in that direction. Quite often the seedlings produced by self-fertilization in a fastigiated plant are *all normal*. Again, pendula varieties may " sport back " to normal—a phenomenon which reminds us strongly of what we see in Cratægomespilus or in Adams laburnum.

In many plants the " habit " of the flowering branches differs strikingly from that of the rest of the plant, and this change is irreversible. When we make cuttings of flowering stems of the ivy, the bushes formed from them will seldom or never revert to climbing ivy. In many plants, such as cypress or coffee, only the erect-growing branches when budded or rooted will give rise to normal upstanding trees: the material cut from horizontal branches will give rise to trees that grow in every direction except upwards. In all those cases seedlings will again reproduce normal plants. Such " sports " cannot be reproduced from seed any more than can the chimeras.

Where vegetative reproduction is possible, the gardener wants only one individual seedling, or one individual " sported " bud, to reproduce the novelty. This is a great advantage for the amateur plant breeder, as the fixing of a novelty reproduced from seed calls for considerable equipment. Enforced self-

fertilization, where this is possible, combined with progeny testing, will do the trick. The bigger firms even to-day often prefer to leave things to chance; they isolate their numbers by scattering them between plants of different kinds.

In all kinds of flowering plants cross-breeding is the commonest and best method of producing novelties, in plants always grown from seed. I want to repeat here that this not only means that by cross-breeding we can obtain novel recombinations of existing characters, but also the actual production of qualities never before seen in the genus. From what I have seen in argemone, in antirrhinum and in digitalis—to name only a few groups—I am absolutely convinced that what are called " mutations " are often the result of novel combinations of genes present in the two species crossed.

The great value of newly imported plant species—plants that have never before been imported—does not at all lie in the presence of striking novel qualities. They may be wholly inconspicuous, but they may carry genes, new for the group, or they may even carry some common genes in a different chromosome or in different positions on the same chromosome. All this will be sufficient for the origin of wholly new qualities: differences in flower colour, in shape, in doubleness, differences in size and habit, in flowering time—in every quality we can name.

Flowering bulbs—hyacinths, amaryllus, lilies, tulips, daffodils—seem to be in a class apart. This, I am convinced, is true only because it takes a lot of patience and technical knowledge to grow novelties from seed. In this group the warning I have so often given should be taken to heart by the specialists. Their eternal preoccupation with crossing is greatly exaggerated; it pays to sow self-fertilized seed or seed that " just happens ". This is especially true in cases where the breeder has indulged in a cross with a " botanical " tulip or hyacinth. First-generation hybrids that fail to satisfy our requirements should never be scrapped when they have been made with a deliberate idea in the mind of the breeder. They should be cherished and self-fertilized to give a large second generation.

Another counsel: one should never consider a freakish novelty ugly. Tastes differ! When I grew a few double-

flowered nasturtium plants from seeds bought in a cheap packet in 1908 in California, I carefully pulled out those plants. And see what happened twenty years later!

There is no accounting for tastes, even in flower-show judges. Striking novelties are always worth preserving for further breeding work.

The flower trade all over the world makes the production of good flowers a very paying business. The sale of seeds, bulbs and shrubs to amateur gardeners is only one side of the picture. The flower shows are closely bound up with this. But the professional florists are potential customers who look at plants in a very different way, and whose requirements should be reckoned with by the plant breeder.

The professional florist wants his flowers to be adapted to the requirements of the flower market. He needs plants that will give him what the public demands, and so will enable him to make a profit. In dahlias and roses the specialists produce hundreds of novelties every year, and the amateur gardeners buy them at paying prices. They admire thousands of varieties at the big flower shows, where named bunches of cut flowers are displayed. On the other hand, it is surprising to see how very, very few roses or dahlias are really used in the cut-flower trade. This may be partly due to plain conservatism, but most of this conservatism is wholly justified. Even after a rose or a dahlia has won the highest honours at the shows, it will take at least five years of careful experimentation before the florists know whether or not there is " bread " in it—whether it can be grown profitably in competition with the usual sorts. A good florist's dahlia must give a good succession of perfect blooms, that will keep on coming till the very end of the season, in spite of sun or rain. It must be showy, long-stemmed and disease resistant.

Very, very few roses or lilacs are fit for dual purposes, for garden use and for the cut-flower trade. Exactly the same is true of tulips and begonias.

Chapter Forty-four

Tropical Fruit-trees and Tree-crops

This is an enormously varied subject that no single book could begin to do justice to. The different trees often fall into quite different categories, both from the point of view of the economical exploitation and from that of the plant breeder; and both standpoints ought always to be kept in mind. Some species that were known as typical forest trees of which the products were collected by primitive natives (oil-palms and Hevea) may suddenly find themselves in plantations directed by sleek city men in luxurious offices.

