

from the as yet hardly developed study of comparative genetics. Mutation is not a completely autonomous process, but is integrated with the other genetically controlled physiological processes of the organism. Like them it is under the influence of natural selection and of other forces controlling the frequency of genetic types in populations.

## CHAPTER IV

### Natural Selection and Variation in Populations

SINCE ITS EXPOSITION in the classic work of Darwin, the theory of natural selection has had a tortuous history. In the half-century following the publication of the *Origin of Species*, this theory was regarded as the cornerstone of evolutionary biology, and nearly all of the research on evolutionary problems involved studies either of adaptation and selection or of the phylogenetic relationships between organisms. The proponents of selection undoubtedly went to unjustified extremes in their attempts to show the all-inclusiveness of this principle. In the early part of the present century, however, the prestige of the selection theory declined until many biologists regarded it not only as a relatively unimportant factor in evolution but in addition as a subject not worthy of study by progressive, serious-minded biologists. The reasons for this decline lay partly in the excesses of speculation committed by the extreme selectionists of the previous generation. But a more important cause was the impact on biological thinking of two fundamental discoveries in genetics. The first of these was the discovery of mutations by De Vries, and the second was the demonstration by Johannsen that artificial selection is ineffective in a pure line of completely homozygous organisms. These two workers and their followers maintained that all true evolutionary progress comes about by sudden mutational steps, which create at once a new race or species. Selection was regarded as a purely negative force, eliminating the new variants which are obviously unfit, but not taking part in the creation of anything new. The prestige of these two geneticists, as well as the rapid strides being made by the science they helped to found, caused their views to be accepted widely and often uncritically, so that the mutation theory was often looked upon as a modern substitute for the largely outmoded hypothesis of Darwin.

This negative attitude toward natural selection has again become reversed during the past twenty years. The prevailing concept of evolution at present is the neo-Darwinian one, in which mutation and selection are looked upon, not as alternative, but as complementary processes, each essential to evolutionary progress and each creative in its own way. This revival of belief in natural selection as a creative force has resulted from four different trends in the development of genetics. These are the following.

In the first place, our increased knowledge of mutation has made necessary a considerable broadening of our conception of this phenomenon as compared to the opinions about it held by De Vries, Johanssen, Bateson, and other early geneticists. Geneticists now realize that the great majority of mutations with a large effect on the phenotype — the only type that could possibly produce the "elementary species" visualized by De Vries — are in the nature of semilethal or at least less viable abnormalities. They are comparable to the "sports," the existence of which Darwin fully recognized, though he rejected them as of little significance in evolution because of their usually inadapative character. On the other hand, evidence which has accumulated from various sources now indicates that mutations with small effects are very common, occurring perhaps at a greater frequency than the conspicuous type, as discussed in the preceding chapter. Furthermore, as will be brought out in more detail below, the nature of inheritance in crosses between natural races and species indicates that the formation of these groups has involved mutations with a small effect far more often than it has involved the conspicuous ones. The "elementary species" of De Vries is either a fragment of the imagination or a phenomenon peculiar to plants with self-pollination and an anomalous cytological condition, like that of *Oenothera*, or some other deviation from normal sexual reproduction and cross-fertilization as found in most organisms.

Second has been the realization that the pure line, which according to Johanssen represents the limit of selection, is approached in nature only in organisms with self-fertilization, and is therefore completely absent in the higher animals and in most of the higher plants. Self-fertilization is relatively frequent in those plants which form the most suitable material for experiments on genetics and plant breeding, namely the annual grains,

vegetables, and flowers commonly grown in the garden and field. Strains which approach the condition of a pure line are to be expected in such plants. However, these groups are not typical of the higher plants. Study of the wild relatives of the self-pollinated crop and garden plants shows that most of these relatives and presumable ancestors are frequently or regularly cross-pollinated, often being self-incompatible. In these organisms heterozygosity for a large number of genes is the normal condition in nature, and selection may be carried on in one direction for many generations without exhausting the possibilities inherent in the supply of genetic variation present in a population. This fact has now been well demonstrated by the experiments of Winter (1929) on maize, of Goodale (1942) on mice, and particularly of Payne (1920) and Mather (1941, Mather and Wigan 1942) on *Drosophila*. We can no longer think of mutation as the primary source of directive tendencies in evolution and of selection in the purely negative role of eliminating unfavorable tendencies. On the contrary, the direction of evolution is determined largely by selection acting on the gene fund already present in the population, the component genes of which represent mutations that have occurred many generations ago. New mutations are important chiefly as a means of replenishing the store of variability which is continuously being depleted by selection.

The third line of genetic knowledge which has restored our belief in the creative importance of natural selection has been obtained from studies of the genetics of natural populations. From such studies has come the realization that most differences between natural races and species are inherited, not according to simple Mendelian ratios, but in a manner indicating that they are controlled by multiple factors or polygenes. This evidence is discussed in detail by Dobzhansky (1941, pp. 68–82), Huxley (1942, pp. 62–68), and Mather (1943). Without the action of some guiding force, the individual mutations making up the multiple factor or polygenic series will be combined in a multitude of different ways, of which only a small percentage will produce a noticeable effect on the phenotype. Natural selection, if not the only guiding force, is at least by far the most important agent in producing the regular accumulation of these small genetic changes. To be sure,

always acts by eliminating genes and gene combinations. But just as a sculptor creates a statue by removing chips from an amorphous block of marble, so natural selection creates new systems of adaptation to the environment by eliminating all but the favorable gene combinations out of the enormous diversity of random variants which could otherwise exist. Muller (1947) has correctly characterized mutation as a "disrupting, disintegrating tendency" in natural populations and selection as the force which "brings order out of mutation's chaos despite itself."

Strong support for these generalizations is provided by the work of Fisher (1930), Haldane (1932a), Wright (1940a,b), Tschetwerikoff, Dubinin, and others on the genetics of natural populations. This work, which has been ably summarized by Dobzhansky (1941, Chaps. V, VI, X) and Simpson (1944, pp. 48-74), has brought the realization that evolutionists must think of variation on two levels. The lower level, that of the variation between individuals within an interbreeding population, is the direct effect of mutation and gene recombination, but by itself is of little significance in evolution. The variation most important to evolutionary progress is on a higher level, that between populations in space and time, with respect to their gene frequencies. New variability on this higher level does not originate through mutations alone. Only two agencies are known which can produce differences between populations in gene frequency — the chance fixation of random variation and the directive action of natural selection. These forces obey the rules of the physiology of populations, not of individuals. Dr. Sewall Wright (oral communication) has characterized evolution as "the statistical transformation of populations." Such a transformation can be accomplished to the degree represented by existing races, species, and genera of organisms, with their great diversity of adaptive gene combinations, only through the guiding influence of natural selection acting on the raw material of variability provided by gene mutation and recombination.

Even stronger support for the creative role of natural selection is provided by the fourth trend in genetics, namely, the modern amplifications of Darwin's analogy between artificial selection as practiced by plant and animal breeders and the selective action of the natural environment. Breeders now recognize that, with the

exception of disease resistance, the desirable qualities toward which they are working usually result from favorable combinations of several different measurable characteristics (Hayes and Inner 1942, Lush 1946, Frankel 1947, Lerner and Dempster 1948). For instance, yield of grain in any cereal crop is the result of such diverse characteristics as number of flowering heads, size of grain, fertility, and resistance to disease. Of a similar complex nature are characteristics like milling and baking qualities in wheat, flavor in tomatoes, apples, or other fruits, and fiber quality in cotton.

The survival or extinction of an individual or race in a natural environment is determined by qualities with a similar complex nature. Resistance to arid or desert conditions, for instance, involves such diverse characteristics as depth of penetration of the root system; extent of transpiration surface of the leaves and shoots; size, number, distribution, and morphological character of the stomata; and various physical and chemical properties of the protoplasm which enable it to withstand desiccation. Winter hardiness, competitive ability, seed fertility, and efficiency of seed dispersal are adaptive qualities of equal importance with a similar complex basis. Individual mutations, therefore, even if they produce entirely new characteristics, are important in evolution chiefly in relation to the other characteristics already present in the population.

Furthermore, the effectiveness of selection depends not only on the nature of gene combinations rather than of individual genes; it is also influenced strongly by the degree to which the phenotype can be modified by the environment. This is the basis of the principle of *heritability*, as Lerner and Dempster (1948) have discussed it in relation to animal breeding. Heritability, as defined by animal breeders, is the degree to which the additive genetic effects of multiple factors determine the phenotype, as compared with parallel effects on the same phenotype caused by environmental modification. The direct action of selection is, after all, on the phenotype. If, therefore, the heritability of a character is very low, then strong adverse selection pressure may fail to reduce its magnitude or frequency in a population, since the individuals which die or produce too few offspring because they exhibit this character may have genotypes entirely similar to

or deviating in the opposite direction from those of the surviving individuals. Heritability is particularly important in considerations of selection on the basis of combinations of characteristics which, as was pointed out in the beginning of this chapter, is one of the principal ways that selection works. Lerner and Dempster have presented examples to show that under certain conditions of heritability and genetic correlation of characteristics, a population may be altered with respect to a particular character in the opposite direction to that of the selection pressure which is active. This does not mean, of course, that selection can ever cause a population to become less fit. It merely emphasizes the fact that fitness, and therefore the response to selection, is based on combinations of characteristics, and that the same type of selection pressure does not always alter similar phenotypic characteristics in the same direction.

To students of plant evolution perhaps the greatest significance of the concept of heritability is in connection with the fact brought out in Chapter III, namely, that the degree to which the expression of the phenotype may be modified by the environment differs greatly from one genotype to another. There seems to be good reason for believing that in some species natural selection has favored a high degree of phenotypic plasticity in terms of environmental modification, in spite of the low heritability and consequent inefficiency of selection which this brings about. On the other hand, in other species low phenotypic plasticity and high heritability have been maintained, presumably because of their selective advantage to the evolving population. The study of the distribution of different degrees of phenotypic plasticity and heritability will undoubtedly be one of the important lines of approach to evolutionary problems in the comparative genetics of the future.

#### EXPERIMENTAL EVIDENCE FOR NATURAL SELECTION

As with most other natural phenomena, the most convincing evidence for natural selection is coming and will continue to come from carefully conducted experiments. Unfortunately, however, the number of these experiments, particularly on the higher plants, is as yet very small. This is not because evolutionists have failed to recognize their importance. To perform

them adequately, particularly in relatively large, slow-growing organisms like the seed plants, requires much time, space, and money. Furthermore, while the demonstration that selection has occurred is not excessively difficult, the nature of action and the causes of the selective process are much harder to discover or to prove.

Experiments which can provide valid evidence on the existence and dynamics of natural selection do not have to be performed under completely undisturbed natural conditions. After all, many of the evolutionary changes which are taking place at the present time are doing so under the influence of new environmental conditions brought about by the activity of man. The essential differences between natural selection as it occurs in evolution and artificial selection as practised by animal and plant breeders is that natural selection is the result of the elimination or non-reproduction of individuals through the agency of the environment, whether completely natural or man-made, while in artificial selection certain individuals are selected and segregated consciously from the population by the hand of man, and only the offspring from these individuals are allowed to form the next generation. The experiments to be discussed, therefore, all involve subjecting populations containing different genotypes to various more or less artificial environments of which certain features are known and recorded, and observing the effect of these environments on the genotypic composition of the populations concerned.

Since the normal type of population in nature consists of heterozygous, cross-breeding individuals, experiments with this type of material will in the long run tell more about the role of selection in evolution than will those with self-fertilized species, or with asexually reproducing clones. Unfortunately, however, only two experiments dealing with such cross-fertilized plants are known to the writer. Sylven (1937) showed that when strains of white clover (*Trifolium repens*) originating from Denmark and Germany were planted in the more severe climate of southern Sweden, they became adjusted to this climate over a period of two years through selective elimination of the less hardy individuals. This adjustment became evident through a marked increase in yield of green matter. The increase, however, took place only

in two varieties which had not previously been subjected to artificial selection, and which were therefore highly heterozygous at the start of the experiment. A more highly selected, relatively homozygous strain did not respond to this change in climate.

The second experiment is that of Clausen, Keck, and Hissey (1947) on *Potentilla glandulosa*. They planted under cultivation in their three standard environments — Stanford, Mather, and Timberline — clonal divisions of each of 575 individuals belonging to an F<sub>2</sub> progeny derived from a hybrid between subsp. *nevadensis* and subsp. *reflexa*. Over a period of 5 to 8 years some of the individuals were eliminated at each station, and as expected these were different in most cases. On the other hand, some of these F<sub>2</sub> genotypes showed the unexpected ability to survive and produce seed at all three stations, which was not true of either of their original parents. In this experiment only one generation was tested in this fashion. The continuation of such an experiment over several generations of natural reproduction would be very desirable.

