CHAPTER X

Apomixis in Relation to Variation and Evolution

THE TERM APOMIXIS is a general one, covering all types of asexual reproduction which tend to replace or to act as substitutes for the sexual method. The more familiar term parthenogenesis, though better known to most biologists, applies to only a part of the apomictic phenomena found in plants. In most animals higher than the Protozoa, the Porifera, and the Coelenterata parthenogenesis is the only possible method of regular asexual reproduction. It appears in various groups of animals, such as rotifers, crustaceans, Hymenoptera, and aphids, but is by no means as widespread as it is in plants. This is in accordance with the principle, developed in Chapter V, that the relatively simple structure and development of plants, as well as their tendency for indeterminate growth, increases the selective value in them of genetic systems which deviate from continuous sexual reproduction and allogamy.

Careful analyses of the apomictic phenomena in a number of plant genera, and more or less casual surveys of apomixis in many more, have shown that numerous methods of apomixis exist in the plant kingdom, and that their genetic nature and evolutionary origin are both multiform and complex. The earlier reviews of the literature on apomixis by Rosenberg (1930) and the writer (Stebbins 1941a) have now been superseded by the vastly more thorough, complete, and discerning review and analysis of Gustafsson (1946, 1947b,c). This chapter, therefore, will be based chiefly on this review, particularly in respect to the factual material included, and for more detailed information on every phase of this subject, as well as for a complete list of literature, the reader is advised to consult Gustafsson's work.

METHODS OF APOMICTIC REPRODUCTION

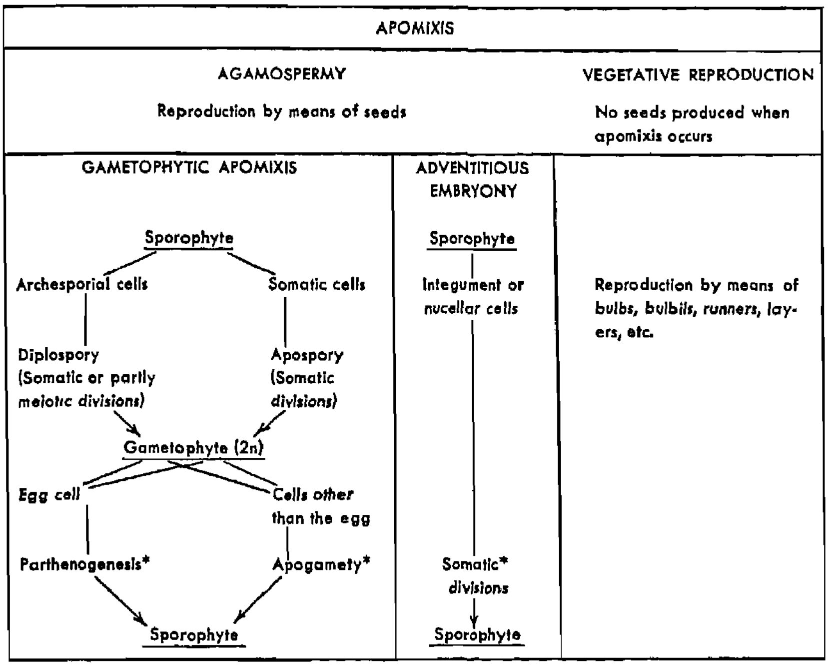
On the part of botanists not specializing in this field one of the chief barriers to an understanding of the apomictic phenomena has been the highly complex terminology it has developed, as well as the differences of opinion which have arisen among specialists as to the correct usage of terms. There are two reasons for this. In the first place, the phenomena themselves are complex and in many ways quite different from any which are regularly encountered in organisms reproducing by normal sexual methods. Secondly, the early research on apomixis was carried out before the morphological nature and the genetic significance of the various parts of the normal sexual cycle were fully understood by most botanists, so that many terms were used uncritically and were defined in ways that included erroneous interpretations of the phenomena they purported to describe. We owe chiefly to Winkler (1920, 1934) the first classifications and terminology of the apomictic phenomena which show correctly their relationship to corresponding sexual processes. In particular, Winkler first stressed the all-important point that since the normal sexual cycle of the higher plants includes two entirely different and equally essential processes, meiosis and fertilization, which are separated from each other by the entire period of growth and development of the gametophyte, these two processes can be expected to be influenced by entirely different environmental and genetic factors. Every harmonious apomictic cycle must therefore provide either a single substitute for both of these processes or a separate substitute for each of them, with coordination of these two substitutes. Thus, parthenogenesis through development of the egg cell without fertilization is not possible unless previously some process has occurred which has circumvented the reduction of the chromosomes at meiosis and has produced an embryo sac and egg cell with the diploid chromosome number. On the other hand, the mere occurrence of various altered developmental processes which lead to diploid gametophytes and egg cells does not ensure the occurrence of parthenogenesis and apomictic reproduction, as has been shown in a number of organisms.

Nevertheless, the terminology of Winkler is not complete, since some of the modifications of meiosis which lead from an archesporial cell in the ovule to a diploid embryo sac have not been recognized. For these reasons, Stebbins and Jenkins (1939), Fagerlind (1940a), and Stebbins (1941a) proposed amplified terminologies, in which names were given to as many as four different ways of circumventing meiosis and producing a diploid embryo sac. Gustafsson (1946) has pointed out that Fagerlind's karyological classification is difficult to apply because of the numerous intermediate situations which exist between the various recognized modifications of meiosis. In addition, he shows by the clarity of his lengthy exposition of the apomixis phenomena that a relatively simple terminology is sufficient for all practical purposes.

Gustafsson does not include in his classification of the apomixis phenomena those isolated occurrences of haploid parthenogenesis which have been reported from time to time in plants as well as in animals. Since these occurrences are known only in laboratory cultures and are without evolutionary significance, this decision is correct, and the chart presented by the writer (Stebbins 1941a, Fig. 1) may therefore be simplified to that extent (Fig. 36).

The classification of Gustafsson includes two principal types of apomixis, vegetative reproduction and agamospermy. The former may be considered as apomixis whenever the normal sexual processes are not functioning or are greatly reduced in activity. This may come about through a variety of causes, both phenotypic and genotypic, as was discussed in Chapter V. Under such conditions, structures like stolons, rhizomes, and winter buds, which normally act only as accessory methods of reproduction, may assume the entire reproductive function, so that the species under these conditions is essentially apomictic, although the same genetic types may under other conditions be normal sexual organisms. Gustafsson cites a number of species, such as *Elodea canadensis, Stratiotes aloides, Hydrilla verticillata,* and various members of the family Lemnaceae which in northern Europe reproduce wholly by such asexual means, but elsewhere are normally sexual.

More striking, and perhaps of broader significance, are those methods of vegetative reproduction in which the propagules occur within the inflorescence and replace the flowers. This phenomenon, often termed vivipary, is well known in such genera as *Polygonum (P. viviparum), Saxifraga, Allium, Agave,* and some



*The processes at this level can take place either autonomously or by pseudogamy, i.e., under the influence of pollen tubes or endosperm development.

FIG. 36. Chart showing the interrelationships of the processes of apomixis found in the higher plants. Modified from Gustafsson 1946.

genera of grasses, particularly *Poa* and *Festuca*. Species or races with this mode of reproduction may fail entirely to produce seed, and therefore from the genetic point of view may be quite comparable to the obligate apomicts which reproduce by seed.

Agamospermy includes all types of apomictic reproduction in which embryos and seeds are formed by asexual means. The essential feature of all types of agamospermy is that meiosis and fertilization are circumvented, so that the embryo (or embryos) which develops in the seeds is usually identical with its maternal parent in both chromosome number and genic content. The simplest method is adventitious embryony, in which embryos develop directly from the diploid, sporophytic tissue of the nucellus or ovule integument, and the gametophyte stage is completely omitted. This phenomenon is best known in various species of the genus *Citrus*, but it is also found in *Alchornea* *ilicifolia* and *Euphorbia dulcis* (Euphorbiaceae), in *Ochna serrulata* (Ochnaceae), in *Eugenia jambos* (Myrtaceae), in *Sarcococca pruniformis* (Buxaceae), in *Opuntia aurantiaca,* and in species of *Hosta* and *Allium* (Liliaceae) and of *Nigritella, Zygopetalum,* and *Spiranthes* (Orchidaceae). References are given by Stebbins (1941a) and Gustafsson (1946). For some reason, adventitious embryony seems to be relatively frequent in species native to warm temperate or tropical climates.

