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.

As Huxley (1942) has indicated, comparative genetics and comparative evolution are for the most part sciences for the future, and most statements concerning them must at present be largely hypothetical. Nevertheless, the gathering together of facts and opinions on these subjects is desirable at this early date, even if only to form a basis for future discussion and for the design of critical experiments. Viewed in this light, the last chapter of Darlington's book *The Evolution of Genetic Systems* stands out as a pioneering effort in which the most important principles of these sciences have already been stated.

The first of these principles, which brings out the importance of recombination in relation to the genetic system, is given on page 127 of this book, as follows: (The italics are those of the present author.)

> In a word, the unit of variation is not the unit of selection. Changes in the chromosomes are determined by conditions of molecular stability. They are biologically at random. *The combinations of these changes together with the selection of environments is what takes us from the chemical level of mutation to the biological level of adaptation.*

Next in importance is the principle of compromise, which, as Darlington points out, is a "corollary of integration in the genetic system." The most important compromise is that between the need for constancy as opposed to that for regulated change. The latter, as Cuénot (1911) and Goldschmidt (1933, 1940), as well as Darlington, have pointed out, involves the need for the formation of preadapted gene combinations. This need for preadaptation requires that all species populations of the more complex organisms should include individuals which are not perfectly adapted to the immediate contemporary environment of the species, but may be adapted to new environments to which the species will become exposed. As shown by Mather (1943), immediate selective advantage is gained by the *fitness* of the particular individuals exposed to the selective forces, but the survival of the evolutionary line in a changing environment depends on its *flexibility*, expressed in terms of its ability to produce new gene combinations at a definite rate per unit of time. In all evolutionary lines, a compromise is necessary between the conflicting requirements of fitness and flexibility. Furthermore, no one level of compromise is equally advantageous for all types of organisms. Depending on the length of their life cycle, the complexity of their development, and other factors, different groups have established compromises at very different levels, some in the direction of maximum stability and fitness at the expense of flexibility and others with immediate fitness of all offspring sacrificed to the maintenance of flexibility.

The third principle established by Darlington is that of anticipation. This is similar to preadaptation as defined by Cuénot and Goldschmidt, but emphasis must be placed on the fact that the selective advantage of a particular genetic system benefits, not the individual in which it arises, but its posterity. Whether an individual produces offspring of many different types or all similar makes no difference to the organism itself, but may have a profound effect on the survival of the race. Hence, the evolution of genetic systems involves competition, not between individuals, but between evolutionary lines. The time factor is therefore of vastly greater importance than it is in the evolution of morphological and physiological adaptations. The various mechanisms composing the genetic system must have arisen before they possessed selective value as members of this system. Either they arose by chance, or else they possessed at the beginning a different use from their present one.

Another important point about the genetic system is that it affects not only the survival of a group of organisms but also their capacity for evolutionary change. In many cases organisms may survive over long periods of time even if their genetic system is ill-adapted to their evolutionary progress. Such species are doomed to conservatism and are tied to the habitats in which they originally existed, but even with such restrictions they may survive for millions of years. Hence, in discussing the selective value of genetic systems we must consider primarily the advantages a particular system gives to the progeny of those who have it and the evolutionary possibilities which it holds out to the race. The immediate advantages or disadvantages of the system are of secondary importance.

Before a survey can be made of the genetic systems adopted by organisms of different types, the concept of flexibility must be defined more explicitly. It may be thought of as evolutionary opportunism and expressed in terms of the number of gene combinations which a population occupying a given area can form in a given unit of time. The latter must be expressed chronologically rather than in terms of generations of the organism concerned, since alterations of the external environment are largely independent of the character of the life cycle of the organism undergoing selection. Furthermore, the area which a population occupies is more important than its numbers, since competition restricts environments spatially and with reference to the available food supply. If flexibility is defined in these terms, then the size of the organism and the length of its generations are among the major factors affecting this quality. Small organisms with short life cycles will possess a considerable degree of flexibility simply on account of these characteristics, while in large, slowly developing ones other factors favoring flexibility will have a correspondingly higher selective value. These factors consist chiefly of the methods of reproduction, in so far as they affect cross-fertilization and panmixy. Mutation rate, however, is by no means a negligible factor, particularly in small, rapidly breeding organisms.

MUTATION AND EVOLUTION IN ASEXUAL ORGANISMS

The genetic system most strongly promoting immediate fitness at the expense of flexibility is that in which sex is absent. This is found as an occasional aberration in higher plants, which will be discussed in Chapter X, on apomixis, and occurs similarly among animals in some phyla of Metazoa. It is, however, much more widespread among the thallophytes, both algae and fungi, and in the Protozoa.

Biologists have commonly believed that two classes of organisms, the bacteria and the Cyanophyceae or blue-green algae, are universally and primitively asexual (Fritsch 1935, Copeland 1938). This belief has been based on the facts that no complete sexual cycle has as yet been observed in any of these organisms and that their nuclear substance seems to be relatively poorly organized and incapable of undergoing the precise type of mitotic division found in the higher organisms. Recently, however, both genetic and morphological evidence for the existence of sex in some bacteria has been brought forward (Lederburg and Tatum

1946, 1947, Lederburg 1947, Dienes 1947). How far our concepts concerning these organisms will have to be revised is not yet clear, but the assumption is still fairly safe that sexual fusion is very rare or absent in many, if not the great majority, of bacteria.

In other lower organisms, such as the flagellate Protozoa, many of the unicellular green algae, some multicellular algae (such as the golden greens or Chrysophyceae), and most of those fungi classed as *fungi imperfecti,* sexual reproduction is unknown or extremely rare. And as we ascend to more complex plants, such as lichens and bryophytes, we find many examples of species in which the sexual cycle is well known, but asexual reproduction by means of various types of vegetative propagules is far commoner than the sexual method. There is no doubt that asexual reproduction is far more widespread in plants than it is in animals and that in the nonvascular plants its frequency is inversely correlated with the complexity of the vegetative plant body.

HAPLOIDY AND THE EVOLUTION OF DIPLOIDY

The most striking difference between the sexual cycle of animals and those found in plants is that, with the exception of a few Protozoa, animals are diploid at all stages and their only haploid cells are the gametes themselves; while nearly all plants possess a haploid stage of greater or less duration. Furthermore, the sequence of types of alternation of generations, involving the gradual increase in emphasis on the diploid generation, is one of the best-known features of plant evolution. The striking fact is that in each major phylogenetic line of plants this increase in diploidy has occurred independently, in every case correlated with the increase in complexity of the plant body.

The simplest nucleate organisms, the flagellates, at least those with sexual reproduction, are strictly haploid except for the zygote. The same is true of most of the filamentous algae, green and brown, and most of the fungi with the least differentiated plant bodies, namely, the Phycomycetes.

The diploid generation has undoubtedly evolved independently many different times, apparently through some physiological adjustment changing the first division of the zygote from meiosis into a diploid mitosis (Svedelius 1929, Kylin 1938). The opposing theories of plant morphologists as to whether this generation first appeared as an entirely new set of vegetative structures interpolated into the life cycle of the plant (Bower 1935, Chap. XXIV) or whether a series of existing morphological structures merely became transferred from the haploid to the diploid condition by a delay in the timing of meiosis (Svedelius 1929) will be discussed later. It may be remarked here, however, that much recent experimental evidence, which is discussed in Chapter VIII, has shown that the transformation of tissues or organs from the haploid to the diploid or polyploid condition never produces a radical change in their external morphology, so that the mere formation of a diploid generation could not give that generation a distinctive external appearance unless mutations should occur which affected it alone.