A far larger number of experiments is available which deal with competition between constant biotypes such as are found in apomictic species, like *Taraxacum*, and in essentially homozygous, self-fertilized species like the cereal grains. This is partly because of the economic importance of such plants, and partly because the technique of experimentation and the recording of results is far easier in experiments with them than it is in experiments with cross-fertilizing species. The results of experiments on intervarietal competition are therefore presented here in detail not because they represent the best possible evidence on the action of natural selection in plants, but because they are the best which is available at present.

The experiments of Sukatschew (1928), showing differential survival of different apomictic clones of *Taraxacum* under different cultural conditions, have already been discussed in detail by Dobzhansky (1941). The most significant features of Sukatschew's results are, first, that the survival of any race depended on a complex combination of factors, including type of soil, density of planting, and the amount and type of competition, and, second, that the ability of a race to produce abundant seeds and so perpetuate itself was not directly related to the ability of the individual plants to survive.

These results immediately emphasize the point that two equally important but somewhat different factors are involved in the success of a race or species under natural conditions; first, the ability of the individual plants to survive and grow to maturity, and, second, their capability of reproducing and disseminating their offspring. This point will be discussed in more detail later in this chapter.

The most extensive experiment yet performed on natural selection in the higher plants is that of Harlan and Martini (1938) on barley. In this experiment, a mixture containing equal quantities of seed of eleven different commercial varieties of cultivated barley (*Hordeum vulgare*) was planted in each of ten different experiment stations located in various parts of the United States. The seeds were sown on field plots prepared under as nearly uniform cultural conditions as possible. At the end of each growing season, the mixed crop was harvested in bulk, the seeds were thoroughly mixed, random samples of 500 seeds each were extracted, sorted into varieties, and the number of seeds of each variety was counted. The remainder of the mixture was saved for planting in the following spring at the same rate as that of the preceding season. The length of the experiment varied from four to twelve years, depending on the locality.

A part of the results is shown in Table 2. The most obvious

TABLE 2  
SURVIVAL OF BARLEY VARIETIES FROM THE SAME MIXTURE  
AFTER REPEATED ANNUAL SOWINGS AND COMPETITION  
OF VARIOUS DURATION <sup>a</sup>

	Arlington, Va. (4 yrs.)	Ithaca, N.Y. (12 yrs.)	St. Paul, Minn. (10 yrs.)	Moccasin, Mont. (12 yrs.)	Moro, Ore. (12 yrs.)	Davis, Calif. (4 yrs.)
Coast and Trebi <sup>b</sup>	446 T	57 T	83 T	87	6	362 C
Hannchen	4	34	305	19	4	34
White Snymra	4	0	4	241	489	65
Manchuria	1	343	2	21	0	0
Gatani	13	9	15	58	0	1
Meloy	4	0	0	4	0	27

<sup>a</sup> Condensed from Harlan and Martini 1938.  
<sup>b</sup> The records on these two varieties were combined because of the difficulty of distinguishing between their seeds. The figures marked T indicate a predominance of Trebi, those marked C, predominance of Coast.



feature of this table is that in nearly every station the majority of the seeds at the end of the experiment consisted of one variety and that the surviving variety differed according to the locality. Equally significant, however, are two other facts. In the first place, the number of varieties which survived varied considerably from one locality to another, even when these localities differed relatively little in their climate. For instance, the locality at which the largest number of varieties survived in reasonably large percentages was Moccasin, Montana. Yet, in Moro, Oregon, with a similar dry, cold climate, and having the same dominant variety, namely, White Smyrna, the number of surviving varieties is the smallest of any of the localities. Secondly, the individual varieties, which approximate pure lines consisting of one or a few very closely related biotypes, differ considerably not only in their tolerance to a particular climate but also in their ability to tolerate a variety of climatic conditions. For instance, the variety Hannchen, though dominant only at St. Paul, Minnesota, survived at least in small percentages at each locality. On the other hand, Manchuria, which was highly successful at Ithaca, New York, apparently has a much narrower range of tolerance and was a failure at nearly every other locality.

This experiment provides suggestive analogies to competition between the different species in any community, as well as that between different biotypes of one cross-breeding species. The first analogy is obvious. Examples of localities rich as well as poor in species are well known to students of plant distribution, as are also species with wide and with narrow ranges of climatic tolerance (Mason 1936, 1946, Cain 1944). The analogy to competition between interfertile biotypes of the same species is indirect, but possibly of greater significance. Some of these barley varieties differ from each other as much as do the different subspecies of a wild species, but in the degree of their morphological and physiological differences from each other some varieties are more comparable to the different individuals of a cross-breeding population. The results of this experiment might lead one to predict, therefore, that if a similar experiment were performed on a heterozygous, cross-breeding population, some localities would retain a high degree of genetic variability, while others, though containing at the end of the experiment a large number of vigor-

ous, productive plants, would nevertheless select out a population containing many fewer genetic variants. Furthermore, natural selection should permit the survival of some genes and gene combinations over a wide range of environments, while restricting others to particular localities, where they might nevertheless be highly successful. Actually, such conditions do exist in nature, so that the experiment of Harlan and Martini suggests a way of showing how patterns of this type of intraspecific variation can be produced by natural selection.

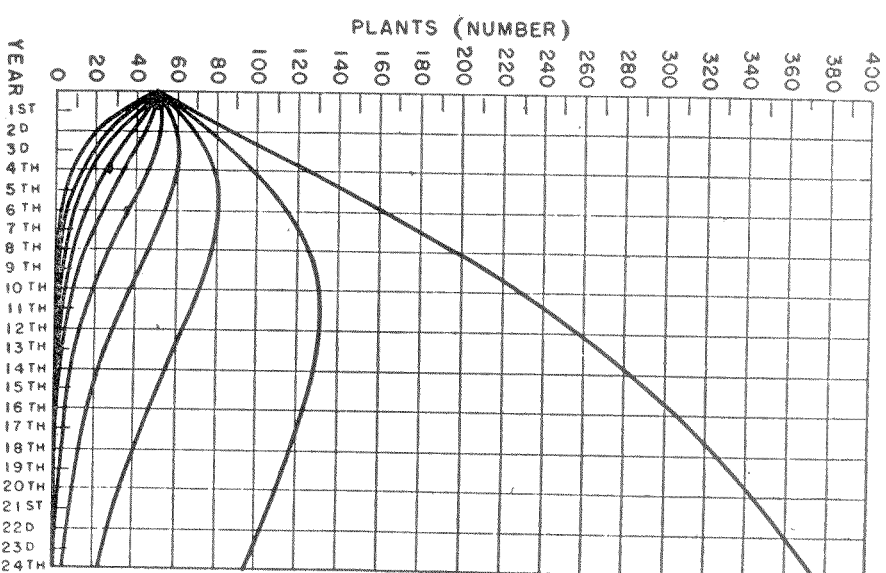


FIG. 13. Theoretical curves of natural selection based on an equal mixture of ten varieties of cereals differing by five kernels each in their productivity per plant, the poorest plant producing 45 seeds. From Harlan and Martini 1938.

Another set of facts brought out by Harlan and Martini concerns the rate at which the unsuccessful and the partly successful varieties become eliminated. Three different types of curves were found for the yearly change in percentage of seeds of a variety (Figs. 13, 14). The most successful ones rose rapidly and rather evenly throughout the experiment. Those of intermediate adaptive value at any locality rose rapidly at first, reaching a rather low peak, then declined equally rapidly, but the rate of this decline always slackened toward the end of the experiment.

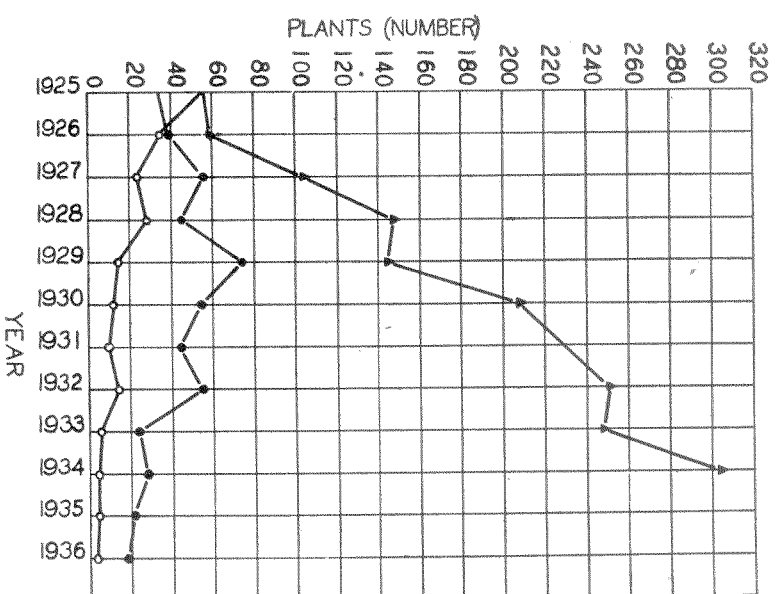


Fig. 14. Actual curves showing the change in number of plants of representative varieties of barley initially sown in equal quantities in a mixture. Triangles, a dominant variety, Hannchen at St. Paul, Minn.; solid circles, a better than average variety, Hannchen at Moccasin, Mont.; open circles, a poor variety, Meloy at Moccasin, Mont. Redrawn after Harlan and Martini 1938.

Finally, the unsuccessful types declined rapidly at the beginning of the experiment and then more slowly, so that toward its end some of them retained a very small number of seeds in the mixture for several generations. These results, which agree in general with theoretical expectation, form a practical demonstration of a principle similar to that brought out by Fisher (1930) and Haldane (1932a) for the survival of alleles in a heterozygous population. Selection acts very rapidly at intermediate gene frequencies, but much more slowly at very high and very low ones. The fact that a large proportion of rare and localized wild species are actually ancient relicts (Fernald 1931, Cain 1944, Chap. XV) is due at least in part to this principle. Many of these rare types, by avoiding the keenest regions of competition and the most rigid types of selection, have lengthened greatly their existence.

A final fact of practical as well as theoretical importance is that the variety surviving at any locality is not necessarily the one which gives the highest yield at that locality when grown in a pure stand by the farmer. For instance, the most successful commercial variety near Ithaca is similar to Hannchen, which in the mixture survived best at St. Paul, Minnesota, while at the latter locality the best agricultural variety is Manchuria, which in Harlan and Martini's experiment survived best at Ithaca. Summerson and Wiebe (1942) tested four different varieties of barley and five of wheat over periods of four and eight years, respectively, in pure stands and in a mixture grown under identical conditions at Davis, California. They found that of the four barley varieties Vaughn, which survived in the smallest percentage in the mixture, had in a pure stand the highest mean yield over the eight-year period. On the other hand, Atlas and Club Marjout, which ranked first and second in the mixture, were second and fourth in yield in pure stands. The differences among the wheat varieties were comparable. These results are comparable to those of Sukatschew, when he found that an apomictic strain of *Taraxacum* which gives a large amount of seed when competing with itself in a pure stand may grow very poorly when raised at the same density in competition with other strains. Together these experiments emphasize the complexity of the factors entering into natural selection and the difficulties involved in finding out the specific basis of selection of any particular characteristic.

Suneson and Wiebe, although well acquainted with the morphological characteristics and the manner of growth of the varieties they used, were unable to explain satisfactorily the reason for the differences between the behavior of these varieties in mixtures and in pure stands.

Laude and Swanson (1942), in similar experiments involving competition between two varieties of wheat (Kanred vs. Harvest Queen and Kanred vs. Currell), found that during the first two years the change in percentage of the two varieties was relatively slight, that for the next five years the decline of the less competitive variety was rapid, but that for the final two or three years of the experiment the rate of change was again slow in the event that one variety had not yet been eliminated. They also showed that elimination or reduction in frequency could occur at the vegetative stage, at the reproductive stage, or both, and that the various causes of elimination were not necessarily correlated with each other. Competitive ability was therefore found to be the result of the interaction of several different, independently inherited characteristics, and as in the other experiments was not necessarily related to the yield of the variety in a pure stand.