More common are methods of agamospermy which include from the morphological viewpoint a complete sporophyte-gametophyte-sporophyte cycle of alternation of generations, but in which diploid gametophytes arise as a result of some method of circumventing meiosis. These were collectively termed *agamogony* by Fagerlind (1940a) and Stebbins (1941a), a term which, as Gustafsson pointed out, had been used previously by Hartmann in a totally different sense. Fagerlind (1944b) then suggested the substitute term *apogamogony,* which Gustafsson rejected as illogical. He himself refers frequently to those types of agamospermy which are not adventitious embryony by the rather long and awkward phrase "apospory and diplospory followed by parthenogenesis." Since a collective term is obviously needed, the suggestion is here made that the term *gametophytic apomixis,* that is, apomixis via a morphological gametophyte, which sometimes can function sexually, is both descriptive and appropriate.

There are two principal ways of circumventing meiosis: apospory, in which a diploid embryo sac is formed directly from a cell of the nucellus or of the inner integument by a series of somatic divisions; and diplospory, in which the embryo sac arises from a cell of the archesporium, but in which meiotic divisions are either entirely omitted or are so modified that pairing and reduction of the chromosomes does not occur. These various modifications and the omission of meiosis have frequently been designated according to the plant in which they were first found (*Antennaria* scheme, *Taraxacum* scheme, etc.), but Fagerlind (1940a), Stebbins (1941a), and Battaglia (1945) have used special terms for them. Which of these methods of terminology is the more desirable, or whether any special terms are needed for these phenomena, is a matter outside of the present discussion of apomixis in relation to evolution. Whatever the method of formation of diploid gametophytes, the end result, from the evolutionary point of view, is essentially the same. Figure 36 shows a modification of the simplified terminology recognized by Gustafsson to describe the phenomena included in agamospermy, or apomixis with seed formation.

Diploid gametophytes formed by apospory or by diplospory may give rise to embryos through the multiplication of either the egg cell (parthenogenesis) or some other cell (apogamety). The former phenomenon is by far the most common one in the seed plants, but apogamety is frequent in ferns. Both processes, as well as adventitious embryony, are in some plants autonomous, but in others require pollination and the development of pollen tubes. Such apomicts are said to be pseudogamous. Like sexual forms, they will not seed unless pollination has occurred, but the plants formed from such seed are maternal in character. The effect of pollination appears to vary with the species concerned. In most pseudogamous species, such as *Allium odorum* (Modilewski 1930), *Potentilla collina* (Gentcheff and Gustafsson 1940), *Poa* spp. (Håkansson 1943a, 1944a), and *Parthenium incanum* (Esau 1946), the embryo begins development autonomously and even precociously, but the endosperm will not develop unless it is fertilized. Pollination and partial fertilization are therefore essential for continued growth of the embryo. Gustafsson nevertheless cites some examples, particularly the species of *Ranunculus* investigated by Häfliger, in which fertilization of the endosperm possibly does not take place. When parthenogenesis is autonomous, development of the embryo, the endosperm, or both are very often so precocious that at the time when the flowers open and the stigmas are ready to receive pollen the formation of the embryo and seed has already started.

One of the most conspicuous features of many apomictic plants is the disturbance of the meiotic divisions of both megasporogenesis in the ovules and microsporogenesis in the anthers. This is present occasionally in plants which reproduce by vegetative means or by adventitious embryony, but it is not characteristic of them. In plants possessing apospory ("somatic apospory" of Fagerlind and of Stebbins 1941a), meiosis is likewise either normal or characterized by slight abnormalities, such as a small number of univalent and multivalent chromosomes, in both microsporogenesis and the formation of the megaspore tetrads and embryo sacs which become replaced by the products of apospory. This comparative regularity may be connected with the fact that most of the aposporous apomicts have pseudogamous embryo development. On the other hand, in some of the American species of *Crepis,* which combine apospory with autonomous development of embryos and seeds, the archesporial tissue of the anthers develops so abnormally that the pollen mother cells degenerate before they reach the stage of meiosis (Stebbins and Jenkins 1939).

The most striking abnormalities of both micro- and megasporogenesis are found in those plants which combine some form of diplospory (including "generative apospory" of Stebbins 1941a) with autonomous development of embryos and seeds. These abnormalities have been intensively studied in *Hieracium, Taraxacum, Antennaria, Calamagrostis,* and some species of other genera. This work was reviewed by Stebbins (1941a) and even more carefully by Gustafsson (1947b). The most frequent abnormalities are failure of chromosome pairing, failure of contraction of the chromosomes, retardation of meiosis, and precocity of the meiotic divisions. These abnormalities, which were found thirty years ago by Rosenberg (1917), were considered by Ernst (1918) as strong evidence for his hypothesis that apomictic forms are of hybrid origin, and therefore that apomixis is caused by hybridization. Further knowledge of these phenomena, however, has made such an opinion untenable, although some of the abnormalities may be a direct or indirect result of past hybridization between species.

The most conspicuous feature of these abnormalities is that they are often, and perhaps usually, different in the male and the female organs of the same species. In *Antennaria fallax,* for instance (Stebbins 1932b), the occasional male intersexes found in nature have microspore meiotic divisions which are essentially regular, with a high degree of bivalent formation and normally contracted chromosomes. But in the ovules, meiosis is either entirely omitted or may in some ovules occur in a very abnormal fashion, with practically no chromosome pairing. In such an example, it is quite clear that the failure of pairing has nothing to do with the lack of homology between dissimilar chromosomes, but is connected with some disturbance in the normal development of the ovular and archesporial tissue. Meiosis in the anthers of various *Hieracium* apomicts has been studied by several workers, and a series of abnormalities has been described; but these are not duplicated in the ovules. Finally, Nygren (1946) has found that in *Calamagrostis lapponica* meiotic divisions occur in the anthers, although these are irregular and characterized by a varying number of univalents, while in the ovules the divisions are essentially mitotic; but in *C. chalybaea,* the reverse is the case, since the divisions of the pollen mother cells are essentially mitotic, while those of the megaspore mother cells are more like meiosis, although the formation of restitution nuclei causes them to produce diploid megaspores and gametophytes. In *Hieracium,* the reversion toward mitosis in the pollen mother-cell divisions is accompanied by great precocity in the time when they begin, while the same change in the ovules is associated with a delay in the onset of the divisions. In *Calamagrostis,* mitosislike divisions in the pollen mother cells may be associated either with a delay in their onset or with precocity.

The complexity and multiformity of these disturbances of meiosis, as well as the differences between anthers and ovules of the same plant, can be explained only if we assume that the normal course of meiosis requires the carefully synchronized occurrence of a series of developmental processes, and that it can be upset in a number of different ways by various environmentally and genetically controlled disturbances of one or more of these processes. They provide a wealth of material for studies of the differences between mitosis and meiosis and their causes, which still has by no means been exploited to its full extent.

One of the results of this diversity in the nature of meiotic abnormalities in apomicts is that not infrequently some ovules of a plant may produce diploid embryo sacs through failure of meiosis, while in other ovules of the same plant successful completion of the meiotic divisions will yield haploid embryo sacs and egg cells. The former ovules contain diploid egg cells capable of parthenogenetic development, usually through pseudogamy; while the latter will not form seeds unless fertilized. Such plants will therefore produce some completely maternal progeny through apomixis and other offspring by the normal sexual process. They are termed *facultative apomicts.* In plants which form diploid embryo sacs by means of apospory, facultative apomixis may also occur because in certain ovules the aposporic embryo sac either does not develop at all or develops so slowly that it does not crowd out the haploid one derived from the megaspore.

GENETIC BASIS OF APOMICTIC PHENOMENA

A number of hybridizations have now been performed between sexual types and related facultative or obligate apomicts of the same genus. Segregation in later generations from these crosses has shown in every case that the apomixis of the species is genetically controlled, but the basis of inheritance has been different in the various groups studied. The simplest situation is that found by Levan (1937b) in the predominantly apomictic *Allium carinatum,* a species in which the flowers are largely replaced by bulbils which reproduce it vegetatively. A cross between *A. carinatum* and the sexual species *A. pulchellum* showed that bulbil production in the former species is largely controlled by a single dominant gene, although the expression of the character may be greatly modified by other genes and by various environmental factors. Gustafsson's brief analysis of the meager data on the inheritance of adventitious embryony in *Citrus* has led him to the suggestion that in this group the inheritance is more complex, and apomixis is recessive to sexuality.

The most extensive genetic data on apomixis have been obtained in the complexes of *Poa pratensis* and *P. alpina* and in the genus *Potentilla.* In both of these groups the mechanism of apomixis is aposporous or diplosporous (in *Poa alpina*) gametophyte development followed by pseudogamous or (in some species of *Potentilla*) autonomous development of the embryos. The genetic basis in both is complex, as revealed through several publications by Müntzing and by Akerberg on *Poa,* and by Müntzing, Christoff and Papasova, and Rutishauser on *Potentilla* (see Gustafsson 1947b,c, for complete list of references). In *Poa,* crosses between facultatively apomictic and sexual biotypes, as well as between different facultative apomicts, yield a great predominance of sexual plants, showing that apomixis is recessive to sexuality (Müntzing 1940). Furthermore, since progeny from such crosses yield some plants which possess apospory, but not regular pseudogamous embryo development, and others which have little apospory, but yield a high percentage of haploid progeny through pseudogamous parthenogenesis (Håkansson 1943a), the various processes of the apomictic cycle are in this genus controlled by different genes, and successful apomictic reproduction is "due to a delicate genetic balance" between a series of factors.