In most unicellular organisms, both plant and animal, the life cycle is either entirely haploid except for the zygote or strictly diploid except for the gametes. This indicates that the change from haploidy to diploidy in these organisms took place in a single step, without the intermediate condition of an alternation between haploid and diploid generations, such as that existing in many higher plants. There is no doubt that the diploid Protozoa and the unicellular algae known to be diploid are in general more complex in structure than haploid unicellular organisms. The ciliate Protozoa or Infusoria have particularly large and structurally complex cells, while the diatoms, which are diploid, are probably the most complex and structurally diversified of the unicellular algae. In both groups, the independent origin of diploidy accompanying an increase in structural complexity seems to be a likely hypothesis.

Among the groups with an alternation of generations, three different types can be recognized: those with similar haploid and diploid generations (*Ulva, Dictyota, Polysiphonia*), those with a relatively small diploid or sporophytic stage (*Cutleria, Nemalion* and other red algae, Bryophyta, Ascomycetes), and those with the sporophyte large and conspicuous (Laminariales and many other brown algae, Basidiomycetes, vascular plants). The first type is found only among the algae. Among the algae showing this type are filamentous forms, like *Ectocarpus,* as well as forms with more complex thalli, like *Polysiphonia,* but most of these algae have a more complex vegetative structure than the algae which are strictly or predominantly haploid. The existence of these forms with morphologically identical haploid and diploid generations is perhaps the best evidence in favor of an explanation of the evolution of diploidy based primarily on the genetic properties of the diploid condition. In mosses, ferns, seed plants, and even in the predominantly diploid brown algae, the origin of the diploid sporophyte might be interpreted on the assumption that this generation, because of its new structural characteristics, performed functions of value to the plant which could not be carried out by the haploid gametophyte. But in the case of such algae as *Cladophora* and *Polysiphonia* such an interpretation is impossible, since the sporophyte, except for its reproductive characteristics, is structurally and functionally equivalent to the gametophyte. The establishment of a mutation or mutations producing this identical diploid generation must be based on the existence of a selective advantage for this generation, simply and solely because of its diploid condition. And if this advantage does not result from its structural or physiological properties, it must reside in the genetical properties inherent in the diploid sporophyte. That this sporophyte could have evolved and become established independently in a number of different groups purely by the chance accumulation and establishment of mutations is highly improbable.

In those groups with a prominent gametophyte and a reduced sporophyte, not only is the plant as a whole more complex than that in strictly haploid groups, but in addition the sporophyte usually includes the most complex and diversified structures of the plant body. The gametophyte of the mosses and the liverworts is undoubtedly more complex than the plant body of the haploid green algae, from which they are probably descended (Fritsch 1916). But at least in mosses, the elaborate structures of the diploid spore capsule are more complex than any part of the gametophyte, and it is these diploid structures that are sufficiently diverse to provide diagnostic characteristics for families, genera, and in some cases species.

A life cycle with the diploid generation predominant or exclusively present has appeared at least three times in the evolution of multicellular plants: in the order Siphonales of the green algae, in the brown algae, and in the vascular plants. Although these three groups are as different from each other as plants can be in their structure and physiology, they have one characteristic in common: each group contains on the average larger and more complex plants than do the nearest relatives of that group.

This fact is least obvious in the Siphonales, but such genera as *Codium* and *Caulerpa* certainly have among the most complex plant bodies of any green algae. The Laminariales and the Fucales, on the other hand, contain unquestionably the largest and most complex plant bodies of all the algae. In fact, such genera as *Laminaria, Nereocystis,* and *Postelsia* are the only plants outside of the Tracheophyta or "vascular plants" which have a marked differentiation of tissues, particularly within their stalks.

In the vascular plants, the increasing dominance of the diploid sporophyte in groups successively better adapted to life on land formerly led many botanists to think of adaptation to land life as the direct cause of the rise of this sporophyte (Bower 1935, Pincher 1937). Now, however, the well-known diploid condition in the strictly aquatic algae mentioned above, as well as the haploid state of the vegetative body of such strictly terrestrial forms as most Ascomycetes and in particular lichens, shows us clearly that the causal relationship between diploidy and life on land in the vascular plants is an indirect, not a direct, one. This connection is through the fact that a plant cannot attain any appreciable size on land unless it has a relatively complex vegetative body, equipped with conducting, supporting, and storage tissues.

In the fungi, comparison between the ascomycetes and the basidiomycetes gives us just as good an example of increase in size and complexity following the appearance of a condition similar to diploidy as does comparison of the bryophytes and vascular plants among the archegoniates. In most fungi, however, "diploidy" occurs in an anomalous form, the dikaryotic condition, in which the parental haploid nuclei do not fuse, but remain side by side in each cell and divide simultaneously as new cells are formed. As Buller (1941) has pointed out, the genetical properties, and consequently the evolutionary possibilities, of the dikaryotic diploid cell are very similar to those of the synkaryotic cell. The dikaryotic condition is advantageous in the fungi chiefly because, as Buller (1941) has shown, it is the most efficient way of fertilizing and converting to diploidy fully developed mycelia.

The mycelium, or vegetative portion of the plant body, in the Basidiomycetes differs from that in most Ascomycetes only in its prolonged life in the dikaryotic condition. The increase in prominence of the dikaryotic diploid generation in this group is associated with the increase in size and complexity of the basidiomycete reproductive body. As a matter of fact, the elaboration of these large, relatively complex structures, such as the mushroom of the Agaricaceae and the perennial "bracket fungus" of the Polyporaceae, was probably made possible by a gradual increase in size and longevity of the mycelia from which they arise.

HETEROKARYOSIS AS A GENETIC SYSTEM

In certain fungi, particularly the Ascomycetes and their asexual derivatives classified as *fungi imperfecti,* the plant body may contain nuclei of two different types and may therefore exhibit segregation by means of a series of processes not involving sexual fusion at all. This is through the fusion of hyphae belonging to different mycelia and the passage of nuclei from one mycelium to another, regardless of the sex or mating type of the mycelium, a phenomenon known as *heterokaryosis.* The implications of its existence have been realized by mycologists for some time (Brierley 1929), but it was first clearly demonstrated by Hansen and Smith (1932) in the imperfect fungus *Botrytis cinerea.* When single-spore cultures were isolated repeatedly, three different types of mycelium were obtained. One of these produced normal conidia, or asexual spores, in abundance, and mycelia from these conidia were uniformly conidial. A second type produced extensive mycelial growth, but very few conidia, and remained constant like the first type. The third type was intermediate in its amount of conidia formation and continued to segregate conidial, mycelial, and intermediate types. When conidial and mycelial strains were grown in mixed cultures, isolates from such cultures produced all three types. The authors observed frequent anastomosis of hyphae in their cultures and concluded that the intermediate type of mycelium owed its peculiar properties to the presence in the coenocytic hyphae of two genetically different types of nuclei, one capable of producing the conidial strain and the other the mycelial type of strain. The coenocytic character of these fungi makes it possible for many nuclei to exist side by side in the same cytoplasm and to pass from one end of the mycelium to the other with the streaming of the protoplasm. Although cross walls are present, they are perforated and serve only to strengthen the hyphae.