The date-palm of the South Arabian desert oases is grown in flourishing Californian plantations in which Hollywood Arabs on " location " are grudgingly admitted for the shooting of Hall Caine dramas.

The enormous advances in production and quality obtained in rubber, oil-palms, and coconuts in Sumatra, in tea and coffee in the Javanese Government experiment stations show what can be done in the tropics by a few geneticists.

The four or five plant species enumerated here happen to belong to a group in which reproduction by seeds is about the only common factor. In such plants success by means of selection tends to be phenomenally rapid. I can think of no other field of applied genetics where a geneticist can be so certain of success.

Most tropical fruit-trees in the narrower sense—mangoes, alligator pears, mangosteen, citrus fruits and custard apples,

to name but a few—are generally propagated by vegetative methods, by cuttings and tjankokans, or by budding. Native horticulture everywhere tends to preserve the very best of chance-found wild seedling trees, as well as the valuable " sports " that are noticed on valued individual trees (rambutans and kapulassans in different colours).

In all tropical countries plant importation in the hands of Europeans amounts to only a fraction of what is going on in the hands of some of the humble villagers in Asia, Africa and South America. Phytopathologists are up against the most serious problems, which they share with the entomologists everywhere.

Very few fields of agriculture promise as much profit for private enterprise (and incidentally for world economics) as the establishment of collections of exotic plants, as the history of some of the oldest botanic gardens will abundantly prove (Kew, Buitenzorg, Colombo, Washington). And tree crops are very conspicuous in those lists of exotic immigrants.

The only real difference between tropical tree crops and non-tropical agriculture and horticulture lies in the circumstance that rapid reproduction and the presence of pioneer conditions and undeveloped areas make it possible for enthusiastic explorers and plant breeders to follow up their results during a sufficient number of generations of trees. But the methods used do not differ from those employed in the improvement of pears or cherries.

Over-production in some crops (coffee) or the competition by chemicals (Cinchona) or by other crops (Hevea against Ficus rubber), may quickly make some crop unprofitable, and this often makes it possible to substitute another plantation crop that has approximately the same requirements as far as climate and the available labour are concerned. A moderate collection of other crops and a little plant-breeding work can be recommended to every plantation manager.

In long-lived tree crops plant pathology is of the very greatest importance. Unchecked virus diseases may easily wipe out all profit, and the same is true of some insect pests (coffee, cacao). The change-over from plantation production to cultivation by thousands of scattered small cultivators may spell ruin to

certain crops (cacao). The remedy—if one exists—is obvious. It consists of a hunt for trees that will, in the midst of disease and devastation, escape because of an inborn resistance. Here I want to repeat what I have perhaps repeated all too often: when such disease resistance is insufficient in our cultivated trees, wild related species should be included in the experiments. The qualities of such wild material are really unimportant, so long as the resistance is there, provided we can obtain fertile (or even partially fertile) hybrids.

Chapter Forty-five

Non-tropical Fruit

A rough division between the breeding of tropical and non-tropical fruit-producing plants is useful only in so far as the two groups of plants are likely to be worked with at different experiment stations and in different countries.

In the general chapters—especially on vegetative reproduction—much has been said which need not be repeated here. For some reason or other, the breeding of new apples and pears has given rise to a great many unwarranted generalizations, and this might well be that part of plant breeding in which the theoretical geneticist may do most good to help the breeders avoid costly mistakes.

What I said about the need for awaiting a second generation if we want to combine the good qualities of two kinds of plants, applies to the breeding of fruit-trees more than to any other field. If we want to produce apples fit for very cold latitudes, it is encouraging to find crab apples in Northern Siberia that will thrive in very high latitudes. It has been shown that hybrids of such winter-hardy crab-apples and our cultivated varieties are quite fertile enough to give us some seeds for large numbers of second-generation seedlings. It would seem that there is no reason whatever for submitting the first-generation hybrids to situations where almost all of them will die. Hundreds of hybrid trees have been winter killed, while it would have been quite simple to grow them at some more sheltered spot, where they would have been producing seeds or pollen to

be used for further breeding work. The majority of plant breeders interested in extending the northern limit of apple culture must have been thinking in terms of first-generation hybrids only. It is true that it would be very handy to find a few genes that could be used in back-crossing work, so as to combine the qualities of well-known and popular apples and pears with greater winter hardiness. But certainly the second generation, derived from first-cross trees, would give us all sorts of combinations of fruit quality and winter-hardiness to choose from.