The results in *Potentilla* are similar when diploid apomicts are crossed with each other or when apomicts with a low chromosome number are crossed with sexual forms. On the other hand, crosses between two high polyploid apomicts or between a polyploid apomict and a sexual form with a low chromosome number yield mostly apomictic progeny. Several genes for apomixis, therefore, may in the case of *Potentilla* dominate over a smaller number for sexuality. In *Rubus,* as in *Poa,* crosses between two facultative apomicts give sexual progeny.

In the genus *Parthenium,* the apomicts are pseudogamous. Although no hybrids between sexual and apomictic biotypes have yet been reported, evidence has been obtained to indicate that the two essential processes of apomixis — development of gametophytes with the unreduced chromosome number and of embryos without fertilization — are genetically independent of each other. This evidence consists of the behavior of a particular strain, No. A42163, described by Powers (1945). Meiosis fails and unreduced embryo sacs are formed in 90 percent of the ovules, but the eggs of these gametophytes cannot develop without fertilization as well as pollination. As a result, the offspring of this plant and its progeny consist of 65 to 90 percent of morphologically aberrant, dwarf triploids. The parental plant has 72, the progeny, 108 chromosomes. These triploids, in their turn, produce only unreduced gametophytes and egg cells, and progeny with still higher chromosome numbers (about 140) and more aberrant morphology. In crude language, this line polyploidizes itself out of existence.

Dominant factors for apomixis have been reported in *Hieracium* by Ostenfeld (1910) and Christoff (1942), but their evidence is considered doubtful by Gustafsson, since it deals with a cross, *H. auricula* × *aurantiacum,* involving a diploid sexual and a polyploid apomictic species. In general, the sum of evidence from

Hieracium suggests a genetic basis for apomixis similar to that in *Potentilla,* in which crosses between two polyploid facultative apomicts are likely to yield apomictic progeny.

Summing up, we may say that as a rule the apomictic condition is recessive to sexuality, although increasing the chromosome number often increases its tendency toward dominance. However, this recessiveness is not usually that of a single gene, but is due to the fact that a successful apomictic cycle is produced by the interaction of many genes, so that any cross between an apomictic form and a sexual one, or between two apomicts having different gene combinations controlling their apomixis, will cause a breaking up of these gene combinations and therefore a reversion to sexuality, sterility, or some abnormal genetic behavior. It is only in the relatively simple types of apomixis, like vegetative reproduction and adventitious embryony, that simple genetic behavior can be expected.

APOMIXIS, HYBRIDIZATION, AND POLYPLOIDY

The first hypothesis developed to explain apomixis was that of Ernst (1918), who believed that it is caused by hybridization between species. His evidence consisted mainly of the fact that disturbances of meiosis and of other developmental processes in the development of the sex cells are widespread in apomictic forms, and often simulate the same phenomena found in interspecific hybrids. As was pointed out earlier in this chapter, this evidence by itself is by no means conclusive. Supporting evidence produced by Ernst centered in the great polymorphism in apomictic groups and the difficulties of delimiting species in most of them. The latter situation has now been confirmed in many groups besides those known to Ernst, and in some of them, such as *Rubus, Poa, Crepis, Parthenium,* and *Antennaria,* convincing evidence has been obtained for the hybrid origin of many of the apomicts. Nevertheless, there is no evidence at all that hybridization by itself can induce apomixis. Hybrids between different sexual species of *Rubus* (Peitersen 1921), *Antennaria* (Stebbins 1932a), *Potentilla* (Christoff and Papasova 1943), *Taraxacum* (Poddubnaja-Arnoldi 1939a,b, Koroleva 1939, Gustafsson 1947b), and other genera have in no instance shown any clear indications of apomictic reproduction, even though their parental species may be closely related to known apomictic forms.

A similar situation exists in respect to the relationship between apomixis and polyploidy. Many groups of plants are known in which the diploid species are exclusively sexual and the polyploids, largely apomictic. This correlation is not, however, complete; all of the different types of apomixis are now known to occur in diploid forms. Diploid species with vegetative apomixis by means of bulbils or similar structures ("vivipary") are known in *Allium, Agave,* and *Lilium,* although in all these genera apomictic polyploids occur with equal or greater frequency. In a larger number of genera with this type of apomixis (*Polygonum viviparum, Ranunculus ficaria, Cardamine bulbifera, Saxifraga* spp., various species of *Festuca, Poa, Deschampsia,* and other Gramineae), all, or nearly all, the apomicts are polyploid.

Among agamospermous apomicts, those with adventitious embryony contain a relatively high proportion of diploids. *Citrus* is the classic example of this situation, but others are *Nothoscordum bivalve, Alnus rugosa, Sarcococca pruniformis,* and some species of *Eugenia.* In the latter genus, polyploids with adventitious embryony occur also, but *Ochna serrulata* and *Nigritella nigra* are the only polyploid species with this type of apomixis which are not known to have diploid relatives also possessing it.

Among the numerous groups of apomicts with gametophytic apomixis only three are known in which some of the apomictic forms are diploid. These are *Potentilla,* particularly *P. argentea* (A. and G. Müntzing 1941), the *Ranunculus auricomus* complex (Häflinger 1943, cited by Gustaffsson 1947b), and a form of *Hieracium umbellatum* (Gentscheff, cited by Gustafsson 1947b). In both *Potentilla* and *Hieracium,* the polyploid apomicts far outnumber the diploid ones, and polyploid apomicts also occur in *Ranunculus.* On the other hand, the list of apomictic groups given by Stebbins (1941a) includes 24 of this type, in which the apomicts are exclusively polyploid. Additional groups of this nature which may now be cited are *Parthenium* (Rollins, Catcheside, and Gerstel 1947, Esau 1944, 1946, Stebbins and Kodani 1944), *Rudbeckia* (Battaglia 1946a,b, Fagerlind 1946), *Paspalum* (Burton 1948), and probably *Crataegus* (Camp 1942a, b), although the latter genus is badly in need of careful study.

On the other hand, evidence obtained recently makes very unlikely the assumption that polyploidy directly initiates apomictic reproduction. Autopolyploids of *Taraxacum kok-saghyz* produced by Kostoff and Tiber (1939), by Warmke (1945), and by the writer (unpublished) show no signs of apomixis, although all of the triploid and tetraploid "species" which are closely related to *T. kok-saghyz* and live in the same region are apomictic (Poddubnaja-Arnoldi and Dianova 1934). Similarly, Gardner (1946) found complete sexuality in a high polyploid form of *Parthenium argentatum*, although closely related strains of the same species are apomictic.

The usual close association between apomixis, on the one hand, and polyploidy, interspecific hybridization, and polymorphy, on the other, must be explained on an indirect rather than a direct basis. Hybridization promotes apomixis in two ways. In the first place, the combinations of genes necessary to initiate an apomictic cycle are probably put together most easily by hybridization, either between species or between different forms of the same species. A genetical model illustrating how this could happen is presented by Powers (1945). He conceives of a minimum of three pairs of genes, as follows: Gene pairs *A* vs. *a* control, respectively, normal meiosis and failure of chromosome reduction; *B* vs. *b* control fertilization of the egg (whether haploid or diploid) and failure of fertilization; while *C* vs. *c* control failure of the egg to develop without fertilization vs. autonomous (usually precocious) development of embryo and endosperm. Apomixis will occur regularly only in the triple recessive homozygote, *aabbcc*. Gustafsson points out that pairs *B, b* and *C, c* control processes closely integrated with each other, and which might be expected to be controlled by the same genes. Since the action of any of the three alleles *a, b,* or *c* would be lethal or strongly deleterious to the individual unless the other two were present, such alleles would be likely to survive in natural populations only if they were recessive. Either inter- or intraspecific hybridization would be essential to put together such gene combinations.

Conditions similar to those which would be expected in two of the single recessive homozygotes postulated by Powers are known as isolated instances in a few plant species. In *Scolopendrium* (Andersson-Kotto 1932) and *Leontodon hispidus* (Bergman 1935b) recessive mutant forms are known which produce gametophytes by apospory, but these cannot produce new sporophytes without fertilization. According to the scheme of Powers, these would have the combination aaBBCC. The form of *Parthenium argentatum,* described in the previous section, which produces only triploid offspring is probably also of this constitution, as are the occasional aposporous, but not parthenogenetic, individuals which have been found in *Oxyria digyna, Antennaria dioica, Coreopsis bicolor,* and *Picris hieracioides* (cf. Stebbins 1941a). Håkansson (1943a) studied a sexual plant of *Poa alpina* derived from a cross between a sexual biotype and an apomictic biotype, and he found in it a tendency to produce up to 15 percent of haploid embryos by pseudogamous parthenogenesis. Hagerup (1944) found that in *Orchis maculata* haploid embryos frequently arise, due to precocious division of the egg cell. Both these forms can be considered to possess the combination AABBcc.