These observations were extended by Hansen and Smith (1935) and Hansen (1938) to a large number of different species of imperfect fungi, including thirty genera. In some species, the phenomenon was found in only a small proportion of the strains analyzed, but in others, such as *Phoma terrestris,* it is apparently always present. Hansen concludes that in these coenocytic organisms the nucleus, rather than the cell, must be considered the basic unit of the individual. A multinucleate spore is analogous to a group of individuals in other organisms, and the "segregation" observed in cultures derived from conidia of the intermediate type strains is actually the separation of individual genotypes from a mixed colony enclosed in a single cell wall. But, as will be pointed out below, this concept cannot be strictly held to, since in respect to its physiological properties, a heterokaryon containing two different types of nuclei behaves like a genetic heterozygote.

The nature of the heterokaryotic condition has been greatly clarified by observations on the genus *Neurospora,* in which the true genetic behavior connected with the sexual cycle is well known, and in which many mutants, both morphological and biochemical, have been isolated, as well as produced artificially. Lindegren (1934) found that certain mycelia of *N. crassa* contained both (+) and (—) nuclei, but were unable to produce perithecia and ascospores because of the presence of self-incompatibility ("self-sterility") factors. Dodge (1942) produced in *N. tetrasperma* heterokaryons between an X-ray induced dwarf mutant and a number of normal, though slow growing, strains, both of the same sex and of the opposite sex. These showed conspicuously greater growth than either of the homokaryotic strains from which they were obtained, thus demonstrating the condition of heterokaryotic vigor, which is entirely analogous to hybrid vigor or heterosis in genetic heterozygotes. Beadle and Coonradt (1944) showed that heterokaryons containing nuclei which bear mutations for the inability to synthesize specific growth factors plus other nuclei bearing their wild-type alleles grow normally in the absence of these growth factors, and that the heterokaryon is maintained by natural selection in a medium not containing these factors. They concluded, therefore, that dominance is exhibited in the relationships of two allelomorphs contained in the different haploid nuclei of a heterokaryon, just as it is in typical nuclei of other organisms. Pontecorvo (1947) has described heterokaryons in *Penicillium* and *Aspergillus,* and has shown that when the uninucleate conidiospores are produced in the latter genus, they may in the case of some color mutants assume the color determined by the joint action of the two genes present in the previous heterokaryon, and in the case of other such mutants the color may be determined by the gene present in the single nucleus which has become segregated into the conidial hypha ("autonomous" gene action).

Data of considerable evolutionary significance have been obtained in respect to the relative frequency of the two types of nuclei in a heterokaryotic mycelium. Pontecorvo (1947) found that in a heterokaryon between two X-ray mutant strains of *Aspergillus oryzae* the ratio between the two types of nuclei was relatively constant, fluctuating between 1:2.7 and 1:3.1. Beadle and Coonradt (1944), on the other hand, found that the ratio of two types of mutant nuclei in different isolates of the same heterokaryotic combination of *Neurospora crassa* varied in one example between 1:1.6 and 1:17.6, and in another between 1:2.2 and 5:1, but that these variations had no effect on the growth rate of the heterokaryon. Finally, Ryan and Lederburg (1946) and Ryan (1947) found that in *N. crassa* heterokaryons between a normal strain and one containing a mutant unable to synthesize the amino acid leucine, although able to grow normally on a minimal medium without leucine, showed depressed growth in a medium containing a limiting concentration of leucine. They demonstrated that this is due to the fact that in the presence of leucine, selection occurs in favor of the leucineless nuclei, and those parts of the mycelia which have grown the length of a test tube on such a medium contain only nuclei of the latter type. This shows that heterokaryotic mycelia have one important property of populations of individuals: their genetic composition can be altered by natural selection.

The evolutionary possibilities of the heterokaryon have been discussed by Lindegren (1942), Beadle and Coonradt (1944), Sansome (1946), and Pontecorvo (1947). Since dominance relations hold here as in diploid plants, recessive genes can persist indefinitely in populations, and the possibilities for recombination are on genetic grounds as great as they are in diploid organisms. Heterokaryons thus have the flexibility of diploids. But they have also the immediate fitness of haploids, since the heterokaryon can at any time be resolved into its haploid components, provided these are adapted to the surrounding medium, and furthermore the mycelium can become homokaryotic by natural selection. From the genetic and physiological point of view, therefore, heterokaryons have all the advantages of both haploid and diploid organisms, a condition amply shown by the number, diversity, and ubiquitousness of saprophytic and pathogenic species of Ascomycetes and *fungi imperfecti*. But Lindegren has pointed out that heterokaryons are at a disadvantage when it comes to the formation of complex morphological structures, since the presence of mixtures of nuclei militates against integration of a definite series of genetically controlled growth processes, which is necessary for the development of such structures. It is perhaps significant in this connection that in 30 isolates representing four genera of Ascomycetes, all of which are regularly sexual and most of which form relatively complex fruiting bodies, Hansen (1938) found all to be homokaryotic.

Beadle and Coonradt (1944) have suggested that heterokaryosis might represent a stage in the evolution of sexual reproduction, although they state clearly that the fungi could hardly represent the group intermediate between asexual and sexual organisms. But Sansome (1946), who found that in *Neurospora crassa* heterokaryons between mycelia of opposite sex are difficult or impossible to obtain, concluded that the heterokaryotic condition could not have been a step in the evolution of the heterothallic sexual system, since the sexual, or "mating type," factors tend to suppress heterokaryosis.

Lindegren (1942) has pointed out that the dikaryotic condition existing in the Basidiomycetes, in which each cell contains just two nuclei of opposite sex, approaches the diploid condition of the higher plants and animals in that cells of this type can cooperate to produce the integrated development of complex morphological structures. But a conspicuous difference is in the possibilities for competition between nuclei of the same sex. In diploid organisms, the zygote and the resulting individual must be entirely the product of a single fusion between two particular haploid nuclei. But in a dikaryotic mycelium, fusion with other mycelia of different genetic constitution can occur at any time, and one of the nuclei of the original dikaryon may be replaced by "invading" nuclei of the same sex but genetically different. Thus, the vegetative mycelium of a dikaryon possesses some of the flexibility afforded to the heterokaryon by natural selection between nuclei of the same individual mycelium. Fungi, therefore, possess two genetic systems which are *sui generis* and are adapted to their particular method of vegetative growth. These systems form most interesting intermediate conditions between haploidy and diploidy.

CROSS-FERTILIZATION AND SELF-FERTILIZATION IN THE HIGHER PLANTS

In nearly all animals, cross-fertilization is necessary. Although some of them are hermaphroditic, the great majority of these are incapable of fertilizing themselves. In plants, on the other hand, the hermaphroditic condition is the usual one, and species which regularly fertilize themselves are by no means uncommon. But in nearly every major subdivision of the plant kingdom some species require cross-fertilization, and if self-fertilized produce either no offspring or else weak and degenerate ones, while other species, often closely related, are regularly self-fertilized and seem to suffer no ill effects from this continued close inbreeding. This fact is particularly obvious among higher plants in the grass family, in which a relatively large number of species has been studied genetically (Beddows 1931, Jenkin 1931, 1933, 1936, Nilsson 1933, Smith 1944). The fact is well known that cereal rye (*Secale cereale*) is normally cross-pollinated, is highly self-incompatible, and produces weak and abnormal offspring when forcibly inbred, while wheat (*Triticum* spp.), which is so closely related to rye that the two can be intercrossed, is normally self-pollinated, so that the older commercial varieties of this crop are almost completely homozygous when kept pure. Similar examples may be found among many wild species of this and other families of angiosperms. They might be explained purely on the basis of chance, that is, random fixation of genes for self-incompatibility in some species and for self-fertilization in others. In that case, however, the two types of reproduction should be distributed at random with respect to other characteristics of the species concerned. This is by no means the case. To illustrate this point, Table 4 has been prepared, showing the degree of cross- or self-pollination in the species found in the United States of the genera *Bromus, Festuca, Lolium,* and the tribe Hordeae as compared with their habit of growth and the length of their life cycle.