It so happens that in three different parts of the world I have met with a firm belief in correlations between quality of fruit-trees and such characters as spininess and leaf-colour or size. The reason for this seems to lie in the inability of the plant breeder to keep his thousands of seedlings until he can really judge them. This means that he is likely to start weeding out his seed-beds, rejecting plants with elongated leaves, with spines, with unpopular leaf colours, etc., etc. In other words, he selects a few plants that show some resemblance to popular apple and pear varieties. Then, when he has only a few seedling trees left, he may find that 20 per cent. of them are worth naming and propagating. If he started with a thousand seedlings, and has twenty left out of the hundred he let grow up, this does not prove that he actually picked the only twenty fair ones out of a thousand. It is much more probable that he threw away one hundred and eighty that were on the average just as good as his twenty.

We must, of course, distinguish between causal correlations and prejudice. It is quite possible that triploid apple-trees may average better in quality and fruit size than diploids. But if this is true it will be simple enough to save all the triploids for further testing, picking them out by means of size of epidermal cells.

At the plant-breeding station of Svalöf, Nilsson-Ehle, starting from the fact that so many of our best European apples are triploid, some years ago began a search for tetraploid seedlings in the descendance of the triploid Dutch variety " Goudreinet " (synonym " Belle de Boskoop "). A tetraploid tree, once it has been found, must necessarily produce nothing but triploid seedlings from crosses with ordinary diploid apples.

Both in the apple and the pear, excellent qualities, such as winter hardiness and resistance to different diseases and pests, have been obtained by cross-breeding with imported foreign kinds, but too often the choice has been restricted to first-generation hybrids only.

What I said in Chapter 26 on sowing *versus* crossing applies particularly to fruit-trees. It is very much worth while looking over the quality of great numbers of seedlings produced from good commercial kinds. I make this last restriction, because seedling cherries and seedling plums are often grown in enormous quantities from rather inferior stock, just because the seed is cheap or because those seedlings have a good reputation as standards upon which to graft superior stocks.

Here is another field in which the amateur plant breeder can do some very interesting and potentially useful work. To grow some hundreds of seedling trees until they come into full bearing, with the knowledge that one is bound to weed out the great majority, may not appeal to the amateur. However, he may have a few strong old trees in his orchard upon which he can graft dozens of seedlings. The amateur gardener, who does not want to wait for ten years to see his results, may buy a row of seedlings from a reliable nursery that will be able to tell him from what varieties the seeds or stones were derived, and he can then graft suitable scions cut from those seedling trees all over the crown of an old tree in full bearing. This should give him some fruit in two or three years. An old tree covered with thirty or forty branches representing as many different potential new varieties is a wonderful sight, both when in flower and when ripening its fruit.

Finding a new, promising peach or pear or cherry is, of course, only the first step. Some of our present commercially grown varieties have very serious faults. The apples may be ripening very early and sell well, but the tree may die off in a few years; the peach may be luscious and a good shipper, but the tree may stand late frosts very badly in many years. Some trees are quite self-sterile, and will need interplanting with another inferior kind. Only long experience over a period of a great many years will tell us whether a new seedling fruit-tree is worthy of planting on a commercial scale, and even then

it may never be able to make any headway against an older kind to which the factories have adapted themselves.

This last consideration makes it imperative for the plant breeder to study the good points and the weaknesses of widely grown commercial varieties. His best bet will always be to improve upon widely known varieties, especially if he can—*e.g.* by repeated back-crosses—reproduce them exactly, while improving them in one or two points where they are weak.

Somatic mutations are far from rare in fruit. Anyone familiar with the phenomenon will find mutated branches upon apple-trees, in black currants, in apricots and almonds. Nurserymen must always be on the look-out for such mutated branches if they want to avoid selling their customers trees that depart from the accepted standard.

On the other hand, a somatic mutation may give rise to a valuable "sport". Such sports have one advantage over seedlings: they are generally very much like the parent tree, and if this belongs to a commercially accepted variety, the "sport" will be likely to show similar virtues. A white-fleshed peach may give a branch that will breed true for yellow colour. This new kind will almost certainly be a clingstone or a freestone, very similar to the parent; it will flower and fruit at the same time; it may be quite acceptable to the packing industry. It will remain true. Of course the best varieties have so many points in their favour that "sports" found upon them will almost certainly be inferior. But this is never quite sure; it always pays to be on the look-out for such novelties.

In most cases fruit-trees are highly heterozygous: they will not come true from seed. It is evident, however, that in some groups we should save time and money if we could reproduce the young trees from seed. This is especially true in those cases in which we can easily obtain the seed in good quality and quantity—for instance, from the canning industry. Some plums (greengages and German jam-plums) are mostly reproduced from seed. And there are indications that the same can be done in some of the raspberries and strawberries, in which vegetative reproduction is difficult, or in which virus infection is widespread.

Chapter Forty-six

The Potato and Other Agricultural Tubers

There exists a long list of plants, the tubers of which are grown for human food or for stock-feeding, of which most are confined to tropical countries. These plants all have this in common: that they are propagated by replanting some of the tubers or shoots formed, that new varieties are almost exclusively grown from seeds, and that it is often rather difficult to obtain such seeds.