Powers's hypothesis thus seems to be the most plausible one yet developed for the genetic explanation of apomixis, although the situation in many apomicts may be even more complex. Each of the separate processes, and particularly the failure of meiosis, may in some instances be affected by more than one gene.

The second way in which hybridization promotes apomixis is through the greater vigor and tolerance of a wide range of ecological conditions possessed by hybrid genotypes of which the parents differ greatly in their ecological preferences. This has been demonstrated clearly by Clausen, Keck, and Hiesey (1945b) in the case of such crosses as *Poa pratensis* × *P. lapponica* or *P. ampla,* as well as in hybrids between widely different sexual ecotypes in *Potentilla glandulosa* (see page 108). The immediate selective advantage of a mechanism tending to preserve and reproduce such well-adapted genotypes is obvious.

After reviewing all the evidence in relation to polyploidy and apomixis, Gustafsson has reached the plausible conclusion that, although apomixis can be induced in diploids by favorable gene mutations, the action of many of these apomixis-inducing genes is stronger on the polyploid level than it is on the diploid level. The best evidence for this is obtained from ferns, particularly the work of Heilbronn (1932) on *Polypodium aureum.* The sporophyte of this species normally produces haploid spores and gametophytes by means of regular meiosis. Such normal gametophytes, like those of most ferns, cannot develop further unless the egg is fertilized to form a new sporophyte. But diploid gametophytes may also be formed aposporously by regeneration from pieces of leaves. These, like their haploid counterparts, produce eggs which are capable of fertilization and yield tetraploid sporophytes. But in addition they can under certain environmental conditions produce diploid sporophytes directly from their vegetative tissue, a process known as apogamety (see diagram, Fig. 36). Tetraploid gametophytes, produced aposporously from tetraploid sporophytes, are almost incapable of producing sex organs, and they reproduce regularly by apogamety. A somewhat similar tendency has been described by Springer (1935) in the moss *Phascum cuspidatum.*

That this property of increasing apomixis with higher levels of polyploidy is not a general one is evident from the comparative studies of Beyerle (1932), which have demonstrated that sporophytes of different fern species differ greatly from each other in their capability for regeneration. Wettstein (1927) has in addition found that the tetraploid, octoploid, and even 16-ploid gametophytes of *Funaria, Bryum,* and other genera of mosses are normally sexual and quite different from those of *Phascum cuspidatum.*

In the flowering plants, Levan (1937b) has produced a polyploid form similar to the bulbilliferous species *Allium oleraceum* by crossing two varieties of the diploid, nonbulbilliferous *A. paniculatum,* and he is of the opinion that the polyploidy was directly responsible for the bulbillifery. Turesson (1930, 1931b) noted that in *Festuca ovina* the degree of vivipary increases with increase of the chromosome number, but in other species of Festuca, such as *F. rubra, F. californica,* and *F. arundinacea,* hexaploid, octoploid, and even decaploid forms exist which show no sign of vivipary. There is good evidence, therefore, that polyploidy can reinforce the action of genes favoring such types of apomixis as vivipary or other forms of vegetative reproduction.

Adventitious embryony is the one type of apomixis which seems to be more common in diploid than in polyploid plants. We should expect, therefore, that the action of genes for this type of apomixis would not be favored by polyploidy. But, in the case of gametophytic apomixis, we should expect a particularly strong reinforcing action of polyploidy on genes for its component processes. There is, however, relatively little evidence for this from the flowering plants. Gustafsson does not cite any examples from the angiosperms of the reinforcement by polyploidy of a genetic tendency for nonreduction and the formation of diploid gametophytes. In *Hieracium hoppeanum,* Christoff and Christoff (1948) have obtained evidence for a tendency away from nonreduction after artificial doubling of the chromosome number. The form investigated is a pentaploid with the somatic number 45, and like all apomicts of *Hieracium* subg. *Pilosella* it produces unreduced gametophytes by apospory. A form with 90 chromosomes obtained from colchicine treatment also reproduces in this manner to a large extent, but it yields in addition offspring with 45 chromosomes, which resemble the undoubled form. Apparently embryo sacs with the reduced chromosome number have been formed, and eggs from these develop parthenogenetically. Embryological studies showed that in both typical *H. hoppeanum* and the doubled form, the products of meiotic division of the archesporial cell degenerate and are replaced by embryo sacs derived from the integument and the nucellus. In the doubled form, however, some of the nucellar cells expand and go through meiosis, thereby producing embryo sacs with the reduced chromosome number.

Evidence that a tendency toward pseudogamous parthenogenesis may be induced by increasing the chromosome number was produced by Håkansson (1943a, 1944) in *Poa alpina.* He obtained hybrids between a sexual race of this species with $2n = 24$ chromosomes and an apomict having $2n = 38$. Some of the F_1 plants, resulting from the fertilization of unreduced egg cells, had 41 to 43 chromosomes. These plants, although they always produced by meiosis embryo sacs with the reduced chromosome number, nevertheless yielded a high proportion of haploid offspring through parthenogenesis. Their sister plants with the normal complement of 30 chromosomes obtained from haploid gametes of the parental forms were not parthenogenetic at all. Håkansson and Gustafsson assumed that this situation could not be explained on a genic basis, since the F_1 offspring capable of parthenogenesis receive twice as many genes from their sexual parent, but the same number of genes from their apomictic parent as do those which are purely sexual.

In artificial autotetraploids of some purely sexual angiosperms eggs with the reduced chromosome number may develop parthenogenetically. This was found by Randolph and Fischer (1939) in maize and by Warmke (1945) in *Taraxacum kok-saghyz.* In every instance, the number of parthenogenetic diploids was very small, but nevertheless the fact is demonstrated that polyploidy may promote the autonomous development of the egg cell into an embryo.

Fagerlind (1944a) has suggested that in some, perhaps the majority of, agamic complexes the apomixis first arose on the diploid level. The present association between polyploidy and apomixis is believed to be secondary, and due to the fact that polyploids, particularly of unbalanced chromosomal types, can reproduce themselves more efficiently when apomictic than when sexual. This may be a partial explanation of the correlation in some groups, but it seems hardly applicable to such complexes as *Antennaria, Rubus, Potentilla,* and *Poa,* which contain a considerable number of sexual polyploids.

SOME TYPICAL AGAMIC COMPLEXES

Whatever may be its causes, the connection between apomixis, hybridization, and polyploidy is so intimate that it cannot escape the observation of anyone who studies thoroughly a group of apomicts and their closest sexual relatives. Species groups in which these three sets of processes have been operating possess a characteristic variation pattern, not unlike that described in Chapter VIII for polyploid complexes, but more intricate, and with fewer discontinuities between entities which can be recognized as species. Such groups were characterized by Babcock and Stebbins (1938, Stebbins and Babcock 1939) as *agamic complexes,* on the basis of their study of a typical example, the American species of *Crepis.* This complex remains the only one which has been studied in its entirety from both the systematic and the cytological point of view. But in other agamic complexes, particularly *Poa, Potentilla, Rubus, Parthenium, Taraxacum,* and *Hieracium,* portions of them have been studied much more intensively than *Crepis* from the cytogenetic as well as from the taxonomic point of view, and variation patterns have been revealed which deviate considerably from those found in *Crepis.* The best conception of the variation pattern in such complexes can therefore be obtained by summarizing first the situation in *Crepis,* and then indicating the ways in which various other agamic complexes depart from it.