TABLE 4

TYPE OF FERTILIZATION AND GROWTH HABIT OF CERTAIN GRAMINEAE IN THE GENERA *Bromus*, *Festuca*, *Lolium*, *Elymus*, *Agropyron*, *Sitanion*, AND *Hordeum*

	NUMBER OF SPECIES			
Type of fertilization	Rhizomatous perennials	Caespitose perennials	Annuals	Total
I. Plants more or less self-incompatible, predominantly cross-fertilized	13	13	0	26
II. Plants self-compatible, but flowers chasmogamous and cross-fertilization frequent	1	39	3	43
III. Plants self-compatible, flowers often or always cleistogamous, normally self-pollinated	0	5	27	32
Total	14	57	30	101

These groups have been selected merely because they are better known to the writer than other grasses. Some familiarity with other genera throughout the family indicates that many of them would have served equally well.

The following generalizations may be made from this table and a study of the distribution of the species included. In the first place, as is well known for angiosperms as a whole (Raunkiaer 1934), annual species are relatively uncommon in cool temperate regions and predominant in warm, dry ones, with seasonal rainfall. Second, while the perennial species may be either cross- or self-fertilized, depending on the species, the annuals are almost exclusively self-pollinated. Third, among the perennial species those with rhizomes are almost exclusively self-incompatible and cross-fertilized, while the caespitose, "bunch-grass" types show various degrees of self- or cross-fertilization. These last two generalizations hold with few exceptions throughout the grass family. Finally, among the caespitose perennials, the 44 species inhabiting cool temperate regions include 12 (27 percent) self-incompatible cross-fertilizers, while among the 12 species of hot, dry climates with winter rainfall only one (8 percent) is of this type. This relationship becomes more evident when other groups of grasses are considered. For instance, such familiar caespitose grasses of cool temperate regions as *Dactylis glomerata, Phleum pratense*, and many perennial species of *Poa* are self-incompatible, while the xerophytic "bunch grasses" in such genera as *Stipa, Aristida,* and *Triodia* are largely self-fertilized.

THE CHROMOSOMAL MECHANISM AND THE GENETIC SYSTEM

The three primary elements of the genetic system which have been discussed already are the presence or absence of sex, haploidy vs. diploidy, and cross-fertilization vs. self-fertilization. The fourth and final one of these elements is the chromosomal apparatus, particularly the number of chromosomes and their behavior at meiosis. Darlington (1939, p. 77) has pointed out that the amount of genetic recombination in any particular intermating group is determined by the chromosome number of the species and by the amount of crossing over in each chromosome, which is determined in turn by the chiasma frequency. He has therefore suggested that the "sum of the haploid number of chromosomes and of the average chiasma frequency of all the chromosomes in a meiotic cell" could be considered as a *recombination index.*

It is obvious that the larger the recombination index, the greater is the number of new gene combinations which can be formed by segregation and recombination *in a limited number of generations.* The smaller this index, the greater is the number of generations over which a given favorable gene combination could be expected to persist. A high recombination index, therefore, promotes flexibility, and a low one fitness over a short time.

The factors making up the recombination index have not been studied carefully or extensively in any of the cryptogams except for a few isolated species of fungi. The pattern of distribution of these factors, therefore, is known only in certain groups of animals and seed plants. Here, however, evidence is available that this distribution is not a random one, but, like the distribution of sex, diploidy, and self- or cross-fertilization, is correlated with various characteristics of the growth and longevity of the plants themselves.

The writer has noted previously (Stebbins 1938b) that among the flowering plants or angiosperms the basic haploid number of woody genera, regardless of their phylogenetic position, is significantly higher than that of herbaceous genera. This suggests that among long-lived plants, a high recombination index is favored. On the other hand, no significant difference was found between the basic chromosome number of herbaceous perennials and that of annuals. This apparently contradictory evidence can be largely explained by the fact mentioned above that a large proportion of annual species are predominantly self-pollinated. The relation between self-pollination and the recombination index will be discussed below. Evidence that within strictly cross-pollinated groups annual species tend to have lower recombination indices than perennial ones is difficult to obtain at present, but certain data from the tribe Cichorieae of the family Compositae are suggestive. The fact that the annual species of *Crepis* have on the average lower chromosome numbers ($x = 4$ and 3) than the perennial ones is now well known (Babcock and Cameron 1934, Babcock and Jenkins 1943). Furthermore, cytological studies of annual species, as well as closely related perennial species, of *Crepis* have shown that they all have relatively low chiasma frequencies (Koller 1935, Richardson 1935, Jenkins 1939, Tobgy 1943). Such annual species as the three-paired *C. capillaris* and *C. fuliginosa,* therefore, have the lowest chiasma frequencies which the genetic mechanism is capable of producing. In such strictly perennial genera as *Prenanthes, Hieracium,* and *Taraxacum,* on the other hand, the basic chromosome numbers are consistently $x = 9$ or 8, and such evidence as is available (Gustafsson 1932, 1935a) indicates that the chiasma frequencies of the sexual species are also relatively high. Furthermore, in *Lactuca* and

Sonchus there are many annual species with haploid numbers of 8 or 9 or even (as in *S. oleraceus*) with polyploid multiples of these. Many of these species, however, have been found to be self-compatible, so that in them constancy can be secured by self-pollination and homozygosity. The possibility exists, therefore, that most annual species possess one of two types of genetic systems: either they are largely self-fertilized and have a high recombination index or they are cross-fertilized and have a low one.

THE SELECTIVE VALUE OF GENETIC SYSTEMS

The material summarized in the preceding pages illustrates two points. First, we can find among plants many different types of genetic systems, in which the elements of sexuality, diploidy, cross-fertilization, and free recombination vs. genetic linkage are developed to various degrees. Furthermore, although many evolutionary lines have progressed from one genetic system to another, few if any of the systems now found among plants can be considered obsolete or inadaptive. Nearly all are found among at least some groups of common and widespread organisms. Second, the distribution of types of genetic systems is by no means at random throughout the plant kingdom, but is correlated with various features of the adult morphology, life history, and habitat of the plants themselves. These points lead to the hypothesis that in each group of organisms a particular type of genetic system is established as a result of the genetic potentialities of that group and of the action of natural selection. The most important feature of each genetic system is the level of compromise it establishes between the need for fitness, in order to secure immediate survival, and that for flexibility, as a means of potential adaptive response to future changes in the environment. The length of time during which any evolutionary line can exist on the earth and the amount of diversification and evolutionary progress of which it is capable are influenced to a great extent by the degree of harmony achieved between the level of compromise in the genetic system and the morphological and developmental characteristics of the organism.

The discussion already presented of the five primary elements of the genetic system has brought out two important correlations, which hold more or less regularly throughout the plant kingdom.