The potato is perhaps the most widely grown and the most typical plant of this group, and what relates to the potato is to a great extent applicable to the improvement of all the other tuber-producing plants of this group.

One of the most interesting plant-breeding problems is that of the " degeneration " or " running out " of the older potato varieties (and of many other vegetatively propagated plants, from the apple to the raspberry). When it was discovered that true seedlings were often very vigorous for some years, after which they started to degenerate, many authors were of the opinion that we were dealing with a true senescence. Every clone was thought to represent one single individual plant, and every individual plant has only a limited number of years allotted to it, just like every other individual.

A later hypothesis may have originated with me. I am no great stickler for priority, but in 1912, in my first plant-breeding book, I stated it as my opinion that in those cases we were not dealing with ageing at all, but with disease and infection,

and we can say that this hypothesis is now generally accepted. We now know what was not known around 1912: that virus diseases rather than invasion by micro-organisms cause the majority of cases of this " degeneration ".

Seedlings are generally vigorous, or rather, in seedling lots we can generally select a good many vigorous individual plants that may be worth growing, and sowing potato seeds has become of great importance. I may say that in some countries, notably in Holland, sowing potato seeds has become a veritable hobby of a large number of young farmers. The central Plant-breeding Institute furnishes potato seed, the farmers sow the seed and bring the plants to maturity, promising novelties are planted in an infected field for Dr. Oortwyn Botjes to test their resistance to " wart " while their resistance to a great many virus diseases and to Phytophthora is also systematically tested.

The sowing of potato seed can be strongly recommended to amateur plant-breeders. It is easy to find seed-balls in potato-fields, although some varieties never produce seed. The seedlings can be grown under glass and potted up like tomatoes to be set out when all danger of frost is past. A very good idea can be obtained of the shape, colour, and even of the yield of the plants in the first summer if they are planted far enough apart in the field. No two will be alike. It is a fascinating hobby, and the amateur has as good a chance of winning a prize as the professional.

As I explained in another chapter, deliberate cross-breeding has been done so often with potatoes that very good success can be expected from just sowing the self-fertilized seed that happens to be found in the field. Seed from the middle of a field should be better in this respect than seed from plants adjacent to a potato field with another variety.

There are two ways of combating the " degeneration " of potatoes by virus infections. One is the time-honoured method of growing the seed potatoes in a climate where there is little chance of infection (very few plant lice) and where the growers have learned special methods of selection. The other is breeding for virus resistance.

To keep healthy stock free is the business of the professional

seed-potato firms. Islands in exposed positions have a very good reputation. Prince Edward Island does a thriving business furnishing the New England States with chit potatoes, Texel does the same for Holland, and many of the Scottish potatoes are island grown. High altitude has the same effect to a great extent (see chapter on " Virus "). The method of selection consists mostly in growing the plants in rows that are very far apart, and rejecting any row in which even one plant shows any evidence of infection.

Breeding for virus resistance to a certain extent could be called a process diametrically opposed to this business of keeping the stocks free from infection. It consists of finding plants and strains that will be able to live with the virus—in fact there is some evidence that a virus which is obviously injurious to many plants can be a normal constituent of the cells of some other plant.

The virus specialists have named and numbered several noxious viruses, and the potato breeders strive to combine immunity against most of them into new seedling varieties. They are gradually building up resistance by combining into one plant the specific immunity of several.

In all sorts of plants it has been shown that one of the most promising methods of obtaining virus immunity is to dip into the relatively unexplored reservoir of wild species. This has been found true in the case of sugar-cane and of Phaseolus—to name only two—but it is certainly true of manioc and of the potato. The Andean potato species have proved to carry important genes that can help the breeders of potatoes in their work of producing frost-resistant and disease-resistant potatoes.

Plant-breeding work on such plants as the potatoes tends to be centred in a very few places, probably because of the fact that specialists of the calibre of Salaman are rare. It should be emphasized here that every potato-growing country should do at least some testing of numerous varieties, to find a few that really suit local conditions. To continue the importation of Scottish or Canadian tubers in order to grow them for just one or two seasons seems a very inefficient method of agriculture. The example of the sugar-cane shows that adaptation even to extremely trying tropical conditions is largely a matter

of disease resistance, and I am convinced that the solution of potato-culture in tropical countries must be sought along plant-breeding lines.