In contrast to the higher plants, some of the fungi and bacteria are particularly favorable material in which to study natural selection, because of the rapidity of their cell generations and the relative simplicity of their growth and development. Winge (1944) and Pontecorvo and Gemmell (1944) have independently pointed out that in colonies of yeasts and molds which have originated from a single spore and are growing at an even rate on a uniform artificial medium, the selective value of mutations in relation to the wild type can be determined by the shape of the sector they form in the colony. Unsuccessful mutations form a lens-shaped inclusion within the circular mass of the colony; slightly inferior ones form a sector with convex margins, due to the slackening of their growth as the colony gets older, and their position is marked by a slight indentation of the margin of the colony. Mutants with a growth rate equal to that of nonmutated cells form straight-edged sectors, while the superior ones form sectors with concave margins which become expanded near the periphery of the colony and produce a bulge in its margin (Fig. 15). Actual examples of all these types of mutations are illustrated by Winge

in yeast and by Pontecorvo and Gemmell in *Neurospora*, while other fine examples are shown by Skovsted (1943) in the yeast relative *Nadsonia richteri*. These organisms are excellent material for experimental studies of the selective basis of individual muta-

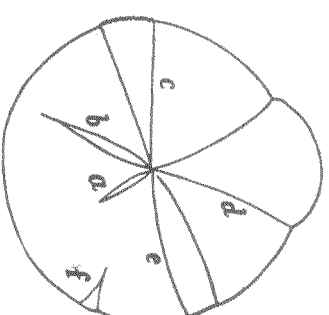


FIG. 15. Different types of mutant sectors in yeast colonies: a, b, and c, with selective value lower than the nonmutant strain; c, with the same selective value; d and f, with selective value higher than the non-mutant strain. From Winge 1944.

tions, as well as of the dynamics of selection, but as yet they have been little used for this purpose.

More accurate quantitative data on selection rates can be obtained in the case of mutations which affect the ability of the organism to grow in the presence of some known chemical component of the substrate. For instance, Spiegelman and Lindegren (1944) showed that in a genetically heterogeneous haploid culture of yeast, adaptation to the fermentation of the sugar galactose, with consequent ability to grow on this medium, increases over a 48-hour period at a regular rate. This rate can be expressed in linear fashion by a logarithmic equation, which was derived on the basis of the assumption that certain cells of the original culture were growing faster than others because of their greater ability to ferment galactose. In the bacterial species *Staphylococcus aureus* Demerec (1945a,b) showed that resistance to low or moderate concentrations of penicillin increased at a rate which would be expected on the assumption that mutations to resistance were occurring and being selected. He further proved experimentally the random occurrence of these mutations and the greater resistance of the strains which had been selected. In this



organism, the mutation and selection is progressive, each selected mutant having a greater resistance to penicillin than its progenitor. Here, therefore, we have an example of directed evolution by means of random mutation and selection through a particular environmental factor, all taking place in a single test tube in the course of a few days.

In a similar manner Braun (1946a,b) demonstrated that the phenomenon of dissociation in *Brucella abortus*, involving the appearance and spread of rough cells in bacterial cultures of the smooth type, is due to mutation and selection. Different clones of this organism have different and characteristic rates of dissociation. These appear to be determined only to a minor extent by the rate of mutation. Genetically determined growth rates, which can be modified by various types of changes in the environment, are much more significant. In particular, the rate of dissociation is affected by the period at which the number of viable cells the medium can support reaches its maximum, and after which there is a steadily increasing ratio between the total number of cells and the number of viable ones. Because of their greater viability in relation to smooth types, the rough cells increase relatively rapidly under the latter set of conditions.

Even more striking from the evolutionary point of view are the experiments of Emerson and Cushing (1946, Emerson 1947) on the resistance of *Neurospora* to drugs of the sulfonamide type. Cultures of this mold grown on a medium containing these drugs became adapted to growth on this medium by means of the occurrence and establishment by selection of mutations resistant to its toxic effects. One of these mutations, moreover, mutated still further into a strain with such highly specialized properties that its optimal growth occurred only on a medium containing sulfanilamide. Here we have an example of extreme specialization occurring within the course of a few days.

Finally, Ryan and Lederberg (1946) have demonstrated competition and selection between nuclei of different genetic constitutions within the same organism. In the mold *Neurospora*, as in other Ascomycetes, hyphae from mycelia of different genetic constitutions may fuse to form a heterokaryon, that is, a mycelium containing within its coenocytic hyphae nuclei derived from the two mycelia which have fused and therefore are different in their

genetical constitutions. Similar heterokaryons will be produced by mutation in single nuclei of such coenocytic mycelia. Ryan and Lederberg found that the "leucineless" mutant—that is, one unable to grow in a medium lacking the amino acid leucine—could be combined in a heterokaryon with the normal wild type, and that this heterokaryon would grow normally on a minimal medium lacking leucine. In such a medium, however, the nuclei derived from the wild type mycelium divide so much more rapidly than those containing the leucineless mutant that the latter become eliminated, and after reaching a size of about 4 cm in diameter the mycelium was no longer a heterokaryon but a typical "wild" mycelium. Physiological adaptation in microorganisms, therefore, in colonies and even within single organisms, is very often produced by mutation and selection, and sometimes in a series of successive steps forming a miniature evolutionary sequence.

#### HISTORICAL EVIDENCE FOR NATURAL SELECTION

Because of the difficulty of carrying out adequate experiments on natural selection in the higher animals and plants, much of our knowledge about the action of selection in these organisms will have to be derived from studies of changes in the genetic composition of populations over periods of many years which accompany recorded changes in the character of the external environment. Examples of such historic changes in the composition of populations are well known in animals and have been fully discussed by Dobzhansky (1941, pp. 190–196). Even more striking examples have been described recently. In the hamster, a gopherlike rodent of eastern Europe, Gershenson (1945a,b) described marked fluctuations in the frequency of the melanic form, which differs from the normal brown type by a single gene. The frequency of melanics in parts of southern Russia varies both from year to year and from one season to another of the same year. These variations are regular and are very similar in different districts; they cannot be ascribed to random fluctuation or to migration. Some of the changes, particularly the seasonal ones, are so rapid that very high selective pressures must be acting to produce them. Similar high selection pressures must be responsible for seasonal changes in frequency of different inversion

types in populations of *Drosophila*. This has been demonstrated experimentally by Dobzhansky (1947a,b, Wright and Dobzhansky 1946) for western American populations of *D. pseudoobscura*, Dubinin and Tiniakov (1945, 1946) have data on *D. funebris* in Russia which can be explained in a similar fashion.

The only comparable evidence in higher plants known to the writer is that given by Kemp (1937) as a result of observations on a pasture in southern Maryland. This pasture, after having been seeded to a mixture of grasses and legumes, was divided by its owner into two parts, one of which was protected from livestock and used for hay, while the other was heavily grazed. Three years after this division had been made, Kemp dug up plants of blue grass (*Poa pratensis*), orchard grass (*Dactylis glomerata*), and white clover (*Trifolium repens*) from each half of the pasture and transplanted them to uniform conditions in his experimental garden. He found that the grazed half of the pasture contained a high proportion of biotypes of each species which produced a dwarf, procumbent growth under experimental conditions, while those taken from the ungrazed half were vigorous and upright. This, like the experiments on animal material, indicates that very high selective pressures can be operating in these populations.

#### THE ADAPTIVE VALUE OF DIAGNOSTIC AND DISTINGUISHING CHARACTERISTICS

The evidence presented above, as well as many other examples from the animal kingdom, leaves no doubt that natural selection is an active, directive force in evolution. Those differences between varieties, species, and higher categories which represent either adaptations to different environments or different ways of becoming adapted to the same environment must all have originated under the direction of natural selection. Obviously, therefore, a final estimate of the importance of selection in evolution must depend largely on determining what proportion of interspecific and interspecific differences are of such an adaptive nature. Unfortunately, however, the determination of the adaptive character of many types of differences between organisms is one of the most difficult problems in biology. Failure to realize this fact has been responsible in large measure for differences in

opinion regarding the importance of selection in evolution. The early followers of Darwin, believing that all differences between organisms have an adaptive value which can easily be seen and interpreted, made many unwarranted speculations based on superficial observations of differences between plants and animals in color and form, and many of their examples of protective and warning devices have been justly criticized. But on the other hand a greater number of recent biologists, among whom may be mentioned Schaffner (1929, 1930, 1933), McAtee (1932), and Robson and Richards (1936), with the same oversimplified concepts of the action of selection, have argued that because the adaptive nature of certain characteristics cannot be easily seen or proved, it therefore does not exist.

Conclusive evidence against both of these points of view is provided by the experimental and observational studies of Gershenson, Dubinin, Dobzhansky, and many others, some of which have been discussed in the preceding section. These results show that carefully conducted experiments and observations of changes in the composition of populations can prove convincingly the existence of natural selection as an active force, but that the demonstration of how selection acts, and of the reason for the selective value of a particular character, is a much more difficult task. We are therefore no longer justified in assuming either that all characters are adaptive and can be demonstrated as such or that character differences must be considered nonadaptive and not influenced by natural selection until the basis of selection has been discovered and proved. If we are ignorant of the life history, development, and ecological relationships of a species we must maintain a completely open mind and an agnostic position concerning the adaptiveness or nonadaptiveness of its distinguishing characteristics. Even in the case of better-known species, neither the adaptive nor the nonadaptive quality of a particular character should be assumed unless definite evidence is available concerning that character.

In the case of species in which a large number of biotypes has been compared as to their morphological and physiological differences as well as their reaction to different climatic conditions, fairly safe conclusions may be reached as to the adaptive or non-adaptive quality of most of their distinguishing characteristics.

For instance, in the genus *Achillea*, Clausen, Keck, and Hiesey (1948) were able to conclude that height of plant, leaf texture, size of heads, and number of florets per head are all correlated directly with the environment and therefore must have survival value, while differences in length and width of the ligules of the ray florets, flower color, leaf cut, herbage color, and branching pattern show parallel variations in different habitats and therefore are probably not adaptive in character. Nevertheless, even those characters which are adaptive vary so much in any one locality that their adaptiveness cannot be considered as a fixed quantity. In the words of Clausen, Keck, and Hiesey (1948, p. 108):

The analysis of *Achillea* populations suggests that natural selection is far from being an absolutely rigid process. Many compromises are tolerated, and the fitness of a particular plant depends not so much upon a single character as upon a combination of several. Such a compensatory system of adaptation is flexible, for a relative lack of fitness in one character may be compensated by special suitability in another.

This principle of compensatory systems can explain many apparently irrational features of adaptation. For instance, the greater sensitivity to frost of the vegetative parts of the alpine ecotype of *Achillea* may be of positive selective value, as a means of causing the plant to go into dormancy sufficiently early in the fall to escape severe frost injury. On the other hand, frost resistance of the leaves probably has a positive selective value in alpine races of slow-growing species with thick or leathery leaves, like many of the Ericaceae and some species of *Eriogonum* and *Pentstemon*, which survive the winter as rosettes. There is every likelihood, therefore, that the same morphological or physiological characteristic may under the same environmental conditions have either a positive or a negative selective value, depending upon the other characteristics with which it is associated.

The above data and many more of a similar nature make highly probable the concept that many and perhaps most of the differences between related subspecies and species in their vegetative characteristics have arisen under the guiding influence of natural selection. The systematic botanist and the student of comparative morphology, however, rightly place more emphasis in classification on characteristics of the reproductive structures than on the vegetative structures. For this reason the most important

questions concerning the role of selection in plant evolution center about the degree and the manner in which selection has entered into the origin of the differences between species, genera, and families of plants in their reproductive structures.

The final answer to this vastly more complex question of the selective value of reproductive characteristics cannot be given until a much greater array of precise observational evidence, and particularly experimental evidence, is available on the ecology and the genetics of these differences in reproductive structures. Nevertheless, a number of facts are available which point the way to a solution of this problem.

A very significant observation in this connection has been made by Rick (1947) on a mutant of the tomato, *Lycopersicon esculentum*. This species, along with others of its genus, has the anthers held together into a tube by a series of lateral hairs. The stigma, protruding from the center of this tube, receives pollen directly from the anthers, which normally results in self-fertilization. In a commercial planting of tomatoes Rick found a recessive mutation which was conspicuous on account of its unfruitfulness. This was caused by the failure of the mutant to develop the lateral hairs on the anthers, which consequently were spread wide apart at anthesis and failed to deposit pollen on the stigmas. When cross-pollinated artificially or by insects, the mutant set an abundance of good fruit. Obviously, the presence or absence of lateral hairs on the anthers, one of the reproductive characteristics diagnostic of the genus *Lycopersicon*, is of great selective importance to its species, although this importance would not be realized by anyone studying only normal plants.

#### THE INDIRECT ACTION OF NATURAL SELECTION

The observations reviewed in the last section lead to the hypothesis that the action of natural selection in directing the origin of differences between species, genera, and families in reproductive characteristics, has been more often indirect than direct. An understanding of the indirect action of natural selection may be obtained by studying three processes through which it works. These are *developmental correlation*, *adaptive compensation*, and *selective correlation*.