The first is that between the level of compromise and the length of life of the individual organism. In short-lived, rapidly reproducing organisms the genetic system is usually one which favors fitness at the expense of flexibility, while an increasing length of life, and particularly of the sexual cycle of generations, raises the selective value of genetic systems which favor flexibility at the expense of the immediate fitness of all of the sexual progeny of an individual.

The second correlation is that between the level of compromise and the developmental simplicity or complexity of the organism. In organisms which are structurally or developmentally simple, particularly in terms of the number of different kinds of cells and tissues which are elaborated during development, the level of compromise tends to favor fitness. But with increasing complexity of structure and development, the selective advantage of flexibility, considered in terms of evolution over long periods of time, correspondingly increases.

THE ORIGIN AND DEGENERATION OF SEX AS AFFECTED BY NATURAL SELECTION

Our present knowledge concerning the genetic consequences of sexual reproduction and its distribution within the plant and animal kingdoms makes possible only one type of conclusion concerning its biological and evolutionary significance. There is no longer any reason for believing, as did some biologists of the last generation, that sex exists as a means of rejuvenating the protoplasm, or for any other reason than its function in securing a great variety of genetic recombinations, by which the evolutionary line may adapt itself to new and varied environments. The prime importance of this function of sex, which has been realized by many biologists beginning with Weissmann, has been very aptly stated by Muller (1932) as follows:

> It is not generally realized that genetics has finally solved the age-old problem of the reason for the existence (i.e., the function) of sexuality and sex, and that only geneticists can properly answer the question, "is sex necessary?" There is no basic biological reason why reproduction, variation, and evolution can not go on indefinitely without sexuality or sex; therefore sex is not, in an absolute sense, a necessity, it is a "luxury." It is, however, highly desirable and useful, and so it becomes necessary in a relativistic sense, when our competitor-species

are also endowed with sex, for sexless beings, although often at a temporary advantage, can not keep up the pace set by sexual beings in the evolutionary race, and when readjustments are called for, they must eventually lose out.

If we view sexual reproduction in this light, then we must conclude that those evolutionary lines which have been highly successful over long periods of time in spite of the absence of sex have achieved this success either by securing the necessary flexibility in some other way or because flexibility in terms of the formation of new genetic combinations is less important for their existence or evolutionary progress than it is in sexual organisms. Both of these factors have been important.

Organisms with a short life cycle and rapid reproduction can achieve a certain degree of flexibility simply because of these characteristics. Changes in the environment occur at a definite rate in terms of chronological time and affect all organisms equally at this rate. But the degree of development of sexual reproduction and cross-fertilization determines the rate at which new recombinations can be produced *per generation*. Hence, if the sexual cycle is shortened, the number of gene recombinations produced per generation can be correspondingly reduced without affecting flexibility in terms of the number of gene combinations available in a given unit of chronological time.

The importance of this time-developmental factor may be estimated by comparing directly the length of life cycle of different organisms. In bacteria, the generation may be as short as thirty minutes, making 48 generations possible per day. This rapid rate of reproduction is never kept up, but a constant rate of 100 generations per week would not be excessive for a bacterial population living in a changing environment that would promote evolution. Given equal rates of mutation and recombination, therefore, such a bacterial population could evolve 5,000 times as rapidly as an annual seed plant and 50,000 to 100,000 times as rapidly as the average forest tree. Therefore, except in the highly improbable event of a rapid increase in the rate of useful mutations in these higher organisms, they would have to produce new gene combinations at a rate many thousands of times as high as that of the bacteria attacking them.

Furthermore, in organisms with a short life cycle fitness itself carries a relatively high selective advantage in relation to flexibility. Such organisms, like bacteria, fungi, and the smaller algae, are usually small in size, are destroyed in huge numbers by their enemies, and depend for their survival chiefly on their ability to build up large populations rapidly in a favorable medium. During these periods of increase the production of any organism not adapted to this medium is a wasted effort on the part of a population whose very life depends on reproductive efficiency. Such a growing population cannot experiment with new gene combinations; it must sacrifice flexibility to immediate fitness.

On the other hand, many of the larger plants maintain populations whose size varies relatively little over periods of thousands or even millions of years. In any population of forest trees, for instance, a seedling can grow to maturity only when an old tree dies, leaving room for it in the forest, or in the rare (previous to man) event of a landslide, fire, or other catastrophe. During normal times, therefore, thousands of competitors are available for every niche which may be occupied by an adult individual, and a huge wastage of young in terms of ill-adapted gene combinations is little or no disadvantage to the population. We can say, therefore, that in organisms with a long life cycle a genetic system promoting flexibility is of high selective value, while simple, short-lived, and rapidly reproducing organisms need a genetic system favoring fitness.

The lower selective value of new and complex gene recombinations in many of the asexual organisms is very likely due also to their ability to adapt themselves to new environments in relatively simple ways. Although it is true that many bacteria and protozoa are highly complex and specialized in respect to the physiological activity of their cells, all of them are developmentally simple, in that their ontogeny involves the differentiation of only a very small number of different kinds of cells. If, as was emphasized in Chapter III, we consider the action of genes in terms of their effect on processes rather than on adult characteristics, this fact has important implications. If all of the cells of the organism are alike physiologically, then a particular change in any developmental process will have a uniform effect on the organism as a whole and is likely to have a particular selective advantage or disadvantage as a unit, independently of its relation to other changes in developmental processes. But if the organism possesses a large number of different types of cells, which are produced by a great variety of physicochemical processes acting at different intensities during the various stages of development, then a single change in one process may affect different parts of the same organism in very different ways, some of them advantageous, and some deleterious. Under such conditions, a change which may benefit the entire organism by adapting it to new environmental conditions is most easily achieved through the combined action of several different changes in various ones of the numerous developmental processes. The disadvantageous effects of one change are balanced by the favorable effects of another. The principles of developmental correlation and adaptive compensation, discussed in Chapter IV, are obviously special cases of this more general principle.

For these reasons, we should expect that genetic systems favoring recombination would arise in organisms with structural and developmental complexity even more rapidly than in those with increasing lengths of the sexual generation. This would explain the greater development of sex in animals than in plants, since animals are in general much more complex than plants in both the number and the degree of differentiation of their tissues and in their developmental processes.

A GENETIC THEORY FOR THE ORIGIN OF THE DIPLOID STATE

The idea that the diploid condition became established in the higher plants because of its greater selective value in respect to the production of gene combinations was first advanced by Svedelius (1929). He pointed out that in a strictly haploid organism, in which the zygote undergoes meiosis without any intervening mitotic divisions, each act of fertilization can yield in the following generation only four different gene combinations, since only one meiotic division is possible. On the other hand, the production of a large diploid organism between the time of fertilization and meiosis makes possible the occurrence of hundreds of meiotic divisions in the tissues derived originally from a single zygote. Since the segregation of the genes in each of these divisions will be somewhat different from that in any of the others, each act of fertilization ultimately produces a great variety mutations arose only once in the haploid archegoniates, which were the presumable common ancestors of the Bryophytes and the vascular plants. If the diploid state is of selective value because of the evolutionary potentialities it gives to the plant in terms of greater diversity and complexity, then a great initial advantage would have been granted those archegoniates in which a relatively large proportion of the life cycle was converted at one step to diploidy. Hence, it is easiest to conceive of the vascular plants as having evolved from haploid archegoniates in which mutations at once produced an alternation between similar generations like that found in the modern algae *Ulva* and *Polysiphonia*. Bryophytes, on the other hand, could owe their relatively slight success as a group to the fact that in their ancestors, diploidy first appeared in only a small portion of their life history.