The species of *Crepis* native to North America form a polyploid series based on the haploid number $x = 11$. Eight of them are diploid, but one, *C. runcinata,* is very different from the others and has no polyploid apomictic relatives. The agamic complex, therefore, is based on seven primary diploid species, *C. pleurocarpa, C. monticola, C. bakeri, C. occidentalis, C. modocensis, C. atribarba* ("*C. exilis*"), and *C. acuminata.* With the exception of the last two, these are all much restricted in distribution, and appear as relicts, as shown on the map, Fig. 37. Although their ranges overlap to a considerable extent, they have very different

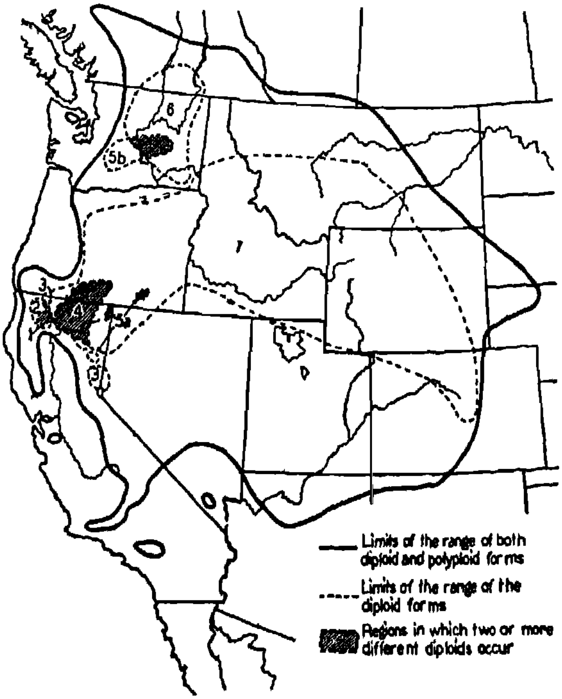


FIG. 37. The relative areas of distribution of diploid sexual forms of *Crepis* species in western North America and of their polyploid apomictic derivatives. From Babcock and Stebbins 1938. Base map copyrighted by Rand McNally Company. Reproduced by special permission.

ecological preferences, and no localities have been found containing two diploid species growing side by side. For this reason, no diploid hybrids between them are known. Since these species are extremely difficult to grow under cultivation, genetic work on them has not been attempted.

These sexual diploids comprise only a minute fraction of the total population of *Crepis* in western North America. Far more numerous are the polyploids, which have somatic chromosome numbers of 33, 44, 55, 77, and 88. All these polyploids which have been tested prove to be apomictic, although some of them are facultative apomicts. They include a certain percentage of forms which resemble closely each of the seven diploids, but the large majority show in their external morphology various combinations of the characteristics of two or more diploids. They thus appear to be allopolyploids, an assumption which is borne out by their cytology, so far as it is known (Stebbins and Jenkins 1939). This hypothesis is also supported by the fact that whenever the ecological and climatic preferences of an apomict have been analyzed, they have been found to fall between those of the diploid species between which the apomict is intermediate morphologically. In geographic distribution, the apomicts as a whole exceed the range of their diploid ancestors, but not to a great extent, because of the wide range of one diploid species, *C. acuminata.* This is the only species of which the nearest apomictic relatives have a narrower geographic distribution than the diploid form. On the other hand, the highly restricted diploids, *C. occidentalis* and *C. modocensis,* possess polyploid apomictic derivatives which are found throughout most of the range of the complex, although most of these seem to contain some genes from *C. acuminata, C. bakeri,* or both.

The most important point about the variation pattern in this complex as a whole is that while each of the seven diploids possesses certain distinctive morphological characteristics not found in other diploid species, none of the polyploids possesses characteristics which cannot be explained as a result of recombinations of those found in the diploid species, plus the effects of polyploidy. Until all the diploids were recognized, the relationships between the different apomicts could be perceived only dimly, and superficial resemblances caused the grouping together in the same systematic category of forms with very different relationships and ecological preferences. But recognition of the seven primary diploids permitted the grouping of the apomicts around them, either as apparent autopolyploids or as allopolyploids combining the different characteristics of various diploids. There thus appeared a variation pattern which resembles that shown in Fig. 34 except that it is more complex. The diploids can be thought of as seven pillars, which by themselves are sharply distinct from each other and so widely different that they appear to have affinities with Old World species which are placed by Babcock in different sections. They are connected by a much larger superstructure of polyploid apomicts, which represent all sorts of intergradations and recombinations of their characteristics.

Another feature of this pattern as observed in *Crepis* is that its diversity is very great in the regions occupied by the sexual species, but much less in the peripheral areas where only apomicts are found. In the latter regions, the same biotype or apomictic clone can often be recognized over distances of scores or even hundreds of miles, while in the vicinity of the sexual types each separate colony seems to possess its own cluster of distinctive apomicts. The apomicts are distributed in just the manner which would be expected if they had been formed by hybridization and polyploidy involving the sexual species and had radiated outward from the areas which the latter occupy.

From the systematic and the phytogeographic points of view, *Crepis* has two advantages over most of the known agamic complexes. The total range of its complex is confined to one geographic area and life zone, namely, the semiarid cold steppe or arid transition zone of the northwestern United States and adjacent Canada. This makes it much easier to comprehend as a single unit than each of the widespread Holarctic or even bipolar complexes, such as *Poa, Rubus, Antennaria, Taraxacum,* and *Hieracium.* Secondly, it is so recent that the diploid species which gave rise to it are all still in existence and are growing in the same regions as their nearest relatives among the polyploid apomicts. In this writer's opinion, many of the apparent divergences from *Crepis* in the variation pattern of other agamic complexes will be found to disappear when these are as fully known.

Although many agamic complexes have variation patterns essentially similar to that in *Crepis,* others deviate from this genus in certain important respects. These are, first, the number of sexual species on which the complex is based; second, the extent to which the range of variation in the complex is covered by modern sexual species; third, the relative frequency of facultative as compared to obligate apomixis; and, fourth, the presence of polyploid sexual species as well as diploid apomictic species.

So far as is known, the agamic complexes found in those genera most nearly related to *Crepis,* namely, *Taraxacum, Hieracium, Chondrilla, Youngia,* and *Ixeris,* differ from it chiefly in the number of sexual species, and therefore in the size and degree of diversity in the complex. The latter three are probably smaller, and the former two are certainly larger than *Crepis.* The two complexes of *Hieracium,* one in the subgenus *Archieracium* and one in subg. *Pilosella,* have been insufficiently explored as to their sexual species, but the range of variation in both of them is very great. In *Taraxacum,* no less than twelve species are known to be diploid and sexual and to have close relatives among the apomicts. But cytological explorations over large parts of the range of this complex are either lacking or are very superficial, and many more diploids undoubtedly exist. *Taraxacum,* therefore, is two or three times as extensive as *Crepis* in the range of its morphological variability, as well as in its geographical distribution. Gustafsson (1947c) has considered that *Hieracium* and *Taraxacum* belong to a different type of agamic complex from that of *Crepis* because the sexual relatives of the apomicts are considered (p. 254) to be "depauperate and relict." This distinction seems hardly justified, since five out of seven of the sexual species of *Crepis* are of this nature and would not have been found if a thorough search had not been made for them. No such search has been undertaken in the case of *Hieracium* and *Taraxacum.*

The agamic complex of *Antennaria* is nearly as extensive as that of *Taraxacum,* since it is based on at least twelve to fifteen different sexual diploid species. Hybrids involving three of these diploids have been found in nature (Stebbins 1932a, 1935), and the one studied cytologically has fairly regular meiosis. The apomicts, which are mostly tetraploid and hexaploid, reproduce by diplospory and by autonomous parthenogenesis. The great majority are obligate apomicts, but the high frequency in certain areas of male plants in apparently apomictic forms of some of the species (*A. parlinii, A. fallax*), suggests that facultative apomicts occur in some regions occupied jointly by sexual diploids and their close relatives among the apomicts. In external morphology, many of the apomicts are intermediate between two or more sexual diploids, and they tend to obscure the original species distinctions, just as in *Crepis, Taraxacum,* and *Hieracium.* A further complication which may exist in this complex is the presence of polyploid sexual species. Bergman (1935c) found $2n = 42$ in *Antennaria carpathica,* which may be related to some of the apomicts of arctic North America. In *A. media,* which possesses both sexual and apomictic biotypes, the writer found $n = 28$ in staminate plants from an apparently sexual colony.

Parthenium differs from all the complexes mentioned above in its smaller size, since its total range is confined to a single desert area, and probably only two original sexual diploid species have entered into it. The basic haploid chromosome number, $x = 18$, is possessed by the relatively restricted sexual forms of both *P. argentatum* and *P. incanum,* and the polyploids include forms with somatic numbers as high as 144, although nearly all the apomicts with numbers higher than $2n = 90$ are dwarf aberrants, which are rare or absent in nature. The method of apomixis is diplospory followed by pseudogamous parthenogenesis, and nearly all the apomicts are facultative. The conspicuous divergence from *Crepis* in the variation pattern of this complex is that the apomicts are grouped around two modes representing the morphological characteristics of the two sexual diploids, and intermediates between them, although clearly identified by the brilliant and painstaking work of Rollins (1944, 1945a, 1946), are less common than types which appear to be autopolyploid. *Parthenium argentatum* and *P. incanum* are sympatric throughout most of their geographic range, but they occupy different habitats and nearly everywhere are distinct enough so that they can be recognized even by people without botanical training. The largest stands of apomicts intermediate between these two species are in parts of Texas in which neither of the parental species is found.