The principle of *developmental correlation* was well recog-

nized by Darwin, and was mentioned several times in the *Origin of Species*. Modern evidence on the nature of gene action, as discussed in Chapter III, tends to emphasize more than ever the importance of this principle. In terms of modern genetics, it can be stated about as follows. The direct action of genes is on the processes of development and metabolism; hereditary differences between adult individuals in visible characters are produced indirectly through the effects of genes on developmental and metabolic processes. Because of this fact, character differences which are affected by the same developmental or metabolic process are necessarily correlated with each other, since they are influenced by the same genes. This is the basis of most if not all of the phenomena which have been termed by geneticists pleiotropy, or the production of manifold effects by a single gene.

The effects of such correlations on the alteration of characters by natural selection are undoubtedly very great, but are practically unexplored. If, for instance, long roots should, because of a change in the environment, acquire a high selective value in one race of a species, mutations producing cell elongation in the roots would become established in that race. Some of these mutations would almost certainly affect cell elongation in leaves and flowers, and would therefore produce interracial differences in respect to these parts. In plants, which produce serially large numbers of similar organs, developmental correlation is to be expected with particularly high frequency, and it is very likely responsible for the origin by selection of many character differences which by themselves have no selective value.

The principle of *adaptive compensation*, the importance of which was recently suggested by Clausen, Keck, and Hiesey (1948), is a direct consequence of the effects on selection of developmental correlation. A gene or series of genes may be favored by selection because of one of their effects, but other effects of the same genes may be disadvantageous to the organism. Under such conditions, still different genes which tend to compensate for the harmful effects of the original ones will have a high selective value. An example of this type is provided by Tedin's (1925) analysis of genetic differences between races of the weed, *Camelina sativa*, as will be discussed in the next section of this chapter.

Once a group of genes have been established in a race because of their role in adaptive compensation they and the initially valuable genes form an adaptive system which must be maintained as a unit if the race or species is to retain its adaptiveness. As Tedin has pointed out, groups of characters will be kept together by *selective correlation*. The relation between these three secondary effects of selection may therefore be stated as follows. Developmental correlation brings about adaptive compensation which results in selective correlation.

The indirect action of selection can be explored both in relation to the differentiation of flowers as efficient mechanisms for securing the transfer of pollen from one plant of a species to another one of the same species and in relation to the differentiation of fruits and seeds as efficient mechanisms for securing the maturation, dispersal, and germination of seeds, as well as the early development of the seedlings derived from them. The discussion of different types of flowers will be deferred to Chapter VI, where they will be taken up in connection with the problem of the origin of species; and to Chapter XIII, where the role of selection in the origin of genera, families, and orders of flowering plants will be discussed. The three following sections will be devoted chiefly to a discussion of the direct and indirect role of natural selection in the origin of differences in fruits and seeds.

#### THE GENUS *Camelina* AS AN EXAMPLE OF THE ACTION OF SELECTION

The example which provides the most evidence on the indirect action of natural selection is that of adaptation in the genus *Camelina*. This example is chosen because it has been carefully studied by three workers, because the adaptive differences within the group involve reproductive as well as vegetative structures, and because the particular selective agents which have been at work in the group are comparatively well known. The present account has been compiled from the careful and discerning study of the different forms of *Camelina* growing in Russia by Zinger (1909), the later more detailed account of the distribution of the same forms by Sinskaia and Bezuhzheva (1931), and from the genetic data obtained on the Swedish forms of the same species by Tedin (1925).

The genus *Camelina*, of the family Cruciferae (mustard fam-

ity), consists of seven or eight species, the majority of which are confined to southeastern Europe, Asia Minor, and southwestern Asia. All are annuals, and all but one are winter annuals, the seeds of which germinate in the fall, form a rosette of leaves existing through the winter, and flower in the following spring and early summer. They are all self-pollinated. The group of forms which has been studied has been classified differently by nearly every systematist who has treated it; of the two most important recent treatments in floras, that of Vassilchenko (1939) recognizes six distinct species, while Hegi (1906) recognizes only one species, with four subspecies. Four entities seem to be sufficiently distinct so that they are generally recognized, as follows (see Figs. 16 and 17):

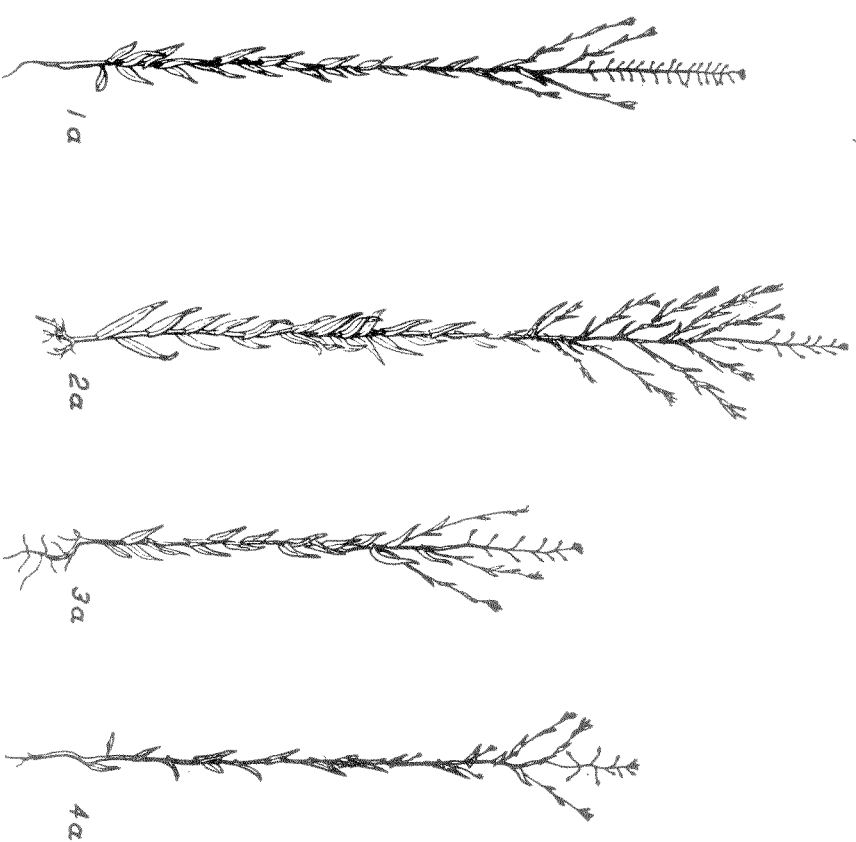


FIG. 16. Growth habits of four "species" of *Camelina*. 1a, *C. microcarpa*; 2a, *C. pilosa*; 3a, *C. sativa*; 4a, *C. sativa* subsp. *linicola*. Redrawn from Zinger 1909.

*C. microcarpa* Andr. — A winter annual with freely branching stems, dense pubescence, inflorescences with numerous, rather crowded pods on ascending peduncles, and rather small pods (mostly 4–6 mm long) with relatively numerous small seeds. This

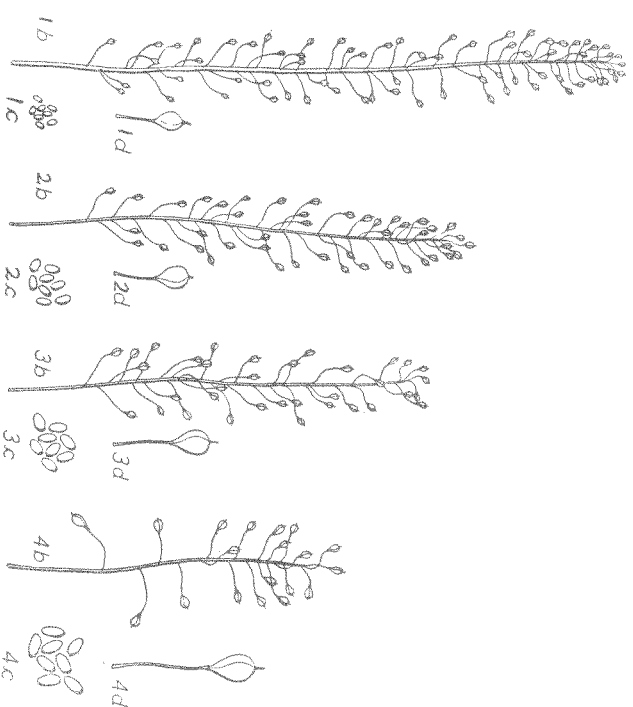


FIG. 17. Inflorescences, seeds, and pods of *Camelina microcarpa* (1b, 1c, 1d), *C. pilosa* (2b, 2c, 2d), *C. sativa* (3b, 3c, 3d), and *C. sativa* subsp. *linicola* (4b, 4c, 4d). Redrawn from Zinger 1909.

occurs as a strictly wild plant on the steppes of central and southwestern Asia and has been introduced as a field weed throughout most of Europe, as well as in North America. Forms with fewer somewhat larger pods less easily dehiscing have been separated as *C. sylvestris* Waltr.

*C. pilosa* (DC) Zinger. — A winter annual with spreading pubescence and large pods approaching in size those of *C. sativa*. Its distribution in eastern Europe is the same as that of *C. microcarpa*, but apparently it is not found in Asia. This form is intermediate between *C. microcarpa* and *C. sativa* and apparently forms exist which connect it with both of the latter species.

*C. sativa* (L.) Crantz. (*C. glabrata* DC and of Russian authors). — A summer annual with less pubescence than the two previously mentioned types and rather large pods (mostly 7–8 mm



long). It is found in northern Eurasia and North America, but everywhere as a weed in fields. Tedin found that  $F_1$  hybrids between this as well as the following subspecies and *C. microcarpa* from Sweden were highly sterile, suggesting that the two are genetically distinct ecospecies.

*C. sativa* subsp. *linicola* (Sch. et Sp.) (*C. foetida* Fr., *C. abyssum* Thell.). — A summer annual differing from typical *C. sativa* in its slenderer, less branched stems with longer internodes; narrower, more glabrous leaves; inflorescences with fewer flowers on spreading peduncles; even larger pods (mostly 9–11 mm long); and large seeds. It is found exclusively as a weed in flax fields. Along with *Spergula maxima*, *Silene linicola*, and several others, this subspecies forms a group of flax "minims," which closely resemble flax in their vegetative characteristics, have large seeds which simulate those of flax, and fruits which dehisce with difficulty, so that the seeds are harvested with the flax crop and threshed out along with the flax seeds. All these characteristics make these types unfitted to grow anywhere except as weeds infesting flax fields. The explanation of their origin has been the principal aim of the students of this group. Tedin has shown that hybrids between *Camelina sativa* subsp. *linicola* and typical *C. sativa* are fully fertile and segregate in the second generation to produce a great array of intermediate types. Sinskaia and Bezuzheva have given abundant evidence that these intermediates exist in nature.

Two additional subspecies of *C. sativa*, subsp. *caucasica* Sinsk. and subsp. *crepitans* Sinsk., infest flax fields in certain parts of Russia. They will be discussed in more detail later.

About the origin of the first three types only a few speculations can be made. Cytologically, *C. microcarpa* and *C. sativa* have been found to possess  $2n = 40$  chromosomes (Manton 1932), and *C. pilosa* probably has the same number. They therefore are probably polyploids and may very well be allopolyploids of ancient hybrid origin. Before the advent of man, *C. microcarpa* and its relatives probably existed as wild plants in the steppes of southeastern Europe and southwestern Asia. Then, with the dawn of agriculture in these regions, *C. microcarpa*, along with many other species of plants, migrated into cultivated fields as a weed. Soon, however, it must have been noticed by man and itself brought into cultivation for the sake of its oil-bearing seeds.

Zinger cites the discovery of seeds of *Camelina* in cave deposits of neolithic age in Austria. In the opinion of Zinger, the absence in a wild state of *C. sativa* or any other summer annual of this genus suggests that the summer annual habit arose as a result of selection by early man. In support of his hypothesis, he showed that when *C. microcarpa* is seeded in early spring, occasional individuals flower and produce seed during the first season. Seed from these individuals produces an even higher percentage of these early-maturing types, while in a similar experiment with *C. pilosa*, Zinger selected in two generations from the original winter annual type a line which bloomed only a little later than typical *C. sativa*. At the time of the beginning of flax cultivation, therefore, *C. sativa* probably existed as a summer annual, grown under cultivation and spontaneous as a weed among other crops.