A word should be said here about seed production. In some plants with edible tubers—such as the potato, the Jerusalem artichoke, ginger, manioc—many good varieties do not set seed. We know that this may simply mean that the plants will not flower, because they need a different latitude (length of day) to flower and set seed. This has been proved abundantly with the potato and the Jerusalem artichoke. In such cases the remedy is obvious: we must grow some of the plants in a different place in order to obtain seed for a (almost always very variable) seedling generation, from which we can again pick out superior and well-adapted varieties. European seed firms interested in the topinambour send their tubers to Madeira to obtain early-flowering plants that set good seed. To a certain extent it will help to shorten (or lengthen) the summer days by shading the plants or, conversely, by giving them artificial light. Shading potato plants under removable sheds and boxes in order to make them flower and set seed is a method that has been used in many different experiment stations.

In this group of plants grown for their edible tubers very wide species crosses have been made repeatedly, sometimes with great success. In potatoes some of the Mexican and Andean Indian potatoes from high altitudes have given the plant breeders very valuable breeding stock. In manioc Dr. Koch has even used a tropical rubber tree, *Manihot Glaziovii*, as one of the parents of a very successful new line of superior varieties for Java.

Plant breeders and amateurs interested in potatoes and similar plants should refer to chapters 17, 26, 34.

Chapter Forty-seven

Brassicas and Vegetables

In the last decade the distinction between market gardening and general farming is much less strict than it used to be. Such plants as cabbages, onions and carrots are often grown in farm-crop rotations. This does not make the plant-breeding methods used in those plants very different from what they always were; the difference lies in the choice of good lines, which must be adapted to the more rough-and-ready methods of cultivation.

In cabbage especially, resistance to fungus and to caterpillar infestation is more important in outlying farm fields than in vegetable gardens. The number of sacks of Brussels sprouts per acre *harvested* by the pickers is more important than the actual yield of sprouts per acre. A reliable guide to uniform earliness or lateness is worth more than even colour or shape to the growers of savoys and drumheads.

In onions some of the American experiments on male sterility are of considerable commercial importance. They have made it possible to use a system of selling hybrid seed that combines very good quality of the resultant onions (hybrid vigour) with high impurity, and great variability in later generations, which keeps the customers from growing their own seed. This male-sterility (femaleness) is transmitted from mother to daughter plant directly through the cytoplasm and outside the nucleus (as in the case of the spotted Japanese hops). By repeated cross-breeding to any ordinary onion we

can at will produce lines of onions *of any breed* that produce no pollen. Such lines can be used as female parents for the production of suitable first-generation hybrids between selected varieties, and the stock of both the female line and suitable pollen-producing stock can be kept separate and pure without any great difficulty.

Chapter Forty-eight

Forest Trees

Wherever the earth has been gutted by thoughtless rape of the soil, afforestation is one of the best and quickest ways to stop erosion and to build up another layer of water-retaining and wind-defying topsoil. This is true almost everywhere, even in places where it would seem that the restoration of something like the original grass-mat would be a better solution. The reason for this lies in the circumstance that grass fires and over-grazing may spoil the prairie more easily than the forest.

In certain cases trees are a valuable crop, counting in production per unit of area. In some countries the same land may produce more profit if we cut down its eucalyptus for railway sleepers every ten years than if we had ten agricultural crops. In countries with poorish soil, as in parts of Canada and Sweden, spruce and poplar for paper-pulp give a more paying crop than the cereal crops that could be grown there.

Special forestry breeding stations have been established, notably in the U.S.A. and in Sweden, to study the quality of certain trees and methods of propagation and plant breeding. I do not suppose there are many countries where a study of forest trees and of breeding trees has not been made the lifework of foresters and geneticists in special experiment stations.

There is one curious fact which strikes every biologist. In general, we find that if a species has a considerable area, so

that it is common in many different countries and latitudes, the trees that thrive best and give us the most profitable forests are the local trees. The best seed is generally that which is collected in our own forests. This is very striking in a comparison of Finnish, Dutch and French pines, when tried out in Finnish, Dutch and French plantings. In every case the trees from home-grown seeds are the most valuable ones in the country where several " provenances " are tested.

In the wild state trees are almost without exception propagated from seeds, but in nurseries vegetative reproduction is often used. This makes it possible to reproduce valuable trees, even if they happen to be heterozygous, and often the trees produced by layering are as large and strong as seedlings of several years of age. Budding on seedlings costs too much in forestry work, but it is now possible to make cuttings root in species from which such cuttings could not be induced to grow ten years ago. Treatment of the cuttings with chemicals sometimes helps. The method described in the chapter on vegetative propagation makes it possible to obtain rooted cuttings even from such trees as beech and oak.

Occasionally mutations are found in wild trees, and a good example of a very valuable mutation in trees is that of the triploid aspen discovered by Nilsson-Ehle in Sweden. Some triploids make phenomenal growth, and the same is true of some species hybrids in the groups of the pines and of the eucalypts. In the absence of a cheap method of vegetative reproduction the utilization of hybrids becomes almost impossible.