The facts presented above suggest that the complexes most similar to *Crepis* are those found in other genera of the family Compositae. The best-known agamic complexes in other plant families, namely, those of *Rubus, Potentilla,* and *Poa,* differ from *Crepis* in most or all of the four characteristics mentioned above. The best known of these is *Rubus,* due to the exhaustive study by Gustafsson (1942, 1943a). Although polyploidy is known in several of the twelve subgenera of this large genus, apomixis is found chiefly in one of the six sections of a single subgenus, sect. *Moriferi* of subg. *Eubatus.* This section has a disjunct distribution, with one series of species in Europe and western Asia and the other in eastern North America, from Canada to Guatemala, plus a single species in Japan. Apomixis is predominant in the European members of this section. The hybridization experiments of Brainerd and Peitersen (1919, Peitersen 1921) indicate that many of the North American species are entirely or chiefly sexual, but the cytological studies of Longley (1924) and Einset (1947b) suggest that apomictic forms also exist, and Einset (unpublished, cited by Gustafsson) has confirmed this supposition.

Gustafsson recognizes five primary diploid sexual species among the European Eubati, but shows that these will by no means account for the amount of variation represented by the polyploid apomicts. The range of variation in these forms goes beyond that of the sexual species in three directions. One series, represented chiefly by the group *Suberecti,* varies in the direction of the North American sexual diploid *R. allegheniensis,* and it could be explained on the assumption that a close relative of this species existed in Europe at some time in the past. The second series, represented by the *Glandulosi,* has its center of variation in the Caucasus Mountains, and further exploration in this area may reveal a sexual diploid with the characteristics necessary to explain the morphological characteristics of this group. The third series centers about the anomalous species *R. caesius,* an apomictic allopolyploid of which the diploid ancestors are completely unknown. *Rubus,* therefore, differs from *Crepis* in that several of the sexual diploid ancestors of its agamic complex appear to be extinct, but may have close relatives still existing in regions not occupied by the apomicts. *Rubus* differs also in the presence of polyploid sexual species, and in the fact that most of its apomicts are facultative, while even the obligate apomicts have such good pollen that they frequently serve as the parents of hybrids.

The wide Holarctic range and disjunct distribution of the section to which the agamic complex belongs indicates a greater geological age than that of the North American section of *Crepis,* but nevertheless some of the sexual members of the *Rubus* complex have remained common, aggressive, and capable of contributing genes on a large scale to its apomictic members, although other sexual ancestors are apparently extinct. Due to the facultative apomixis, the origin of new forms through hybridization between apomicts is taking place on a much larger scale and over a much wider area than it is in *Crepis.* In fact, one whole group, the Corylifolii, appear to be derived from recent (post-human) hybridization between *Rubus caesius* and apomicts belonging to other sections. Thus, although the total range of morphological and ecological variability in the agamic complex of *Rubus* is about the same as that in *Crepis,* and although perhaps only half of the original sexual ancestors are now living within the range of the apomicts, the greater ability for hybridization, plus the vigor of the plants and their adaptability to areas disturbed by man, has kept the complex of *Rubus* in a more "youthful" self-perpetuating condition than is that of *Crepis.*

Neither of the two remaining well-known and extensive agamic complexes, those of *Potentilla* and *Poa,* has been given comprehensive treatment by a single author. The diploid species of the *Potentilla* complex may prove to be more numerous than those in any other, and the range of chromosome numbers, from $2n = 14$ to $2n = 109$ (the latter in the western American *P. gracilis*), is likewise the greatest known in any agamic complex. *Potentilla* is unique in the great development of apomixis through apospory and pseudogamy among two diploid species complexes, those of *P. arguta* (Popoff 1935) and *P. argentea* (A. and G. Müntzing 1941). Like the apomicts of *Rubus,* those of *Potentilla* are largely facultative, and hybridization between them is common in nature. Gustafsson suggests that one whole group of apomicts, the Collinae, like the Corylifoliae of *Rubus,* has arisen through recent hybridization between two other groups. Although sexual diploid species of *Potentilla* related to the apomicts are known, the precise relationships between them have not been worked out, so that the structure and history of this agamic complex is likewise obscure.

The genus *Poa* may contain one or several agamic complexes.

Apomixis is known or strongly suspected in seven sections of this genus, and since these sections are very difficult to separate from each other, and wide intersectional hybrids prove to be vigorous and productive of apomictic seed (Clausen, Keck, and Hiesey 1945b), all the apomicts of *Poa* may eventually prove to be interconnected and to form a single gigantic agamic complex. This would be undoubtedly the largest in the plant kingdom. Furthermore, two North American sections, the *Nevadenses* and the *Scabrellae,* resemble in some respects the neighboring genus *Puccinellia,* which also contains species that may be apomictic. It is not inconceivable, therefore, that this agamic complex is spread over two world-wide genera.

Poa, along with the apparently similar but little-known complex of *Alchemilla* (Gustafsson 1947c, p. 254), is distinctive in that only two sexual diploids are known which are likely ancestors for some of its apomicts. These are *Poa trivialis* (Kiellander 1942) and a sexual diploid of *P. alpina* reported by Christoff (1943). Furthermore, sexual polyploids form a conspicuous feature in two series, those of *P. alpina* and of *P. pratensis.* In both of them there is the additional unusual feature of aneuploidy. In particular, Müntzing (1933) has found somatic numbers of 22, 24, 25, 31, 33, and 38 in European strains of *P. alpina.* The type of apomixis present varies from one group to another. Several species are viviparous; the best-known method, found in *P. pratensis* and *P. alpina,* is apospory followed by pseudogamous parthenogenesis; and other mechanisms are likely to be found. Several species of western North America, such as *P. nervosa* and *P. epilis,* consist entirely of plants with abortive anthers and no pollen over large sections of their range (Keck, oral communication); these must be obligate apomicts with autonomous parthenogenesis. The range of chromosome numbers varies with the section. That in *P. alpina* is probably the lowest; that in the Scabrellae of western North America, with somatic numbers from $2n = 42$ to $2n = 104$, and a mode at 84 (Hartung 1946), is probably the highest. *Poa,* therefore, has more in common with *Potentilla* than with any other agamic complex, and agrees with it to a large extent in geographic distribution. Although additional diploid sexual species of *Poa* will almost certainly be discovered, most of those which contributed originally to the agamic complex are probably extinct. Furthermore, many polyploid sexual species of *Poa* are known, and these may have contributed very largely to the agamic complex. In fact, when this genus is better known, it may have to be regarded as a single huge polyploid complex, which is in part purely sexual, in part facultatively apomictic, and which contains in addition obligate apomicts. Like *Rubus* and *Potentilla,* the bulk of this agamic complex has retained its youthfulness and its ability to produce new forms through the activity of the facultative apomicts.

The agamic complexes just discussed are all classified by Gustafsson in the second of his two series of "apomictic and amphi-apomictic complexes." They are characterized by the statement that (Gustafsson 1947c, p. 235) "The apomicts belong to two or more different complexes which merge into one another," while in the first series (p. 222) "the apomicts are included in a single complex." The distinction between two merging complexes and a single one would seem to be rather difficult to make in many instances. The groups which Gustafsson places in his first series seem to the present writer rather heterogeneous, and many of them are relatively little known. Some, like *Ranunculus ficaria, Allium carinatum-oleraceum, Saxifraga stellaris-foliolosa,* and *Hypericum perforatum,* may be relatively small and simple agamic complexes similar to the larger ones described above. Others, like *Rubus idaeus, Poa bulbosa,* and *P. compressa,* may be portions of the main agamic complex found in each of these genera, and may appear to be isolated only because their relationships have not been well studied. Still others, like *Deschampsia caespitosa* and *D. alpina, Nigritella nigra, Festuca ovina, Stellaria crassipes, Polygonum viviparum, Cardamine bulbifera, Saxifraga cernua,* and *Gagea spathacea,* may be apomictically or asexually reproducing units of otherwise sexual polyploid complexes. Finally, there is the example of *Houttuynia cordata,* which so far as known is an isolated apomictic species without living sexual relatives, and may be the last relict of an ancient agamic complex (Babcock and Stebbins 1938).

CAUSES OF VARIATION IN AGAMIC COMPLEXES

The information reviewed in the preceding section makes possible an explanation of an apparent paradox mentioned by several authors, namely, that partial or complete abandonment of sexual reproduction results in a great increase in polymorphy of the group in which this phenomenon occurs. The causes of this polymorphy may be summarized as follows: first, hybridization and allopolyploidy between the original sexual ancestors of the agamic complex; second, hybridization between facultative apomicts, with the resulting segregation, or between apomicts and sexual species; third, chromosomal and genic changes within the apomictic clones themselves.