CAUSES FOR THE DEGENERATION TOWARD SELF-FERTILIZATION

The occurrence of self-fertilization as well as cross-fertilization in various groups of plants must be explained by a hypothesis different from those used for the origin of sex and of diploidy. There is little doubt that in this case the genetic system promoting greater flexibility, namely, cross-fertilization, is the ancestral one, and that self-fertilized types have evolved repeatedly in various phyla and classes of the plant kingdom, presumably in response to selection pressure in favor of immediate fitness. There are probably two principal reasons for the selective advantage of self-pollination in certain types of organisms. In the first place, short-lived plants with no effective means of vegetative reproduction must produce a good crop of seeds or perish. If an annual plant cannot be self-fertilized, and if in some abnormal season conditions are unfavorable for cross-fertilization at the time when the plant is sexually mature, it may perish without leaving any offspring. We can expect, therefore, that selection in favor of self-fertilization is very likely to occur in all annuals and other short-lived plants living in deserts, alpine or arctic regions, or other extreme environments. These must sacrifice their evolutionary future for the sake of their immediate survival. That this is not the only reason for the evolution of self-fertilization is suggested by two facts. In the first place a number of groups of short-lived annuals, such as many species of the genus *Crepis* and of various genera belonging to the tribe Madinae in the family Compositae, are self-incompatible and must be cross-fertilized, yet set a high percentage of seed even in dry years when their plants are greatly stunted. Second, some long-lived perennials, such as various species of grasses in the genera *Stipa, Danthonia,* and many others, have evolved mechanisms promoting a high degree of self-fertilization, in spite of the fact that the production of a heavy crop of seeds is by no means essential to their survival. An additional hypothesis is therefore necessary to account for the evolution of self-fertilization in such perennials, as well as in annuals living in a climate that is rarely or never unfavorable for cross-fertilization.

Such a hypothesis may be based on the fact that most of the species concerned live in habitats characterized by a great fluctuation in climatic conditions from season to season or in pioneer associations which are constantly changing their extent and position. The populations of such species are therefore greatly reduced in size periodically, and in certain seasons they must be built up very rapidly from the seed available in the ground. Such drastic changes in the populations of annual species in the San Joaquin Valley of California have been recorded by Talbot, Biswell, and Hormay (1939) and are well known to botanists in this and similar regions.

When plants are living under such conditions, they can build up their populations successfully in favorable years only if a large supply of seed is available and if the seedlings produced from these seeds are all or nearly all very well adapted to the conditions which prevail at such times. Such species cannot afford to experiment with a large number of new and possibly ill-adapted gene combinations. In them, a high premium is placed on a genetic system which favors opportunism and enables a favorable gene combination, once it has been achieved, to spread over a large number of genetically similar individuals. Genetic similarity is further favored by the fact that annual species, at least those which have been grown by the writer, have a relatively high degree of phenotypic plasticity as compared with perennials, so that the individual genotype can be enormously modified in respect to size, seed production, and other characteristics, depending on whether the environment is favorable or unfavorable. The great predominance of self-pollination in annual species of grasses and many other flowering plants can therefore be best explained on the basis of the selective advantage this genetic system gives to the species populations of such plants, as well as to the need for security in seed production.

Nevertheless, these predominantly self-pollinated annuals have not lost their capacity for forming new gene combinations. It is a well-known fact that in cultivated wheat from 1 to 3 percent of outcrossing may occur in some varieties under certain climatic conditions (Hayes and Garber 1927, p. 97). And in wild populations of predominantly self-pollinated grasses, the same is apparently true. Harlan (1945a,b) has demonstrated this for the perennial *Bromus carinatus,* while Knowles (1943) has shown that in the annual *B. mollis* the populations found in California, although they have been introduced into the state only about sixty years ago (Robbins 1940), are already differentiated geographically into ecotypes which behave differently when grown in a uniform environment. This would not be possible unless a certain amount of cross-pollination and heterozygosity was present in the species.

The genetic mechanism present in these annual plants apparently works about as follows. A particular family or racial line can maintain itself by self-pollination for scores or hundreds of generations. During this time it becomes completely homozygous and exists as a single biotype consisting of scores, hundreds, or even thousands of genetically similar individuals. Occasionally, however, an individual of such a biotype will produce a few seeds which are the result of cross-pollination with another biotype. If these seeds grow to maturity, they will form hybrid plants of a new morphological type, which will be highly heterozygous. Progeny of these F_1 interracial hybrids segregate extensively, producing a great variety of new genotypes. Some of these may be better adapted to the environment occupied by the parental biotype, while others may be capable of occupying new environmental niches. Following each chance interracial hybridization, therefore, there will ensue a burst of evolution lasting for six to eight generations, during which variability through segregation and consequent natural selection will be at a maximum. The surviving racial lines will gradually lose their remaining variability through inbreeding and will remain static until a new chance hybridization initiates another short burst of evolution.

That this type of evolution has in many instances been highly successful is evident from the fact that many groups of grasses with predominant self-pollination have become differentiated into a large number of species, many of which possess highly distinctive morphological characteristics. Good examples are the subgenera *Eubromus* and *Bromium* of *Bromus*, the subgenus *Vulpia* of Festuca, and the genus *Aegilops*. There is little doubt that a careful study of some of the annual genera in such families as Cruciferae, Leguminosae, Boraginaceae, Scrophulariaceae, and Compositae would reveal genetic and evolutionary patterns similar to the one just outlined for the grasses.

There is, furthermore, evidence that the evolution of a genetic system favoring constancy and fitness has taken place independently in a group of plants entirely unrelated to the angiosperms. Buller (1941) has produced evidence that in the Basidiomycetes, the primitive sexual condition is the heterothallic one, in which cross-fertilization and heterozygosity are obligatory. The heterothallic condition is general throughout the class of fungi, and the evolution of many genera has involved only heterothallic species. Homothallic species, which carry out self-fertilization through fusion of hyphae or gametes derived from the same mycelium, are scattered through various genera and usually appear like sexually degenerate types.

In many groups of fungi, such as the genus *Coprinus* among the mushrooms, no special feature of the homothallic species has been observed which might be looked upon as a causal agent for their evolution in the direction of sexual degeneracy. But in the genus *Puccinia* among the rusts there is a definite correlation between the length of life cycle and the presence of homo- or heterothallism (Jackson 1931). All the rusts of the long-cycle type, like the well-known wheat rust, *P. graminis tritici*, which has alternate hosts and the full complement of five types of spores, are heterothallic. But there are other species of *Puccinia* which are known as short-cycle rusts because they have only one host and three types of spores, the uredospores, the teliospores, and the basidiospores. These are homothallic. In both their life cycle and their genetic system they may be compared with the annual, self-fertilized species of seed plants.