The opinion of Zinger, that the first type to enter flax fields as a weed was *C. sativa*, and that subsp. *linicola* originated in this habitat as a result of the selective forces operating in it, is well supported by the data of Sinskaia and Bezuzheva. They found that in the parts of Russia in which flax growing is intensive and agricultural conditions are good, extreme *linicola* types are found, while in such regions as southwestern Russia, where flax is grown only occasionally, it may be infested by forms which differ little from typical *C. sativa*. We may safely assume that the earliest cultivation of flax for fiber was performed much less efficiently than is this highly specialized culture at present, so that under these conditions *C. sativa* probably was well enough adapted to living in flax fields. In fact, Sinskaia and Bezuzheva report that in parts of the Caucasus and in Armenia, flax and *Camelina* are at present seeded and cultivated together in fields, and their seeds are used for oil. The *Camelina* type sown in the former region is the variety *caucasica*, which deviates in some respects from both typical *C. sativa* and subsp. *linicola*, but has fewer specialized features than typical representatives of the latter subspecies.

Once *Camelina* had entered into flax fields as a weed, the selective forces operating on it, as pointed out by Sinskaia and Bezuzheva, were of three types: climatic factors, phytosociological factors, and the effects of threshing and winnowing the seeds. Of these three, the last two were most important in producing the difference between *C. sativa* and subsp. *linicola*, while

climatic factors have been active chiefly in adapting subsp. *linicola* to the different regions in which flax is grown. The rhythm of growth has been regulated by the selection of combinations of genetic factors which cause the *Camelina* to flower and ripen its seeds at the same time as the flax growing in the same region. Strains of subsp. *linicola* from northern Russia are relatively early, and those from farther south progressively later. Those of the north, growing under relatively moist conditions, have relatively larger leaves and less pubescence than southern strains of subsp. *linicola*. This subspecies, therefore, contains the same type of ecotypic variation in relation to climate that is found in wild species.

The phytosociological factors, resulting from competition in growth with the flax plant, have been the chief selective agents responsible for the differences in vegetative characters between subsp. *linicola* and typical *C. sativa*. The stems of flax, particularly that cultivated for fiber, grow very straight and dense, so that they shade strongly the ground on which they grow. This reduces both the intensity of light for photosynthesis and the amount of water lost from the soil. The only plants which can compete successfully under these conditions are those which grow rapidly, have straight, unbranched stems, and a sufficiently large leaf surface. On the other hand, pubescence and a large amount of supporting fibrovascular tissue are of relatively little value to a plant growing in this habitat.

Zinger raised the progeny of a single plant of *C. sativa* in a garden bed, half of which was planted also to a dense stand of flax. The *C. sativa* individuals growing in competition with flax had slenderer stems, longer internodes, narrower leaves, and less pubescence than their sisters which were not subjected to this competition. Furthermore, the degree of difference in these characteristics, even down to such details as the size of the stellate hairs and the amount of vascular tissue in the stem, was nearly the same in these two lots of sister plants of *C. sativa* as the difference which prevails between typical *C. sativa* and normal subsp. *linicola* when grown under uniform conditions. In other words, if *C. sativa* is subjected to competition with flax, it adapts itself by means of environmental modifications in vegetative characteristics which in character and degree closely parallel the condition

determined genetically in subsp. *linicola*. In the latter subspecies this specialized habit is retained indefinitely when this subspecies is grown apart from flax, as was shown by both Zinger and Tedin.

This parallelism between environmental modification and adaptive hereditary differences is so close that Zinger was led to consider the possibility of the inheritance of the acquired modification. Nevertheless, he believed that the hypothesis of selection of small variations in the direction of these characteristics was more plausible, and this hypothesis is strongly supported by the genetic work of Tedin. The latter author found that a typical pubescent *C. sativa* differs from the most glabrous type of subsp. *linicola* by three Mendelian factors for pubescence, but that other lines of subsp. *linicola* may possess only one or two of the factors for lack of pubescence. Length of internode and width of leaves were not studied genetically by Tedin, but in respect to absolute height, which must bear a direct relation to internode length, the two subspecies differ by a large number of factors, forming a typical multiple factor or polygenic series. And there appears to be no correlation between the factors for height and those for pubescence. We can therefore postulate that the first plants of *C. sativa* which infested flax fields adapted themselves by means of environmental modification of the phenotype, but that very soon genotypes became established which forced the plant into the habit of growth best adapted to these conditions. These mutations gave the plants enough extra vigor so that they became selected. This is another example, similar to those given by Turesson (1922b) of genetic variations in an ecotype which are paralleled by environmental modifications.

The explanation of the origin of these differences as a result of the creation and maintenance by natural selection of a favorable combination of independent genetic factors which arose by mutation is further supported by the evidence of Siniskaia and Beztuzheva on subsp. *caucasica* and *crepilians*. The first subspecies has the slender stems, long internodes, and narrow leaves of subsp. *linicola*, but it is strongly pubescent and much branched. This is associated with and probably results from the fact that in the Caucasus the flax is grown only for seed and oil, and therefore is itself a relatively low, branched type which is grown in more open stands and is often very strongly mixed with *Camelina*.

Subspecies *crepitans* is a type which is now very local, infesting only the fields of *Linum crepitans*, an ancient relict crop now confined to a few districts of southern Russia (Vavilov 1926). This rare subspecies of *Camelina* is well branched when grown by itself, but becomes phenotypically modified to an unbranched type when grown with flax, just as does typical *C. sativa*.

The third set of factors, those connected with threshing and winnowing, are of the greatest interest, since they have played the largest role in causing the differences between the two subspecies in reproductive characteristics. The failure of dehiscence of the pod would have the highest selective value in this connection, since without this character the seeds would drop from the *Camelina* plants before threshing; and therefore would never become mixed with flax seeds. This is verified by the distribution of subsp. *crepitans*, which is restricted in its distribution to the few small areas in Russia in which persists the culture of *Linum crepitans*, a flax with strongly shattering seed capsules. In *Camelina* subsp. *crepitans* the pods dehisce and shatter even more easily than in the wild *C. microcarpa*. This is an adaptation to the procedure of harvesting *Linum crepitans* slightly before maturity so as not to lose its seeds, which are used for oil. If the pods of *Camelina* did not shed their seeds after this treatment as readily as those of the flax, they would not become mixed with them.

More fundamental are the results of winnowing the flax seeds after threshing. By this process most foreign materials, including weed seeds that are very different from those of flax, are eliminated. Winnowing, therefore, exerts a selective pressure in favor of a certain type of seed size and shape, and this pressure becomes progressively stronger as the winnowing is more thorough. Zinger believed that the indirect effects of selection for seed size were directly responsible for the changes in size and shape of the pods which accompanied the origin of subsp. *linicola*. Tedin, however, showed that the size of seeds is governed by a multiple factor series which is independent of those controlling the size and shape of the pods, and furthermore that the factor series controlling length, width, and thickness of pods are likewise independent of each other and of those controlling the position of the peduncles. For this and other reasons Sinskaia and Bezruzheva rightly question the hypothesis of Zinger. Nevertheless, Tedin

found upon examining a large series of herbarium specimens that certain correlations between these genetically independent characters do exist in nature, and that a large proportion of the recombination types which appeared abundantly in the segregating progeny from his hybridizations are actually absent or very rare in natural populations. These correlations he designated *selective correlations*, and they are doubtless what Zinger observed. An understanding of their nature should provide a clue to the way in which selection modifies reproductive characteristics in this and other plant groups.

The primary selective factor which affects the characteristics of the pods and seeds is the size and shape of the latter, as it determines their reaction to the winnowing process. Typical subsp. *linicola* has seeds considerably larger than typical *C. sativa*, and for this reason Zinger assumed that the primary basis for selection was seed size. Sinskaia and Bezruzheva, however, found that the geographic distribution of differences in seed size is exactly the opposite in flax from that in the races of *Camelina* infesting flax fields. In flax, the northern races have the smallest seeds and those from more southerly regions usually have larger seeds. In *Camelina*, on the other hand, the largest seeds are found in the *linicola* types of the north, and the smallest in those of the south, particularly in subsp. *caucasica*. Thus, while seeds of the northern forms of subsp. *linicola* approach in size those of the flax with which they grow, those of subsp. *caucasica* are many times smaller than the flax seeds with which they are associated.

Sinskaia and Bezruzheva found that the explanation for this apparent anomaly lies in the fact that the ability of *Camelina* seeds to become mixed with those of flax depends not on their size per se, but on whether or not they are blown to the same distance by the winnowing machine. This is determined by the relation between size of surface and total weight. Obviously a flat, thin seed will be blown a long distance and a thick, round, or angular seed a relatively short distance, regardless of the total seed size. Now, the relatively smaller seeds of fiber flax grown in northwestern Russia are of the flat, thin type, while the flax seeds grown for their oil content in more southern regions are relatively thick. In the case of *Camelina*, the large seeds of subsp. *linicola* of the north have a relatively large surface area, and so approach

those of fiber flax in size, shape, and reaction to winnowing. But the seeds of the southern and particularly the Caucasian races of *Camelina* are not only smaller but also have a reduced surface area in relation to their weight. They therefore are blown only a short distance by the winnowing machine, as are the flax seeds with which they are associated. In some regions, however, particularly in southwestern Russia and the Urals, small, light seeds of flax are associated with small, relatively thick seeds of *Camelina*. In these regions flax culture is relatively little developed, so that selection has been less intense and has acted over a shorter period of time.

The variations in size and shape of pods which characterize the different races of *Camelina* were in all likelihood produced by the same selective factors which caused the changes in seed size. Tedin has shown that a developmental correlation exists between seed size and number of seeds per pod; the genes for increased seed size tend to reduce the seed number, provided that the genic complex for pod size is unaltered. There is, however, an independent series of genes for pod size, so that selection simultaneously for mutants producing larger seeds as well as those increasing pod size would enable the race to increase its seed size without suffering too great a loss in seed number and therefore in reproductive capacity. Since, however, the genetic factors affecting the different dimensions of the pod are independent of each other, pod size can be increased in a number of different ways. And the evidence from the different selective correlations found by Tedin suggests that this has actually taken place. The two Scandinavian lines of subsp. *linicola* which he found to have the largest seeds and pods were those he designated Nos. 1 and 4. In line No. 1, the pods were relatively long, narrow, and thin, the approximate modal dimensions being 9.7, 5.7, and 3.7 mm, while in line No. 4 the pods were relatively short, broad, and thick, the corresponding dimensions being 8.5, 6.6, and 5.5 mm (Fig. 18). It can be seen that the volume of the pods in line No. 4 would be about  $1\frac{1}{2}$  times that in No. 1, and since the size of their seeds is about the same, the number of seeds per pod is correspondingly greater in line 4. On the other hand, line 1 may actually produce as many or more seeds per plant as line 4, since according to Tedin's illustration the inflorescence of line 1 is

considerably longer than that of line 4 and contains about twice as many pods. This may be associated with the fact that line 1 has a modal height of 95 to 100 cm, while that of line 4 is only 55 to 60 cm. Most of this difference in height is due to the fact that

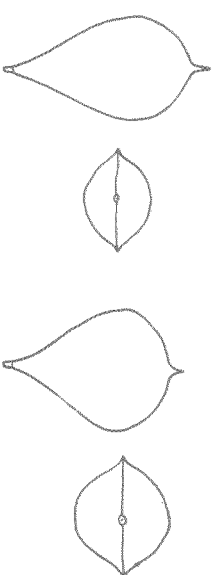


FIG. 18. Pods of the two most common Scandinavian forms of *Camelina sativa* subsp. *linicola*. Reconstructed from the data of Tedin 1925.

line 1 possesses a factor aa, which both increases height and, either through developmental correlation or genetic linkage, produces entire leaves, while line 4 possesses its opposite allele, AA, which produces lower growth and lobed leaves. The pod characteristics of line 1 are those which Scandinavian botanists have designated as var. *macrocarpa*, while line 4 is the type called var. *foetida*.

Tedin grew and classified 215 different lines and studied 290 different herbarium specimens of subsp. *linicola* from Scandinavia. Of these, all but 38 belonged to either the *macrocarpa* or the *foetida* type. This is in striking contrast with the fact that the  $F_2$  generation of the artificial hybrid between lines 1 and 4 produced an enormous array of segregates of all sorts, and the original types were reconstituted in only a small percentage of the progeny. Furthermore, of the 65 lines with pods of the *macrocarpa* type, 41 were more than 70 cm and only 24 less than 70 cm tall, while of the 130 *foetida* lines only 13 were more than 70 cm tall. As expected, there was a larger proportion of lines with lobed leaves among those of the *foetida* type, but this difference was less marked.