When forest trees must be sown, the first requirement is to find a good source of seed. In this respect some species of forest trees have the advantage that the older, selected trees in old forests are very good seed producers. In other species the cheapest seed is produced from young, widely spaced, poorly shaped trees (*Pinus sylvestris* on the moors), and it is almost impossible to judge such trees even as individuals. A system of progeny testing in the female line, with phænotypic selection of parent trees, is about the most efficient system of selection in such trees as beech and oak. This is a very long-drawn-out process. After all, plantings of trees along the roads may

often give us stands that are practically isolated from free intercrossing, and I suppose it would be quite possible to obtain very valuable data for future work if some system of book-keeping would enable us to remember that a certain set of trees was derived from certain specified trees.

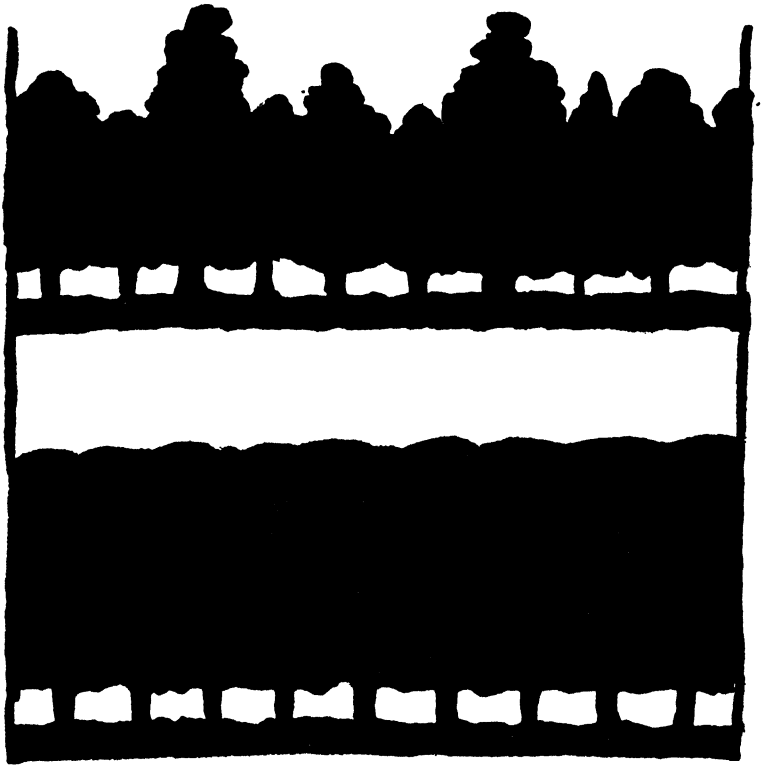


FIG. 10.—Rows of trees along a road. *Above*, trees grown from seed, oak or beech. *Below*, trees grown from layers or cuttings, vegetatively.

In very early flowering and very variable trees, like Robinia, some Eucalypts, Hevea and birches, it would be quite feasible to inaugurate a system of selection according to progeny tests that would work just as well as that worked out for sugar-beets.

In afforestation it is sometimes advantageous to use non-indigenous genera. Eucalypts and wattles have spread all over the world in appropriate climates. Great care should be taken, in the importation of nursery stock, to exclude the possibility of introducing pests, micro-organisms or virus diseases that would affect those trees and might spread to

other, native stands. On the other hand, it is sometimes possible to find a parasite that helps us in the fight against a pest, if we look for this in the country of origin (cactoblastis).

The circumstance that it takes so long to grow a forest to maturity brings its very special difficulties and dangers. I must emphatically warn against attempts to judge immature trees, or even seedlings, by qualities that we think correlates them with the really valuable essential characters which we appreciate in mature trees. It is very tempting to do so: to look for upright shape in oak seedlings and for very quick growth in poplar or spruce grown for pulpwood. Undoubtedly some of those valuable qualities ought to be appreciable in quite young stands, but correlation should be *proved* to exist, and not just taken for granted. After all, the balance of good and bad qualities determines the final value of a forest, and the environment, soil, climate and parasites must be taken into account more than in any other and shorter-lived crop.

If we use the wrong kind of seed, because it is cheap, or because it looks plump and clean, or because it germinates well, our contemporaries may applaud us, while our grandchildren will curse us for our folly. One rule should never be lost sight of: no seed should ever be used for afforestation work unless we have a guarantee that the trees on which it is produced are of very good quality, grown in conditions for which the seedlings are intended. This guarantee can never be given for imported seed, and perhaps it is a safe rule never to use imported seed for any other than experimental purposes. Of course it may be pointed out that imported seed, even from exotic species, has given us extremely valuable additions to local floras. But even in such cases as that of Eucalyptus, of Oregon pines, of the oil-palm, large-scale plantings without preliminary experimentation have been undertaken by planters or by companies that had the courage to take risks. Such risks have often enough resulted in costly failures.