THE SELECTIVE VALUE OF THE RECOMBINATION INDEX

Earlier in this chapter a possible correlation was suggested between longevity and a high recombination index on the one hand, and between the annual habit and a low one on the other. This correlation is an expected one, on the basis of the general principle developed in this chapter. As mentioned previously, genetic homogeneity is likely to have a high selective value in all organisms which are subject to great fluctuations in the size of their populations. But if this homogeneity is achieved by permanent homozygosity through enforced self-fertilization, the evolutionary future of the race is greatly jeopardized. On the other hand, if self-incompatibility and cross-fertilization are retained, an increase in the amount of genetic linkage, through reduction in chromosome number, in crossover frequency per chromosome, or both, can produce an increased homogeneity over periods of a few generations. This is a long enough period to build up the population in response to favorable environmental conditions. But with such a genetic system, new gene combinations can be continuously produced by crossing over, even if at a reduced rate, and the evolutionary possibilities of the race are relatively little affected. We should expect, therefore, that the greatest amount of morphological and physiological diversity among annual species would be found among those with cross-pollination and with relatively low chromosome numbers and chiasma frequencies.

Data recently obtained on chiasma frequencies in certain grass species (Stebbins, Valencia, and Valencia 1946a) suggest that the recombination index most advantageous for self-fertilized species may be much higher than that suited to cross-fertilized species with the same growth habit. The species *Agropyron parishii, A. trachycaulum, Elymus glaucus,* and *Sitanion jubatum,* although they all agree in the number and size of their chromosomes, differ widely in their metaphase chiasma frequencies. These differences are correlated with the degree of self-pollination, since *Agropyron parishii,* which is to a large degree cross-pollinated, has a mean frequency of 2.01 chiasmata per bivalent, while the predominantly self-pollinated *Sitanion jubatum* has 2.79 chiasmata per bivalent, and the two other species are intermediate in both respects. A probable explanation is that in the predominantly self-fertilized species the ability of the rare heterozygous interracial hybrids to produce many new gene recombinations is of particularly high selective value as a means of adapting the species to new conditions. In these species, therefore, fitness and constancy are secured entirely through self-pollination and homozygosity, while the mechanism for flexibility and adaptation to new situations consists of short periods of great heterozygosity, following interracial hybridization. During these periods natural selection is acting with great intensity, and a high recombination index is of great value.

The genetic systems discussed in this chapter are those found in organisms with normal sexual reproduction and without pronounced abnormalities in the pairing and segregation of the chromosomes. In plants, however, the genetic system is often modified by duplication of the chromosome sets, or polyploidy, by substitution of asexual for sexual reproduction, or apomixis, and by permanent heterozygosity for extensive differences in the arrangement of the chromosome segments, or structural hybridity. These phenomena are all of such great importance that they must be treated in separate chapters, and since they greatly affect the nature of species in the groups in which they occur, discussion of them is postponed until Chapters VIII–XI, following the chapters dealing with the species problem in normal diploid organisms.

GENETIC SYSTEMS IN PLANTS AND ANIMALS

One of the most remarkable features of the succession of discoveries which have established and advanced the science of genetics during the past half-century has been the great similarity between the phenomena in animals and those in plants. Segregation, recombination, linkage, crossing over, nearly all the complex cytological processes involved in meiosis, and all the types of progressive change, such as mutations and chromosomal aberrations, have been found in plants as well as in animals, often in the same form. Furthermore, in many respects the difference in genetic behavior between different types of plants is as great or greater than that between certain plants and certain animals. It is for this reason that genetics must be regarded as a branch of biological science separate from either botany or zoology, but forming a powerful connecting link between them.

Nevertheless, there are important differences between the genetic systems found in plants and those characteristic of animals. These differences are correlated with and probably caused by the very different modes of life of members of the two kingdoms. The three differences between plants and animals which have most strongly affected their genetic systems are in complexity of development, in longevity and ability for vegetative reproduction, and in mobility (Anderson 1937a, Turrill 1942a).

The differences in complexity of development and in the diversity of the cells and tissues of the mature organism are very great and extend from the highest to the lowest members of each kingdom. Not only are the systems of organs and tissues vastly more complex in a fly or a man than they are in a dandelion or an oak tree; the complexity of a sponge or a jellyfish is equally great when compared with that of *Spirogyra* or *Neurospora.* The complexity of development is further increased by the different methods of growth and development which prevail in the two kingdoms. The "closed" system of growth found in animals involves the precise, orderly succession of a long, complex series of physicochemical developmental processes, all occurring during the short period of early embryonic growth. Differentiation, youth, middle age, and old age occur in nearly all of the tissues simultaneously. If the genes of an animal are not able to act harmoniously to produce the integration of this complex developmental system, death results. Single mutations with a radical effect on any one process will almost certainly throw the system so far out of harmony that it will not be able to function properly and will produce either death or an ill-adapted monster. New combinations of genes, each having a relatively slight effect, are almost essential to evolutionary progress even in the simpler animals.

On the other hand, the open system of growth characteristic of plants necessitates a much less complex and precise integration of developmental processes. Differentiating and youthful tissues are confined to localized areas like the tips of the shoots, the roots, and the cambial zones. A relatively small proportion of the cells of the plant is undergoing differentiation at any one time. In many algae and fungi, there are never more than one or two types of cells being differentiated at any moment. Even in the vascular land plants the number of physicochemical processes involved in these developmental successions is probably less than that needed for most animals, and the need for the precise integration of the action of many different genes must be correspondingly less. Single mutations could under such circumstances play a relatively important role in evolutionary progress, and the number of adaptive combinations which could be obtained from a relatively small number of genes is probably larger.

All these factors contribute to make gene recombination considerably more important in animals than it is in plants. This is probably responsible for the fact that all animals are diploid (except for the males of some insects) and that the great majority of them, even hermaphroditic types like snails and worms, are normally cross-fertilized. In most animals, indulgence in continued self-fertilization appears to represent evolutionary suicide; in plants it may slow down evolutionary progress, but not necessarily stop it. In animals, furthermore, we should expect basic chromosome numbers and chiasma frequencies to run higher than in plants. This is certainly true of vertebrates as compared with flowering plants; the only numbers in the latter class which equal the ones usually found in vertebrates are obviously polyploid derivatives of the basic numbers, and therefore in a special class. The insects present a different and more complex picture. There is little doubt that a careful comparative cytogenetic study of the orders of insects in relation to their general biology would reveal much concerning the evolutionary significance of genetic systems determined by the recombination index.

The difference between plants and animals in longevity and the development of asexual, vegetative reproduction affects their genetic systems in an entirely different way. In animals, sexual reproduction is as important for maintaining the population of the species as it is for producing new variant gene combinations. This is also true in many plants, such as the annual seed plants, but in other types of plants, particularly many thallophytes, such as various saprophytic fungi and lichens, it is not true at all. A few facts will give an idea of the difference in this respect between animals and many types of plants.

In by far the majority of animal species the length of life of any individual is less than five years, and species of which the individuals live more than a hundred years are truly exceptional. But if we regard the individual from the point of view of its heredity and consider the life span of an individual genotype which has been derived from a single fertilized egg or zygote, then we must recognize that there are many plant species in which a life span of a hundred years is commonplace and a longevity of one or even many thousand years may not be unusual. The most spectacular examples of longevity, and those to which one's attention is most often called, are the large trees like the species of *Sequoia* and *Eucalyptus* (Molisch 1938). But these examples are unusual only if we consider an individual as a single growing shoot or shoot system. There are many species of shrubs and trees which sprout repeatedly from the root crown, so that the age of the individual is far greater than that of any one of its trunks. The species of willows (*Salix*), poplars (*Populus*), and many oaks (*Quercus*) are familiar examples, and even more spectacular ones are found in the crown-sprouting shrubs of dry areas, like the manzanitas (*Arctostaphylos* spp.) of California (Jepson 1939, pp. 29–34), which can be burned repeatedly without being killed. The life span of such individuals cannot be estimated, but barring the interference of man they can be destroyed only by disease, competition with other plant species, or a radical change in their habitat. Molisch (1938) has noted evidence of aging in many species of plants, but excepts those which have natural means of vegetative reproduction or regeneration. In stable plant communities seriously diseased plants are rare, so that the life span of many individuals which are able to sprout from the roots or crowns must approach that of the community itself. There is little evidence that the undifferentiated meristematic tissues of such plants are subject to senescence, as are the completely differentiated tissues of adult animals.