We can therefore conclude that in the Scandinavian population of subsp. *linicola* the problem of increasing seed size and maintaining at the same time an adequate number of seeds per plant

has been solved in two somewhat different ways, which may have originated independently. Both of them illustrate very well the principle of selective correlation as well as that of adaptive compensation. On a small scale, these types of *Camelina* illustrate the probable way in which the same selective agent, acting on somewhat different genetic material, can produce different adaptive systems affecting a number of characteristics besides the one which is the immediate object of selection. The origin of the larger differences in reproductive structures between species and genera is probably of a similar nature.

#### SELECTIVE CORRELATION AND SEED CHARACTERISTICS

Another good example of selective correlation is provided by the work of Gregor (1946) on *Plantago maritima*. He found that plants of this species which are selected under the good growing conditions of a garden or a natural habitat at a high edaphic level have hereditary tendencies toward erectness, numerous scapes and flowers, and relatively large seeds. On the other hand, plants adapted to poorer conditions of growth tend to be decumbent and somewhat dwarfed in their hereditary constitution. The erect, large-seeded plants have a much greater reproductive capacity and therefore a pronounced selective advantage when growing under good conditions. This advantage is increased when they are competing with dwarf plants. On the other hand, the decumbent plants are at a relative advantage under poor conditions, because their seed setting is the least affected by deficient nutrition. In *Plantago*, as in *Camelina*, the habitats available to the plant select out not individual characters, but character combinations, and certain characteristics which appear on the surface to have no imaginable selective value are nevertheless strongly affected by the selection process.

Salisbury (1942) has provided valuable evidence on the action of natural selection in directing the origin of differences in fruits and seeds by showing that among the wild plant species of Great Britain there is a marked correlation between seed size and the habitat of the species. In fact, the contents of his book may be regarded as a model of the type of information which must be gathered and tabulated on an even larger scale before any definite hypotheses may safely be made about the nature of the selective

forces responsible for the differentiation of the various types of reproductive structures found in the plant kingdom. By measuring seed size in several hundred species of the British flora, Salisbury demonstrated that the plants of open habitats, such as fields and areas of disturbed soil, have on the average smaller seeds than those of semiclosed or closed communities, like those of turf and pasture, while larger and larger seeds are possessed in turn by species of scrub and woodland margin, by shade species of the herbaceous flora of woodlands, and, finally, by woodland shrubs and trees. The size of the seed, and consequently the amount of food it contains, is inversely correlated with the amount of light available to the young seedling for the manufacture of its own food by photosynthesis. Exceptions are found where expected, namely, among shade-loving saprophytes and parasites and among Orchidaceae, Ericaceae, and other groups in which the young seedlings are nourished by mycorrhizal fungi.

Examination of the species lists provided by Salisbury shows that the distribution of certain fruit types, and through them of certain families, in the various communities which he describes is according to expectation if it is assumed that the controlling selective factor is seed size. Salisbury (p. 174) points out that in the larger seeds of the closed communities special devices for seed dispersal, such as the hooks on the fruits of *Galium* species, are particularly frequent. Even more striking is the fact that baccate fruits, ideally adapted for dispersal by animals, are absent or rare in the more open habitats, while they are possessed by 25 percent of the herbs of the ground flora of woodlands and by 76 percent of the woodland shrubs.

Turning to the distribution of families in these lists, we find an interesting comparison between the members of the Scrophulariaceae and of the Labiatae. These two families are similar in many respects, the most striking difference between them being that the former family possesses capsular fruits with very numerous small seeds, while the latter has fruits bearing four relatively large nutlets. As expected, the Scrophulariaceae are more common than the Labiatae among the species of open habitats. In his table Salisbury lists 18 species of Scrophulariaceae and two of Labiatae. Among the species of semiclosed or closed communities are listed one of the Scrophulariaceae and five of



Labiatae; among the species of scrub and woodland margin the numbers are three and five; while among the shade species of woodlands there are no Scrophulariaceae and one species of Labiatae. The Caryophyllaceae, with their central placentation, have an ovary structure adapted to the production of numerous small seeds. It is significant, therefore, that they represent 14 percent of the species of open habitats, 5 percent of those of closed or semiclosed habitats, 6 percent of those of scrub and woodland margin, and are not listed among the shade species of woodlands. The Leguminosae, with their single carpel and placentation confined to a suture, are adapted to the production of few, large seeds, often without well-developed means of dispersal. According to expectation, they comprise 4 percent of the species of open communities, 20 percent of the species of closed or semiclosed communities, 10 percent of those of scrub and woodland margin, and are absent from the forest community. Data such as these are obviously of great significance in relation to the selective value of differences between families and genera, and will be referred to in a later chapter.

It is obvious that the conclusions of Salisbury cannot be applied uncritically to plant communities in regions possessing very different climates from that of Great Britain. For instance, the species found in the open communities of the drier parts of California often have exceptionally large seeds. This may be due to the need for the young seedling to establish an extensive root system rapidly in order to obtain water, as was postulated by Salisbury for the seeds of dune plants. Similar differences may exist in relation to reproductive capacity. Salisbury showed that under the relatively favorable conditions for plant growth which prevail in Britain, the reproductive capacity of related species of the same genus, expressed in terms of the number of seeds produced per plant, bears a direct relation to the frequency of their occurrence and the extent of their distribution. But many of the commonest species of the drier parts of California produce relatively few seeds per plant, particularly in dry years. In climates where moisture rather than competition is the most important factor limiting plant distribution, the most significant correlation may well be that between reproductive capacity and available moisture. For this and many other reasons, extension of the data provided by Salisbury is a prime desideratum.

#### SELECTION AND DIFFERENTIATION IN THE COMPOSITAE AND THE GRAMINEAE

In two widely different families of flowering plants, the Compositae and the Gramineae, the writer has noticed correlations of character differences which have led him to the hypothesis that natural selection, operating through the medium of both developmental correlation and selective correlation, has been responsible for the origin of a large proportion of the differences in reproductive characteristics which separate species and genera. Examples will be given from both families.

In the tribe Cichorieae of the family Compositae, to which belong the lettuce (*Lactuca*), the dandelion (*Taraxacum*), the hawkweed (*Hieracium*), as well as *Crepis* and several other genera, the structure of the individual florets at anthesis varies little throughout the tribe. The great diversity of variation, on which genera and species are largely based, is in the involucre bracts or phyllaries, which surround the head of florets, and in the mature fruits, particularly in the system of scales or bristles known as the pappus, which crowns their apex. Many of these structures are obviously adapted to the protection of the seed while it is growing, and especially to its efficient dissemination when ripe.

The first selective correlation evident in this tribe is between the habit of growth or length of life of the plant and the degree to which these protection and dispersal mechanisms are developed. In the genera *Dubyaea* and *Prenanthes*, as well as in the more primitive sections of *Crepis*, all the species are long-lived perennials, living for the most part in the great forest belts which have had a stable climate for long periods of time (Stebbins 1940b, Babcock 1947a). These species are little specialized in their involucre and achenes and for the most part have relatively inefficient methods of seed dispersal. Their seeds are large and heavy and the pappus bristles are relatively coarse and few, so that they are not easily borne by the wind. On the other hand, all the groups of rapidly growing, short-lived annual or biennial species have developed some types of specialization in their involucre or achenes or both. The same high specialization has been developed in groups like *Taraxacum* which, although they have remained perennial, have taken to colonizing disturbed habitats, many of which are more or less temporary. This suggests that the

coexistence in modern times of unspecialized as well as specialized types is a result of adaptive compensation between vegetative and reproductive efficiency. In those types which on the basis of their vegetative structures are fitted to live for a long time in a stable habitat, selection pressures in favor of efficient seed production and dispersal are relatively low, and mutations which might start evolution in this direction do not have a chance to become established. But once the species migrates into or becomes exposed by climatic change to a more unstable habitat, structures which enable it to move about more easily in response to climatic and edaphic changes immediately acquire a relatively high selective value.

The particular mechanisms which are developed must depend partly on the nature of the mutations which happen to occur first in a particular line and partly on the conditions of the environment surrounding the species. In the Cichorieae, nearly all the shorter-lived species of northern and mesophytic regions have highly developed mechanisms for seed dispersal by the wind. The most familiar of these is the achene of the dandelion, *Taraxacum*, with its long beak and spreading pappus bristles, forming a parachute. Nearly as efficient are the achenes of various species of *Crepis*, *Lactuca*, and *Agoseris*, all of which have developed similar adaptations independently of each other. On the other hand, many of the species of this tribe living in warmer, drier regions have developed mechanisms which serve for dispersal either by animals or by both agencies. This has been true in the genus *Sonchus*, of which the largest number of species are found in Africa. One of the best diagnostic features of this genus is the possession of pappus bristles of two types, one straight and coarse, the other fine and crisp. In many species of the genus, like the common sow thistle, *Sonchus oleraceus*, the latter type of hairs, like the similar lint on cotton seeds, adhere to the fur of animals and the clothing of man and so disperse the seeds very efficiently without the aid of the wind. Obviously, the elevation of these adherent hairs on a slender beak, like that of the dandelion and the lettuce, would be a detriment rather than an aid to seed dispersal in the sow thistle, since contact with animals would tend to break this beak and so separate the seed from its dispersal mechanism. There is good reason to believe, therefore, that the

diagnostic characters generally used to separate *Sonchus* from *Lactuca* and *Taraxacum*, namely, the presence or absence of a beak and the character of the pappus, are in each case two parts of an integrated mechanism of seed dispersal and therefore originated through the guidance of natural selection acting on different initial mutations. Furthermore, the direction of evolution taken by ancestors of each of these groups toward more efficient seed dispersal may have been determined by the environment under which they existed.

In other annual species of this tribe, such as *Hypochaeris glabra*, the achenes are of two types. The ones in the middle of the head have the beak and parachute mechanism for wind dispersal common in the tribe, while those on the periphery have no beak and a pappus that is modified into a cobwebby structure. On the other hand, the latter have a sharp pointed base and their surface is covered with tiny upward pointing barbs. All of these are efficient means for securing dispersal by animals, as anybody can testify who has walked through or lain in a patch of the common cat's ear, *Hypochaeris glabra*.

In the genus *Crepis*, the dimorphic achenes present in several of the annual species appear to have a different value in connection with seed dispersal. In such species as *C. foetida*, *C. sancta*, *C. dioscoridis*, and *C. vesicaria* the marginal achenes differ from the inner ones in being nearly or entirely beakless, in having sometimes a reduced pappus, and in being more or less firmly enclosed in the inner bracts or phyllaries. They are not usually dispersed by the wind, but tend to remain in the involucre. There they are protected by the hard enclosing phyllaries and ensure the germination of seedlings in the site occupied by the parent plant. Occasionally the phyllaries may break away from the involucre and may be transported with their enclosed achenes by means of the adherence of their rough hairy outer surface to animals or man. The difference in this tribe between species having monomorphic achenes and those with dimorphic achenes is not merely for the convenience of the classifier, nor is it a random meaningless one. It represents differences in methods of seed dispersal. This, of course, does not determine the life or death of an individual or even of a species, but it does have a great effect on the ability of the species to spread and consequently

to develop the geographic isolation which is the usual prelude to the formation of new species.

In the Gramineae or grass family, as in the Compositae, the parts of the individual flower vary little from one species or genus to another, and the great diversity is in the inflorescence, including the scales or bracts, known as glumes and lemmas, which envelop the flower and seed. And as in the Cichoriceae, most of the differences in these structures are connected with different methods of seed dispersal.

A particularly significant fact, therefore, is that in many tribes or genera of this family there also exists an inverse correlation between the persistence and ability for vegetative reproduction of the plant and the degree of development of its mechanism for

TABLE 3  
RELATION BETWEEN GROWTH HABIT AND SEED DISPERSAL MECHANISMS  
IN 215 SPECIES OF THE GRAMINEAE, TRIBE HORDEAE

	Rhizomatous perennials	Caespitose perennials	Annuals	Total
Awn shorter than lemma, glumes not elongate	48	59	6	113
Awn longer than lemma, glumes not elongate	4	56	7	67
Awn usually longer than lemma, glumes aristate, elongate	0	18	17	35
Total	52	133	30	215
Rachis continuous	52	115	3	170
Rachis fragile	0	18	27	45
Total	52	133	30	215

seed dispersal. In the tribe Hordeae, for instance, the species fall into three types on the basis of their habit of growth: rhizomatous, or sod-forming; perennials; caespitose perennials, or bunch grasses; and annuals. The two principal methods of efficient seed dispersal in the tribe are, first, the roughened awns or "beards"

on the ends of the glumes and lemmas, which cling to various parts of animals, as well as to human clothing, and, second, the tendency of the entire inflorescence or head to break into pieces or to shatter at the nodes of its rachis. This either facilitates the transport of seeds by animals or, as in the squirreltail grasses (*Sitanion*) of the western United States, causes the joints with their clusters of elongate awns and fertile florets to be blown by the wind, scattering their seeds as they go, as in the well-known tumbleweeds.