It is an excellent plan to profit by the successes of the pioneers, and in the absence of well-equipped and well-endowed experiment stations this is the logical way in which all human culture must progress. But I must emphatically warn against taking it for granted that we can use a neighbouring country's pioneer-

ing work in practice (or in science for that matter) as a cheap substitute for local effort, especially in the growing of such long-lived crops as trees.

In so far as the narrower field of the efforts of the geneticist-plant-breeders is concerned, I would like to point out that the " hybrid vigour " so strikingly shown in some tree hybrids can be taken full advantage of only where we can either multiply our stocks by some method of vegetative reproduction that is cheap enough for planting forests, or where we can produce first-generation hybrids by routine methods. The investigation of the methods of propagation is such a very important point that this alone would merit the founding of forestry experiment stations.

If we compare the value of a mature tree with the cost of the dozen seeds that were used to grow the treelets from which this tree survived, we see that not very much can be gained by using cheap seed or cheap nursery stock.

Chapter Forty-nine

Citrus

Plant-breeding in the citrus group has so many curious aspects that it merits a short chapter by itself.

To a great extent some of the very peculiar problems were solved when it was discovered that every citrus seed may contain three to ten embryos, and that of those embryos only one is derived from a fertilized ovum. All those supernumerary plantlets that will grow out of the seed are derived from the maternal tissue, so that sowing the seed will often give us vegetative reproduction.

Swingle and others discovered that there is a discrepancy between the variability in lots of seedlings from self-fertilized seed and that in lots of seedlings after crossing. Self-fertilization in most other plants that are as heterozygous as our common oranges and lemons gives us exceedingly variable offspring. But here it does not! The probable solution lies in the great " hybrid vigour " of cross-bred plants, that win the competition with the purely maternal sprouts, while the self-fertilized " real " seedlings lose the same competition.

The importation of foreign clones can easily be accomplished by means of seeds, and this obviates taking any risks of importing pests or virus diseases. It necessitates separating the plantlets that grow from one seed. Even seedless oranges, grapefruit or mandarines can be propagated from seed, as I do not think there is any exception to the rule that even well-known seedless varieties will occasionally give us a viable seed.

Not only are the widest, wildest crosses possible in Citrus, but the proportion of interesting novelties among hybrids is very great. For this reason, citrus is excellent material for the amateur. Some experimental citrus gardens are really delightful places! On the other hand, the exigencies of the fruit trade are such that one or at the utmost two varieties will suffice in any orange or grapefruit-exporting country. To give the public what it knows, is more important than to give it something of superior quality. Lemons can be crossed with oranges, and either of them with grape-fruit. Many hybrids between mandarines and grapefruit happen to be among the very best oranges! And so it goes. It would not be too difficult to produce oranges of sixteen to the two-cubic-feet box, but some markets prefer quite small ones to large ones.

Curiously enough, some of the best varieties may fit conditions in very diverse circumstances, witness the history of the Brazilian Washington Navel orange.

I am convinced that in citriculture much can be accomplished by careful importation and comparison of many commercial exotic varieties in collections. There is no good reason for trying to establish an export trade in some of the fifth-rate oranges and insipid tangerines that some countries are producing to-day. Even should the export of nursery stock or buds be prohibited or frowned upon, seeds are always exported in the fruit in enormous quantities, and such seeds will certainly reproduce the variety, even if they sometimes give us some novel material in addition to the old.

Disease-resistant and frost-resistant species can be combined in hybrids with commercial citrus groups, and very valuable results should be obtained unless the plant breeder lacks the patience or the insight to value his first generation hybrids even if they fail to be of real individual value.

If I were called upon to find an excellent orange or lemon, adapted to a new citrus-growing country in the tropics, I would certainly not limit myself to the importation of a few excellent subtropical widely known varieties. I would much prefer to collect nursery stock, or preferably fruit in old citrus-growing districts in the tropics, where this could be obtained in very mixed (and perhaps on the whole inferior) orchards.

Chapter Fifty

Micro-organisms

The importance of cultivated micro-organisms in agriculture and medicine is rapidly increasing. Most of them are uni-cellulars, and only in a few cases (yeasts) is it possible to do any cross-breeding to enhance the potential variability. Winge, in Copenhagen, has done a great deal of work on yeasts, and has proved that controlled cross-breeding under microscopical control is quite possible.

In most bacteria and uni-cellular algæ, even in some protozoa, vegetative multiplication goes on for long series of generations, even if occasionally wholly new variability may be the result of what in higher organisms we should call cross-breeding. In the second place, true mutations may occur, and it is even possible that in this material, where the cytoplasm is of great importance compared to the nucleus (or where there may be no nucleus at all), quantitative shifts in the relative proportion between the substances present may be passed on from one generation to many subsequent ones (" Dauermodifikation ").