The same arguments apply with equal or greater force to the clones which represent the individual genotypes of perennial plants with effective means of vegetative reproduction, such as stolons, rhizomes, corms, and bulbs. As genetic individuals, these plants are not only immune to such agencies as age, frost, and fire, which destroy their individual shoots. Their separate vegetative parts or propagules can be carried for considerable distances by water, animals, or other agencies. In this way the individual as a whole is immune to the diseases, competition, or environmental change which may destroy some of its parts; it is practically immortal. Hitchcock and Chase (1931) state that many individual plants of buffalo grass on the western plains are probably the same ones which colonized these plains after the retreat of the glaciers.

The age of the clones of such vegetatively reproducing plants is impossible to estimate unless historical records are available. One such record is that of the saffron crocus (*Crocus sativus*). This "species" is highly sterile as to pollen and seed and is known chiefly in cultivation. Under these conditions, it is normally propagated by its corms. Its minimum age may be estimated from the fact that records of its cultivation for the yellow dye derived from its flowers date back to the ancient Greeks. It must therefore be at least 2,500 to 3,000 years old, and some strains may represent genetic clones of that age. There is every reason to believe that numerous clones of wild plants approach this age. By measuring the size of the clones and the rate of yearly spread, Darrow and Camp (1945) have estimated the age of a clone of *Vaccinium* as at least 1,000 years.

In such perennial plants with efficient vegetative reproduction a high degree of seed sterility is no detriment to the immediate existence of either the individual or the population. Examples are not uncommon of widespread and abundant wild species which over large areas reproduce entirely by vegetative means (Ernst 1918, pp. 569–588). A familiar example is the sweet flag, *Acorus calamus*, throughout Europe and western Asia. Others are such aquatics as *Eichhornia crassipes*, *Anacharis* (*Elodea*) *canadensis*, and *Lemna* spp.; bulbous plants like the sterile triploid form of *Fritillaria camschatcensis* in Japan (Matsuura 1935); and numerous species of lichens in the genera *Usnea*, *Ramalina*, *Cladonia*, and many others. Examples of vegetative as well as agamospermous apomixis, in which asexual reproduction has partly or completely replaced the sexual method, will be cited in Chapter X. In all of these instances, the reproductive potential and the spreading capacity of the species are secured largely through asexual means. Sexual reproduction serves not so much to maintain and increase the species as to produce the necessary genetic variability.

The most important result of this condition is the degree to which it lessens the selective value of complete fertility in sexual reproduction. Highly sterile genotypes may live for such a long time and spread so far by asexual means that they can under some conditions compete successfully with their fully fertile relatives. There is a striking example of this situation in the grass genus *Elymus* in California. *E. triticoides* is typically a rhizomatous grass of bottom lands in alkali soil, and although often not fully fertile, nevertheless as a rule it sets a fair amount of seed when different clones of this self-incompatible species are growing close together. *E. condensatus* is a giant caespitose grass found chiefly along the coast of central and southern California and preferring well-drained hillsides. Although its seed production is frequently very low, this phenomenon appears to be largely environmental rather than genetic, since most plants of this species grown under cultivation set seed rather freely. In addition there are found on hillsides and particularly along railroad embankments and highway margins plants which resemble robust forms of *E. triticoides,* but in their broader, greener leaves and particularly in characteristics of their inflorescences and spikelets approach *E. condensatus.* Since some of these closely resemble the artificial hybrid between *E. condensatus* and *E. triticoides* produced by the writer, they are most likely of hybrid origin. They are very highly sterile under all conditions, and their anthers contain almost entirely aborted and shriveled pollen, in this respect often exceeding the sterility of the artificial F_1 hybrid. These sterile hybrids and hybrid derivatives, because of their great vegetative vigor and their ability to spread by rhizomes, have proved better competitors under the environments produced by man's activity than have either of their parental species and they have spread into areas where neither *E. condensatus* nor *E. triticoides* is found. Some of them have retained the chromosome number 28 found in both parental species, while others have 42 chromosomes in their somatic cells (Gould 1945). Such a situation, which is fraught with considerable evolutionary possibilities, could arise in only a few types of animals. A further discussion of this and of similar situations is presented in Chapter VII.

The mobility of animals, as compared to the sedentary nature of plants, affects chiefly the structure of their populations. The difference between the two kingdoms, however, may not be so great as would seem at first sight. Animals move about mainly in search of food, and in a large proportion of the species of various groups the individuals tend to breed in nearly the same place as that occupied by their parents. This is well known for birds and many species of mammals. On the other hand, plants possess a considerable amount of passive mobility, which is usually most effective in connection with the sexual cycle. There is little doubt that the pollen of many species of trees is borne for many miles by the wind and may function perfectly after such journeys. Seeds are also carried for considerable distances, so that the offspring may grow up and find a mate in some region more or less distant from that occupied by its parents. Furthermore, in plants with effective vegetative reproduction, particularly with such structures as tubers, corms, and small bulbs, these parts may be carried considerable distances, so that a single genotype may simultaneously be fertilizing several other genotypes separated from each other by many miles. In plants as in animals, fertilization is usually between individuals which grew up near each other, but in species of both kingdoms mating between individuals originally separated from each other by long distances occurs fairly regularly, although with a relatively low frequency. There are, however, some species of animals such as ducks (Mayr 1942, p. 241) which because of their mobility and promiscuity have interbreeding populations derived from a much larger area than is ever the case in plants, and it is probably true in general that on the average effectively interbreeding populations of vertebrate animals are spread over a larger area and may reach a larger size than in plants. Accurate comparative data on this point are badly needed.

If this last generalization is true, then it follows that direct adaptation to the environment should be more regularly present in the larger animals than it is in plants, and the effects of isolation and chance fixation of genes should be less widespread. The discussion in Chapter II brought out the fact that in many groups of seed plants the species have a narrower geographical range than is typical for the higher animals and show less tendency to consist of well-defined subspecies. In the following chapter the importance will be brought out of small populations or of "bottlenecks" involving temporary reductions in population size in the origin of the isolating barriers which separate species. These might be expected to occur more frequently in plants than in animals, since animals could migrate more easily to escape temporary vicissitudes of the climate. It is perhaps noteworthy that the nearest approach among plants to the variation patterns found in most of the higher animals is found among forest trees, which have large populations and a maximum mobility of the gametes through wind transportation. Here again, a comparative study of habits of ecology, population size, and the nature of species and the genetic system in various orders of insects would doubtless be very enlightening. It may be that differences in these respects as great as those found between the higher plants and the vertebrate animals exist between different orders of insects. Nevertheless, comparisons between the genetic systems of animals and plants and their relation to the types of evolution found in the two kingdoms will undoubtedly be very fruitful subjects for future research.