Although the causal relationships of hybridization, polyploidy, and apomixis are still to a certain extent matters for debate, there is no denying the fact that in the great majority, if not all, of the known agamic complexes extensive hybridization has occurred in the past between the ancestral sexual species. The products of this initial hybridization were undoubtedly highly sterile, except for those which happened to acquire a combination of genes favoring apomixis. Nevertheless, since the sexual species ancestral to most agamic complexes are rather closely related to each other, their F_1 hybrids might be expected to set occasional seeds, particularly when fertilized by pollen from one or another of their parents, and so to produce a strongly segregating series of backcross types, many of which could be vigorous and well adapted to some natural habitat. Thus, the complex would be likely to possess a high degree of polymorphism, particularly among the partially sterile hybrid derivatives. In such types gene combinations producing apomixis, whether acquired by mutation or by hybridization with apomictic forms, would have a particularly high selective value. Therefore, in any group which possesses the genetic potentialities for apomixis, this process would tend to perpetuate types which because of their sterility would not persist in a sexual group. It would crystallize an initial polymorphism which existed before the onset of apomixis and which, but for the arrival of this process, would have disappeared.

The second process, hybridization between facultative apomicts and sexual forms, or between different facultative apomicts, has been demonstrated experimentally as a cause of variability, particularly in *Rubus, Potentilla,* and *Poa,* in which nearly all of the apomicts are facultative. Gustafsson (1947b, pp. 141–146) has summarized a series of hybridization experiments in these genera, all of which have had essentially similar results. Hybridization between two apomictic forms usually yields sexual F_1 plants and a great range of segregant types in the F_2 generation. Many of these are sterile, inviable, or both, but others are vigorous, and in a few of the individuals in the F_2 or later generations apomixis may be restored. Such plants, if they find an ecological niche to which they are adapted, may be the progenitors of new apomictic clones. Facultative apomixis may therefore give a pattern of variation and a type of evolution which is in some ways similar to that found in self-fertilized organisms. The constancy of such apomictic clones, like that of pure lines, is periodically interrupted by bursts of new variability and selection, caused by hybridization. The major difference between the patterns created by these two types of reproduction is that in predominantly self-fertilized species the modes of variation represented by genetically isolated species are usually maintained, while in agamic complexes the reproductive ability of sexually sterile hybrid derivatives tends to obscure or to obliterate the original species boundaries.

Variability resulting from hybridization is still possible in some obligate apomicts. In the genus *Hieracium*, the classic hybridization experiments of Mendel, as well as the more recent ones by Ostenfeld (1910) and by Christoff (1942), have shown that fertilization of a sexual species by pollen from an apomict yields a great variety of segregant types in the F_1 generation, because of the heterozygosity of the parents. Some of these are wholly or partly apomictic and may give rise immediately to new clones, while others may segregate further and produce still more variant apomicts in later generations. It is obvious, however, that when obligate apomixis has set in, new variability through hybridization and segregation is confined to the regions in which sexual species occur and to those apomicts which still have functional pollen. For this reason, we should expect to find a conspicuous difference between the variation patterns of agamic complexes having facultative as compared to those with obligate apomixis. In the former, variability would be rather evenly spread throughout the geographic range of the complex, while in the latter it would be highly concentrated in those regions containing sexual species. The former situation appears to be true in *Rubus, Potentilla,* and *Poa,* while the latter is the case in *Crepis, Antennaria,* and probably *Taraxacum.*

The total amount of polymorphism would be expected to be greater in complexes containing facultative apomicts as compared to those with obligate apomicts, but this does not appear to be the case. The probable explanation of this situation is that obligate apomicts do not arise directly from sexual forms, but from facultative apomicts. This was postulated by Babcock and Stebbins (1938, Stebbins 1941a) on the basis of their study of *Crepis*. But Gustafsson (1935a) believed that the obligate apomicts arise directly in *Taraxacum* and *Hieracium*. He based this belief on the observation that facultative apomixis is usually associated with apospory, and obligate apomixis with diplospory. He maintained that "an entirely new type of division had to be introduced in the peculiar kind of parthenogenesis occurring in *Antennaria* and *Hieracium*" and that this type of division cannot occur in the same plant with the formation of reduced megaspores through normal meiosis. However, precisely this situation has been found in *Parthenium argentatum* (Esau 1946), fulfilling the prediction of Stebbins (1941a, p. 531). There is good reason, therefore, for believing that much of the polymorphism now found in *Antennaria, Taraxacum, Hieracium, Calamagrostis,* and other complexes with obligate apomixis was produced in an earlier stage of their evolution, when facultative apomixis was still widespread in them.

Various types of chromosomal and genic changes can occur within the apomicts. The first is that postulated by Darlington (1937) as a result of meiotic pairing and crossing over in the megaspore mother cells, with subsequent restoration of the diploid chromosome number in the egg through the formation of restitution nuclei or by some other means. Crane and Thomas (1939) postulate this mechanism for the origin of certain variants in *Rubus,* but do not present cytological evidence. Rollins (1945b) has suggested a similar explanation for variation in the apomictic progeny of *Parthenium.* Gustafsson (1943, 1947c) called the phenomenon autosegregation and discussed several cytological mechanisms, none of which is known to occur in these apomicts. Second, chromosomal aberrations may occur, particularly in the divisions leading to the diplosporous embryo sacs, which will cause the egg to have one or more chromosomes less than the normal number. The best example of this is the series of monosomics found by Sörenson and Gudjónsson (1946) in *Taraxacum*. In *Taraxacum*, as in most other genera, however, these chromosomal aberrants are less viable than euploid plants, and for this reason do not become established in nature. Only in *Poa* and in *Potentilla* are aneuploid apomicts abundant. Finally, apomictic clones may produce new variants by means of somatic mutations. These have been described as occasional occurrences in *Rubus* (Gustafsson 1943, p. 78), but they are better known in *Citrus* (Frost 1926). Because of the genetic heterozygosity of most apomicts, such mutations will usually affect the appearance of the phenotype, and if they occur in the tissue of the inflorescence or flower, they will produce mutant offspring.

SPECIES CONCEPTS IN AGAMIC COMPLEXES

The species concept developed in Chapter VI, which resembles the concepts maintained by the majority of those who desire a truly biological concept of species, centers about the possibility for exchange of genes between members of the same species and the separation of different species by barriers to the exchange of genes. As Dobzhansky (1941) and Babcock and Stebbins (1938) have pointed out, such a species concept cannot be applied to agamic complexes. Free interchange of genes between apomicts is prevented by the very nature of their types of reproduction, while the origin of many apomictic clones is from genotypes which have combined the genes of previously isolated sexual species, and which without apomixis would not be able to persist because of their sexual sterility. It is not strange, therefore, that systematists have not been able to agree on the boundaries of species in such genera as *Taraxacum, Hieracium, Antennaria, Rubus, Potentilla, Poa,* and *Calamagrostis*. In attempting to set up species like those found in sexual groups, they are looking for entities which in the biological sense are not there. Nor are those "splitters" who make a separate species out of every apomictic clone of *Taraxacum, Hieracium,* or *Rubus* likely to provide any better concepts of the variation patterns in the genera concerned. Criticisms of this method have been given by Müntzing, Tedin, and Turesson (1931), by Fernald (1933), by Turrill (1938c), by Babcock and Stebbins (1938), and by Stebbins (1941a). One criticism is that the number of apomicts in any well-developed complex is so large that recognizing them as separate species makes the comprehension of the group as a whole difficult or impossible; "one cannot see the forest for the trees." But more important is the fact that in many complexes the great majority of the apomicts, and in nearly all complexes at least some of them, are only partly or facultatively apomictic. From time to time they reproduce sexually, and on such occasions a whole series of new clones, or "species," may arise in the offspring of a single individual. Such forms may have sexual relatives in which a comparable amount of genetic variation occurs regularly in each generation. A *reductio ad absurdum* would be reached by the treatment as separate species of the apomicts in an entity like *Crepis acuminata*. Here the apomicts, indistinguishable in external morphology from their sexual ancestors, differ from each other in precisely those characteristics which segregate among the sister individuals of any sexual progeny (see diagram, Fig. 38).

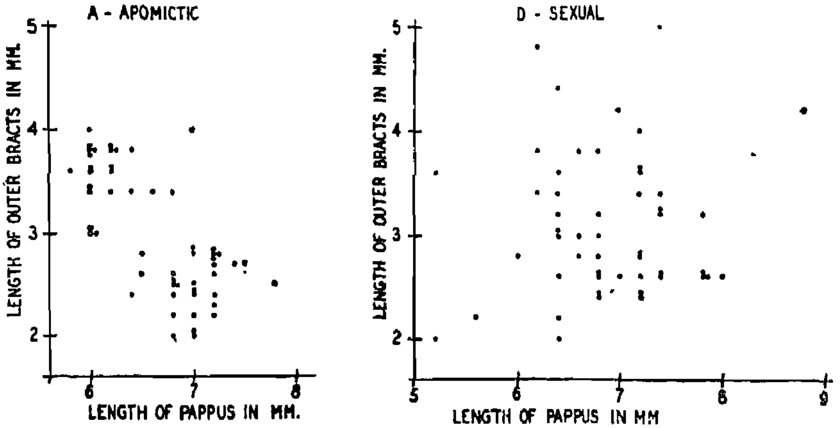


FIG. 38. Diagrams showing the range of variation in respect to length of outer involucral bracts and of pappus on the mature fruits within a colony of apomictic and of sexual *Crepis acuminata*. From Babcock and Stebbins 1938.