The distribution of the different types of seed dispersal in relation to habit of growth in this tribe is shown in Table 3. This was compiled from the grass flora of the United States by Hitchcock, the flora of the U.S.S.R. by Komarov, and Boissier's *Flora Orientalis*, and therefore includes the two regions of the greatest concentration of species of this tribe, namely, the western United States and central to southwestern Asia. This table shows that the efficiency of seed dispersal increases in relation to the decrease in vegetative vigor. That this increase through the development of specialized structures has occurred independently in a number of different evolutionary lines in this tribe is shown both by morphological evidence and by genetic evidence. In the most highly developed of these lines, which culminates in the genus *Hordeum*, or barley, accessory awns for the more efficient dispersal of seed have developed through the sterilization of two of the three spikelets at each node of the spike or head and the reduction of their glumes and lemmas to prolonged awns (Fig. 19, 1A-1C). In another line, represented by the North American genus *Sitanion*, the awns are also much prolonged, so that the head has a "bearded" appearance like that of many species of *Hordeum*, but all the spikelets have remained fertile, and accessory awns have developed through the division of each of the sterile scales or glumes into several parts (Fig. 19, 2A-2C). The evidence from chromosome pairing in interspecific hybrids shows that *Sitanion* is much more closely related to species of *Elymus* and *Agropyron*, which lack these specializations, than it is to *Hordeum* (Stebbins, Valencia, and Valencia 1946a,b, Stebbins unpublished). A third line which has developed a similar type of specialization is represented by the Old World genus *Aegilops*. In this genus, however, the accessory awns are developed through the

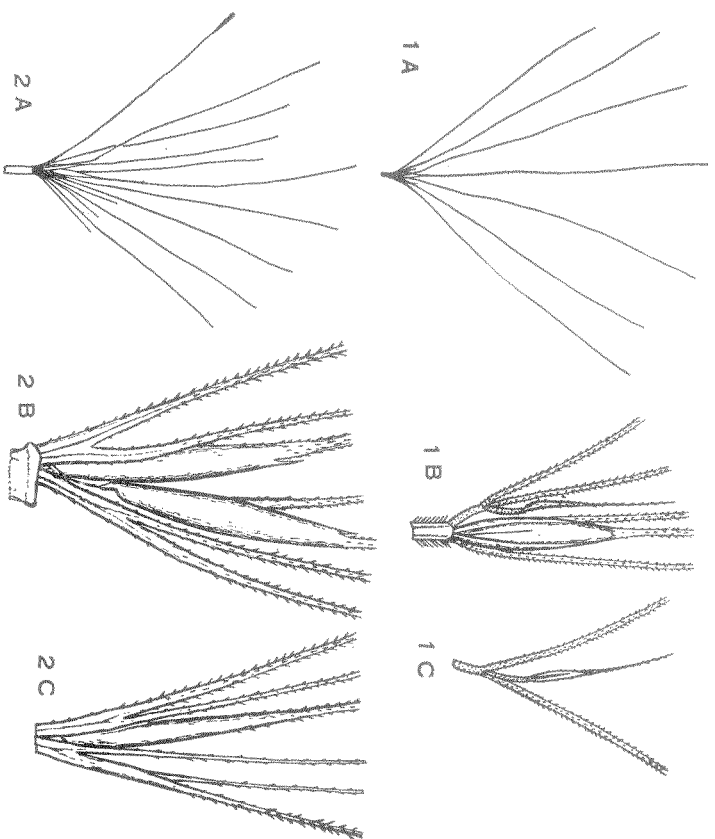


Fig. 19. 1A to 1C, part of fruiting head of *Hordeum jubatum* L. 1A, the three spikelets found at one node of the rachis; 1B, the basal part of Figure 1A, enlarged, with one of the pedicellate sterile spikelets removed; 1C, a single pedicellate spikelet, showing the sterile lemma. 2A to 2C, part of fruiting head of *Sitania jubatum* J. G. Smith. 2A, the two spikelets found at a single node of the rachis; 2B, the basal part of the sterile scales (glumes) and fertile scales (lemmas) of one spikelet; 2C, the second spikelet at the node. 1A and 2A:  $\frac{3}{4}$  natural size; 1B, 1C, 2B, and 2C: 4 times natural size. Original.

prolongation of the nerves of the sterile scales, or glumes, and also of the fertile scale, or lemma. Evidence from many interspecific hybrids (Kihara 1940, Aase 1946, Sears 1941a,b) has shown that *Aegilops* is very closely related to *Triticum*, and through it to various Old World species of *Agropyron* which completely lack awns of any kind.

In this group of grasses, therefore, as in the tribe Cichorieae, some of the most conspicuous of the reproductive characteristics used for the separation of species and genera consist of a series of different devices for the more efficient dispersal of seed, which

have probably arisen in response to increased selection pressures placed upon the ancestral species by changes in its growth habit, its environment, or both. Some acquaintance with other species groups in the Compositae and in the Gramineae has convinced the writer that these are not isolated instances, but represent widespread trends. To be sure, there are undoubtedly both apparent and real exceptions to them in certain species and genera, but nevertheless the correlations hold strongly enough so that natural selection must have played a large part in the development of these groups.

#### NATURAL SELECTION AND MORPHOLOGICAL DIFFERENCES: SUMMARY

Based partly on the examples given above, we may now summarize the various ways in which the origin of differences in external morphology is related to the influence of natural selection.

First, the direct influence of selection, through the immediate adaptive value of the visible changes. This is true of most of the differences between climatic and edaphic ecotypes, as exemplified by *Potentilla* and *Achillea*.

Second, the origin of differences not adaptive of themselves, but developmentally correlated with adaptive characters. A glance at the examples of developmental correlation discussed on pages 87 to 89 will serve to show how far the effects of such correlation can extend. Furthermore, the particular effect of a gene which gives it an adaptive value is probably in many cases very different from the one which is easily seen and measured. An example of developmental correlation which by itself produces a disadvantageous effect is that between increasing seed size and decreasing number of seeds per pod in *Camelina*. Since this negative correlation is probably widespread throughout the higher plants, reduction in number of seeds per ovary, a very common tendency in the seed plants, may often have been caused by selection for increased seed size.

Third, characters not directly adaptive may acquire a selective value as part of a compensatory system of adaptation. Thus, in the origin of *Camelina linicola*, genes for increasing pod size acquired a selective value as a means of offsetting the effect of developmental correlation in reducing seed number along with selection for increased seed size. The development of more efficient means

of seed dispersal in the tribe *Hordeae* may be conceived as a means of offsetting the disadvantages of reduced vegetative vigor and shortened life in the annuals.

Fourth, strictly nonadaptive characters may become established in small populations through the effects of chance. This possibility will be discussed in greater detail in the following section.

#### THE DYNAMICS OF SELECTION AND RANDOM VARIATION

The action of natural selection and its relation to other evolutionary processes will not be fully understood without some comprehension of the rate at which selection acts to change the frequency of genes and gene combinations in populations. The most important factor controlling this rate is obviously the particular selective advantage of individual genes and gene combinations, which has been expressed as the selection coefficient (Haldane 1932a, Wright 1940a, Dobzhansky 1941, p. 219). The relation between selection, mutation frequency, and gene frequency in populations of different sizes has been calculated by the use of mathematical formulae, which estimate the rate of evolution under various assumed values for mutation rate and the intensity of selection.

Some very important conclusions have been reached on the basis of these calculations. In the first place, the same intensity of selection will change the frequency of a gene in a population many times more rapidly when this frequency is in an intermediate range than when it is very low or very high (Haldane 1932a, Dobzhansky 1941, p. 220). This has placed on a quantitative basis the long-recognized fact that individual genes or gene combinations, if present in a very low concentration in large populations, will have difficulty becoming established even in the presence of favorable selection. Another conclusion is that if relatively low rates of adverse selection are operating, these may be partly counteracted by the effects of recurrent mutation, so that unfavorable genes may be present in small concentrations in populations. Finally, Wright has reached the conclusion that in small populations the effects of random fluctuation in gene frequency reduce considerably those of selection (Dobzhansky 1941, pp. 332-336).

The extent to which these conclusions can be applied to actual

situations in natural populations depends primarily on three factors: first, the intensity of selection pressures which prevail at various times, second, the heritability, and, third, the sizes of interbreeding populations. At present, far too little is known about any of these factors. Recent experimental data, however, particularly those of Gershenson (1945) on the hamster and of Dobzhansky (Wright and Dobzhansky 1946, Dobzhansky 1947a,b) on inversion types in *Drosophila pseudoobscura* have demonstrated the existence as a normal phenomenon of selection coefficients many times higher than those postulated by any of the mathematical students of evolution. Selection coefficients under the normal seasonal fluctuations in the environment may range from low figures like 0.001 to very high ones like 0.8 (Gershenson 1945b). The latter figure indicates that under certain conditions the genotype selected against may be considered semilethal (in Gershenson's example this was the normal color form of the hamster as opposed to the melanic form), while the same data have shown that under other conditions the opposite genotype (the melanic hamster) may be equally semilethal. Obviously, therefore, our knowledge about the dynamics of selection will at present be most increased if we obtain actual data on the intensity of selection for various genotypes under different natural conditions.

The third factor, population size, is important chiefly in connection with the effects of random fluctuations in gene frequency. Numerous workers (cf. Dobzhansky 1941, pp. 161-165) have shown that while in infinitely large populations gene frequencies tend to remain constant except for the effects of mutation and selection pressure, in populations of finite size there is a gradual reduction in variability owing to chance fluctuations in gene frequency and random fixation of individual alleles. This phenomenon of "random fixation," "drift," or the "Sewall Wright effect" (Huxley 1942, p. 155) is undoubtedly the chief source of differences between populations, races, and species in nonadaptive characteristics. The extent to which it operates depends, of course, on the sizes of interbreeding populations and the length of time over which these sizes are maintained. As indicated in Chapter I (page 38), our knowledge of these sizes is at present very limited. Nevertheless, such information as we have indicates



that in cross-breeding plants natural populations are rarely maintained for a sufficient number of generations at a size small enough to enable many of their distinctive characteristics to be due to random fixation. The formula developed by Wright (1931) states that in a population of  $N$  breeding individuals, the proportion of heterozygosity would decrease at the rate of  $1/2n$  per generation. This would mean, for instance, that in a population with an effectively breeding size of 500 individuals and containing 200 heterozygous loci, one gene would be fixed or lost about every five generations, although this rate would be slower if the population occasionally received immigrants from outside. Completely isolated populations of this small size are rarely found in the higher plants and are still less often kept at such sizes for many generations. In woody plants and long-lived perennial herbs it is well-nigh impossible. Completely isolated populations of such plants, at least in temperate regions, nearly always contain at least several hundred individuals, as do the groves of the Monterey cypress, *Cupressus macrocarpa*, on the coast of California, and of the giant *Sequoia* in the Sierra Nevada. Since the usual length of a generation in such plants is measured in scores or hundreds of years, the time required for the fixation of even two or three genetic factors would often be measured in tens of thousands of years. In periods of this length the environment would undoubtedly undergo considerable variations, subjecting the population to different selection pressures, which would tend to outweigh the effects of random fixation. In the tropics, where the number of species is much larger and the individuals of a given species in a particular area correspondingly fewer, there would be more likelihood of the establishment of nonadaptive differences between races by means of random fixation. This would be particularly true of tropical oceanic islands, with their small size and diversity of ecological niches. As yet, no plant group has been studied on such islands with Wright's concepts in mind. But such systematic studies as those made in Hawaii, for instance, make very likely the supposition that in some groups of the higher plants, such as *Gouldia*, *Cyrtandra*, and *Bidens*, many nonadaptive differences have been established by random fixation, as seems almost certainly true in land snails, based on the data of Crampton, Gulick, and Welch.

The only plant example known to the writer in which the action of random fixation or drift seems to have taken a prominent part in the differentiation of isolated small populations is that of the complex of *Papaver alpinum* in the Swiss Alps, as described by Fabergé (1943). This species is confined to a series of highly specialized habitats, namely, talus or "scree" slopes of limestone or shale, and for this reason nearly all of its populations are very small and strongly isolated from each other. There is a remarkable amount of geographic variation, much of it in respect to flower color and the character of the pubescence of the scapes, in which alternate characters are distributed more or less at random and seem to be nonadaptive. Furthermore, in contrast to most interracial differences in other species, the character differences in *P. alpinum* are determined to a large extent by one or two pairs of genes. All these characteristics are what would be expected under the action of random fixation of genes.