Of course the possibility of adapting the material to our needs is due to the fact that the cultures are variable mixtures. In this respect " wild " cultures are always furnishing very valuable material for selection if we want novel qualities or if we want to improve existing qualities.

We must always bear in mind that almost always two sets of desiderata exist: the actual quality of the strain for its ultimate purpose, and the ease with which it is multiplied commercially.

To give a striking example. It used to be necessary in the production of penicillin to grow the moulds on the surface of sheets of culture medium. After a while, strains were found that would grow when submerged in a liquid medium, like yeasts, and this made a continuous system of manufacturing possible, and materially reduced the cost of the methods, and so of the final product.

Once a valuable strain is obtained it is of great importance to keep it pure. The ideal method should be the isolation of one single spore, or one single cell. The usual method of the bacteriologists—that of isolating a single colony from a very dilute culture on a semi-solid plate—is also good enough in practice to bring down the potential variability. If we start new cultures continually from very small beginnings we can get round the difficulty of the unavoidable introduction of " wild " strains into our lots.

In vaccination with living microbes, such as in the treatment of young individuals with harmless strains of dreaded infections (contagious abortion in heifers, tuberculosis in human babies), it is evident that only bacteriological methods of isolation and reproduction are good enough. In the commercial production of antibiotics and yeast this is much less pressing. The same is true of nodule-bacteria in legumes.

The preparation of pure cultures for the production of Yoghourt and cheeses that must carry special qualities and aroma is certainly the province of the bacteriologist-specialist.

The use of living cultures of micro-organisms in the fight against diseases is only in its infancy. In many cases where what is called " a mild infection " prepares the animals against " heavy " attacks (coccidiosis in poultry and in rabbits and fur-animals is a good example) veterinary science is bound to progress towards the use of strains of low aggressiveness.

Some micro-organisms can be used to transform cheap material into foods of very high value. I am here thinking of yeasts, capable of making use of predigested wood pulp, and of producing feeding stuffs rich in many vitamins and proteins of very high food value.

I am convinced that the solution of the green-food problem in animals and birds in close confinement can be solved by

the plant breeder who develops suitable strains of unicellular algæ (Chlorella and others).

In a book of this scope I can do no more than point out that the same methods of selection and of progeny testing can be applied to the culture and the breeding of micro-organisms that our breeders of domestic animals and of cultivated plants apply in their work. This is a very new field, and we cannot see where its development may lead us. But one thing is quite apparent, that it promises to become of enormous practical importance.

Chapter Fifty-one

Drugs and Spices

Spices and drugs have the double advantage for the plant breeder that they have not been worked with, and that the product generally brings a very good price. Even plants that are habitually collected from the wild may very well repay cultivation; I am thinking of such plants as Derris, foxglove and valerian, for which there is a steady demand. It will often pay to take such a plant into cultivation, to study its biology and try to produce it in favourable conditions, sometimes in a foreign country. Plants, compared with animals, have the advantage under conditions of cultivation, of staying where we put them; we can devote all our energy to improving their quality and productiveness.

Drugs and spices vary enormously in quality, and it is obvious that it must be the task of the plant breeder to improve both yield and quality. In this matter we are severely handicapped by the peculiarities of the trade. In every plant we must pass through a stage in which the " wild " product brings a much better price than the plantation product. This can be a matter of plain prejudice, in which the buyers know the looks and the smell of the wild stuff, and are suspicious when anything of a new kind is offered. Sometimes matters are reversed after a while (plantation quinine bark) when the trade begins to appreciate the content in an actual, measurable active substance; but, even so, appearance counts for much (lichen and moss on cinchona bark and colour of the pods in vanilla).

Breeding for high quality as expressed in chemical content will always pay in the end if we can find a market which is selling the active principle pure, or that is selling a standardized article (Derris and Digitalis). A good example is the production of tobacco for the manufacture of nicotin. Tobacco species differ enormously in yield per acre: some *T. rustica* lines are remarkable yielders, both in regard to quantity and nicotin content.

It is understood that some drug-plants cannot be compared by actual objective standards. They may have no actual value at all, and the growers of ginseng have no hope of ever getting as good a price for their product as for wild ginseng. Their only hope lies in selecting their cultivated plants and treating them during growth in such a way that they can be palmed off as wild.

Nothing is as fickle as the trade in drugs and spices. The manufacture of synthetic vanillin or alizarin may wipe out the cultivation of the two plants almost entirely, and later on the demand for real vanilla may be so much revived that the cultivation of this orchid again becomes profitable. Certain drugs and condiments have the advantage of being eminently suited for an export trade because they are both light and expensive, like black pepper or saffron. This group of plants merits the fullest attention of the plant-breeders.

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