Although the differentiation of continuously small, completely isolated populations through the action of random fixation of genes is probably a relatively uncommon phenomenon, several other situations occur which would strongly favor the establishment of nonadaptive differences by means of this process. The first of these is the occurrence of great fluctuations in population size. As Wright (1940a,b) has pointed out, the effective breeding size of such a fluctuating population is near the lower limit of its variation in numbers. Hence, if a population is periodically reduced to a few score of breeding individuals, random fixation would take place in it even if the normal size of the population were very much larger. Elton (1930, pp. 77-83) has given a graphic picture of how the completely nonadaptive "blue" mutant could become established in populations of arctic foxes by this method through periodic decimations of the population by famine, and Spencer (1947) has described an example in *Drosophila immigrans* in which the high frequency of a nonadaptive mutant gene is almost certainly to be explained on this basis. In the higher plants, however, this situation would arise relatively infrequently. Their populations are often greatly reduced by extreme cold, drought, or other types of catastrophe, but the plants which perish usually leave behind them numerous resistant, long-lived seeds. Therefore, the new population which is

established upon the return of favorable conditions usually is derived from seeds of a considerable proportion of the original population, rather than seeds from the few last survivors.

An example which might be explained on the basis of long-continued reduction in population size producing *random association* of adaptive characteristics and selectively neutral characteristics is that described by Melchers (1939) in the genus *Hutchinsia* of the European Alps. Systematists have usually recognized in this small genus of the Cruciferae two subspecies in the Alps, *H. alpina* and *H. alpina* subsp. *brevicaulis*. These are distinguished by the shape of their petals, which are clawed in *H. alpina* and spatulate in subsp. *brevicaulis*. The two "species" (as he designated them) were demonstrated by Melchers to be interfertile, and he noted many intermediate forms where they occur together, thus supporting the opinion of most systematists that they are subspecies rather than species. There is no apparent adaptive significance, either direct or indirect, in the difference in petal shape. But in the Swiss Alps *H. alpina* and subsp. *brevicaulis* are separated by a difference which, though invisible, is vastly more important from the point of view of evolution and selection. The distribution of *H. alpina* is entirely on limestone, while subsp. *brevicaulis* grows on granite and other igneous rocks. Melchers showed that this distribution is due to genetically controlled differences in the physiological requirements of the two subspecies, since subsp. *brevicaulis*, when grown in artificial water cultures, will tolerate a much lower concentration of calcium than will *H. alpina*. In the Dolomite Mountains of the southeastern part of the Alpine region, on the other hand, there exists a form of *Hutchinsia* which agrees in petal shape with subsp. *brevicaulis*, but grows on limestone and has the relatively high calcium requirement in artificial culture that is characteristic of *H. alpina* (Fig. 20). Melchers found that the differences both in petal shape and in the requirement for calcium are governed by a relatively small number of genes, perhaps two or three. Furthermore, these genes segregate independently of each other, and there is no evidence for either developmental correlation or genetic linkage.

These facts could be explained on the assumption that at some time in the past, probably during the Pleistocene ice age, the Alpine populations were much reduced and consisted of three

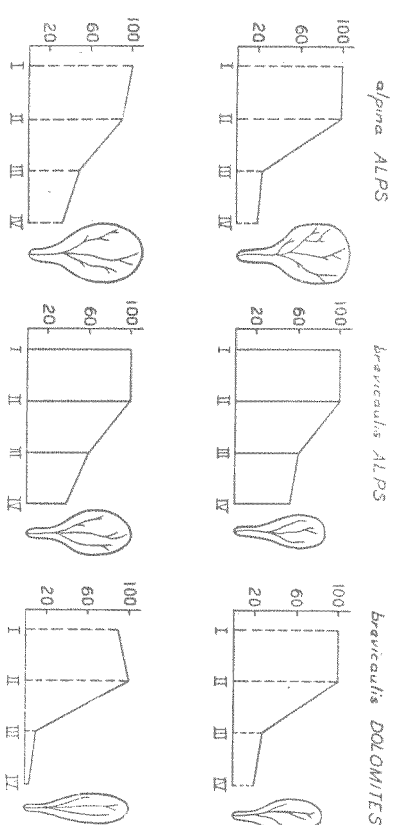


FIG. 20. Diagrams showing reaction to calcium as well as petal shape in six strains of *Hutchinsia*. Roman numerals represent culture solutions containing progressively decreasing concentrations of calcium, as follows: I: 0.000505 molar; II: 0.000253 molar; III: 0.000126 molar; IV: 0.000063 molar. Vertical lines represent percentage of normal growth achieved by the strain represented in the solution concerned. At the right of each diagram is drawn a petal of the strain represented by the diagram. At left, *H. alpina*, from Gschnitzal, northern Tirol. In the center, *H. alpina* subsp. *brevicaulis*; above, from Maureier Tauernal, Austrian Alps, below, from Vikaral, south of Innsbruck, Austria. At right, subsp. *brevicaulis*; above, from Monte Cristallo, Dolomites, below, from Grödener Joeh, Dolomites. After Melchers 1939.

relatively small and strongly isolated fragments, a central one on igneous rock and a northern as well as a southeastern one on limestone. The northern one on limestone acquired by random fixation a high concentration of the gene for clawed petals, while the central and the southeastern one, the former on igneous rock and the latter on dolomitic limestone, both acquired the gene for spatulate petals either by random fixation or through the survival of the original condition of the species. Then, when more favorable conditions allowed the spread of *Hutchinsia* into the glaciated territory, the northern population spread quickly into all of the limestone areas adjacent to it, carrying along the genotype for clawed petals, while the other two populations similarly carried with them into all of the regions available the genotype for spatulate petals.

Another situation in which random fixation and random association of unrelated characters may be expected is during the advance of a species into a territory newly opened to colonization.

Timofeeff-Ressovsky (1940) has pointed out that such an advance will not necessarily be a regular progression of a large population, but that isolated "advance guards" of the incoming population may at first establish small populations, which will then spread and merge with each other. If, for instance, we consider the colonization by plants of the regions left bare by the retreating Pleistocene ice sheets, we realize that this terrain was far from even. There must have been many small pockets with particularly good soil conditions or with protection from winter storms. In such places, some of them perhaps scores of miles north of the southern limit of glaciation, the seeds of a few plants would be transported by wind or animals, and the hardiest of the seedlings coming from these seeds would form the first small plant populations. The sites most favorable for a particular species might be many miles away from each other, so that the species would exist at first in the form of small, isolated populations. These would be subject to rigid selection for certain characteristics, but others, like flower color and petal shape, might be unaffected by selection. Their nature in each newly established population would be determined by the genetic constitution which the ancestors of the population happened to possess. As conditions became more favorable, the small populations would grow and merge, always maintaining their original characteristics. The final result would be a new population which in certain characteristics showed strict adaptation to various environmental conditions, but in others was characterized by regional variation of a purely nonadaptive character. This nonadaptive pattern of variation might be retained in the population for a long time or even indefinitely by means of "isolation by distance."

In *Linanthus parryae*, a small annual species of the Mohave Desert in Southern California, Epling and Dobzhansky (1942) have given an example which may be explained by the past history of the population, as well as by the action of random fixation through isolation by distance. In favorable years the species forms within the area studied a continuous population over an area about seventy miles long and five to fifteen miles broad. Most of the plants in this population have white flowers, but in three distinct areas occur varying concentrations of plants with blue flowers. Within these areas, however, the frequency distribution varies

rather irregularly. Samples containing all blue plants were sometimes found only a mile or less from those with no blues (Figure 21). Summation of all the samples showed a preponderance of those with 0 and with 100 percent of blues and fewer with inter-

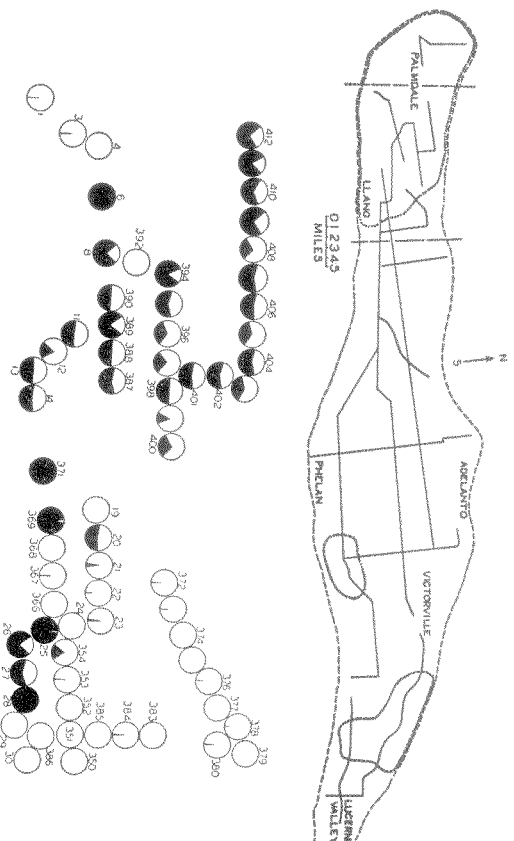


FIG. 21. Above, map showing the distribution of *Linanthus parryae* in Southern California (broken line), the location of the three areas in which blue-flowered plants are found (dotted lines), and the routes taken for sampling the population (continuous lines). Below, enlarged diagram of a part of the western end of the area shown in the map above (that bounded on the west by two vertical broken lines), showing the relative frequency of white- and blue-flowered plants at each collection station in that area. Numbers are those arbitrarily assigned to the stations. Black sectors, blue flowers; white sectors, white flowers. From Epling and Dobzhansky 1942.

mediate percentages, a result which would be expected on the basis of random fixation. A likely explanation is that this population has in past successions of unfavorable years been broken up for many generations into isolated smaller populations, and that the survivors happened to have white flowers in most of these, but blue ones in a few of them. Isolation by distance, resulting from the fact that most plants receive pollen from their immediate neighbors, has kept the random pattern of variation in the population intact through the years when it has been large and continuous.

A final way in which random variations could become estab-

lished in populations is through restriction of cross-breeding by the plants themselves. Many plant species are largely self-pollinated, but occasionally undergo crossing between selfed lines. The effects of such a genetic system, as Wright (1940b) has pointed out, will be the same as those of great fluctuations in size in a cross-breeding population. The further implications of this and other such systems are discussed in the following chapter.

The material presented in this chapter is intended to show that individual variation, in the form of mutation (in the broadest sense) and gene recombination, exists in all populations; and that the molding of this raw material into variation on the level of populations, by means of natural selection, fluctuation in population size, random fixation, and isolation is sufficient to account for all the differences, both adaptive and nonadaptive, which exist between related races and species. In other words, we do not need to seek unknown causes or motivating agencies for the evolution going on at present. And the differences between genera, families, orders, and higher groups of organisms, as discussed in Chapter XIII, are similar enough to interspecific differences so that we need only to project the action of these same known processes into long periods of time to account for all of evolution. The problem of the evolutionist is no longer that of finding unknown causes for evolutionary progress or direction, but of evaluating on the basis of all available evidence the role which each of the known forces has played in any particular evolutionary line. In the future, new generalizations about evolution will come chiefly from comparisons made between specific examples throughout the plant and animal kingdoms.

## CHAPTER V

### Genetic Systems as Factors in Evolution

IN THE PRECEDING chapter the fact was emphasized that in the higher organisms under discussion selection acts primarily on gene combinations rather than on single mutations. This fact inevitably carries with it the corollary that as a force in determining the rate and direction of evolution, recombination is of equal or greater importance than mutation. For this reason, the various factors which influence the rate and nature of recombination must be given separate consideration. These factors are of two sorts, external and internal. The external factors affecting recombination, which consist mainly of the size and structure of the species population, were discussed briefly in the last section of the preceding chapter.

The internal factors together constitute the *genetic system*, as recognized by Darlington (1939, 1940) and Huxley (1942, p. 126). That the chromosomal machinery is only a part of the genetic system, while the type of reproduction — whether sexual or parthenogenetic, with self- or cross-fertilization, and so forth — is equally or more important, was pointed out by Huxley. Both Darlington and Huxley emphasize the fact that the genetic systems of different organisms differ widely from each other and that selection acts to maintain or alter this system, just as it acts on the characteristics of external morphology. We may therefore think of the evolution of genetic systems as a course of evolution which, although running parallel to and closely integrated with the evolution of form and function, is nevertheless separate enough to be studied by itself. In plants, a study of this thread of evolution is particularly important since, as Anderson (1937a) and Turrill (1942a) have pointed out, the diversity of the genetic system in the plant kingdom is much greater than that found among animals.