As Babcock and Stebbins (1938) have pointed out, the needs of classification and the clearest conception of the structure, interrelationships, and phylogeny of the agamic complex are obtained by drawing arbitrary species boundaries which are related to the original boundaries of the sexual species ancestral to the complex. The number of species recognized should not be smaller than the number of sexual ancestors which are known to exist or can be reasonably inferred to have existed in the past. In most complexes, furthermore, the number of species should be larger, since groups of apomicts combining the characteristics of sexual species which are widely different from each other should be recognized as agamospecies (Turesson 1929). The boundaries between these species must be drawn where most convenient, usually on the basis of one or a few easily recognized "key characters" which are known to separate the ancestral sexual species.

If, as in *Rubus* and in *Poa*, the sexual ancestors of the complex are mostly extinct, this method is difficult or impossible to apply. Here the method, suggested by various European systematists and followed by Gustafsson (1943, 1947c, p. 245), of recognizing as "circle microspecies" groups of apomicts morphologically similar to each other, with each species centered about one or a few particularly widespread and common apomicts, is perhaps the only feasible one. Consciously or unconsciously, it has been regularly used in practice. Nevertheless, the use of such a method must be recognized simply as a means of bringing some type of order to a situation which from the biological point of view is incapable of resolution. Disputes between systematists not fully conscious of the biological situation in these groups are particularly academic and futile.

AGAMIC COMPLEXES AND PLANT GEOGRAPHY

There are some features of agamic complexes which make them even better tools for analyses of plant distribution than are sexual polyploid complexes (Gustafsson 1935b, 1947c; Turrill 1938c,d; Babcock and Stebbins 1938; Stebbins 1941a). In the first place, the apomicts must have arisen from sexual ancestors and cannot have diverged very far from them in morphological characteristics. The identification of these ancestors should in most instances be possible by careful morphological and cytogenetical studies. If the apomicts are of allopolyploid origin, the same inferences may be drawn about past distributions of the sexual diploid members of the complex as is possible with sexual polyploids (see page 350). Secondly, *the relative constancy of apomicts through hundreds or* even thousands of generations makes them valuable indicators of ecological conditions, both in their present habitats and in past migration routes.

In the case of agamic complexes like that of *Crepis*, in which all of the sexual ancestors still exist and are concentrated in one or a few geographic areas, these regions must be regarded as primary centers of differentiation, from which migrants have traveled to the peripheral portions of the range of the complex. Obviously, one method of ascertaining centers of migration for entire floras would be to analyze the distribution of the sexual members of all the agamic complexes found in them. This might be particularly successful in floras like those of the arctic regions, which contain many agamic complexes, and in which present distribution patterns are the result of relatively recent migrations. Two suggestions are already possible in this connection.

In *Taraxacum*, the most numerous apomicts of the arctic regions, belonging to the section Ceratophora, have their closest relatives among the sexual species in those from central Asia, particularly the Thian Shan Mountains, studied by Poddubnaja-Arnoldi and Dianova (1934). This central Asiatic *refugium* is therefore the most likely center from which the arctic *Taraxaca* radiated in postglacial times. In *Antennaria*, on the other hand, the most common apomicts in the arctic regions belong to the *A. alpina* group, of which the sexual members are confined to the New World. The probable sexual species (judging by the abundance of male plants) which are morphologically most similar to *A. alpina* and its relatives are *A. monocephala* and *A. alaskana* (Malte 1934). Comparison by the present writer of specimens of these three makes rather likely the hypothesis that *A. alpina* and the arctic American "species" related to it are allopolyploid derivatives of these two sexual species. Since *A. alaskana* is confined to Alaska, and *A. monocephala* is more abundant there than anywhere else, the apomicts of the *A. alpina* complex are best explained as radiants from the Beringian center of Hultén (1937).

As described above, the agamic complex of *Rubus* is one in which certain ancestral diploid sexual species are no longer living in the region occupied by most of the apomicts, but occur in North America. On these grounds, Gustafsson has made the plausible inference that at some time in the past, probably during the latter part of the Tertiary period, some species of *Rubus*, morphologically and ecologically similar to the modern North American *R. allegheniensis* or *R. argutus*, existed in Europe, so as to give rise to the *Suberecti* and related sections. This evidence is in line with much of that from paleontology which indicates that the Tertiary floras of the Old and the New Worlds had considerably more in common than do the modern ones, and it runs parallel to the evidence from *Oryzopsis* allopolyploids (see page 353) that Eurasian species of this genus were once represented in North America.

The constancy of apomicts, and the fact that the ancestry of many of them may be determined, makes them particularly good indicators of past migration routes of floras. Gustafsson (1935b, 1947c) used apomicts of *Taraxacum, Hieracium,* and *Poa* to help solve certain problems of local distribution in Scandinavia, while Babcock and Stebbins (1938, pp. 39–44) have used the apomicts of *Crepis* in a similar manner in connection with the flora of the western United States. If the detailed study and classification of the endless "microspecies," or apomictic clones of the agamic complexes, has any general scientific value, it is in this direction. A broader problem of this nature, toward the solution of which apomicts may be valuable, is that of the disjunct ranges of many species in the temperate zones of the northern and southern hemispheres — the "bipolar" distributions discussed by DuRietz (1940). The fact that apomicts of both *Taraxacum* and *Antennaria* occur in temperate and subantarctic South America, while their possible sexual ancestors occur only in the temperate and subarctic regions of the Northern Hemisphere, indicates that these apomicts must somehow have migrated across the tropics. Because of the relatively narrow limits of ecological tolerance possessed by most apomictic clones, we must suppose that they followed a route which had ecological conditions essentially similar to those found in their present habitat, unless they were dispersed southward by long-distance migration. Some idea of their ability to cross the tropics along the crests of mountain ranges could be obtained by suitable experiments on growing them in such regions, from which they are at present completely absent. By the use of apomicts, therefore, at least one phase of this fascinating and puzzling problem of plant geography is open to experimental attack.

THE EVOLUTIONARY SIGNIFICANCE OF AGAMIC COMPLEXES

Apomixis has three principal effects on the groups in which it occurs. In the first place, it makes possible the survival of many genotypes which are vigorous and well adapted to their surroundings, but which because of their sexual sterility would be unable to survive were it not for this process. In a group of strictly diploid sexual organisms, new combinations of genes for adaptation to new habitats must be formed from a series of separate "gene funds," each of which is largely limited by the isolating barriers which bound the different species. Allopolyploidy permits the "pooling" of the genetic resources of two or more species to an extent limited by the factors which render allopolyploids fertile and constant, and to that extent a polyploid complex is better equipped than a group of comparable diploid species for the colonization of newly available habitats. With apomixis, the possibilities for pooling the genetic resources of several distinct species are still further increased, so that agamic complexes are even better equipped than are sexual polyploid complexes for the rapid evolution of new genotypes adapted to new habitats suddenly made available. They represent evolutionary opportunism carried to its limit. It is no accident, therefore, that apomicts of such genera as *Taraxacum, Antennaria, Hieracium, Rubus,* and *Crataegus* have "weedy" tendencies, and that agamic complexes are prominent in the arctic and subarctic floras which have recently been subjected to alternations of glacial and temperate climates.

Thus, the concept of Darlington (1939), that apomixis is an "escape from sterility," can be taken only in the relatively limited sense that it permits the survival of well-adapted, but sexually sterile, genotypes. Gustafsson (1947b, p. 173) has pointed out that many apomicts are still able to produce viable and fertile sexual offspring, so that the selective value of apomixis cannot be confined to this function.

The second effect of apomixis is similar to that of self-fertilization; it permits the building up of large populations of genetically similar individuals for the rapid colonization of newly available habitats. Thus the "opportunism" of agamic complexes results both from the increase in the number of adaptive genotypes available and from the ease with which such genotypes may be perpetuated. The fact is doubtless significant that apomixis and self-fertilization appear as mutually exclusive genetic systems. So far as the present writer is aware, the sexual ancestors of all known agamic complexes are self-incompatible, dioecious, or possess other mechanisms which promote allogamy. Apomixis has not developed in self-fertilizing plants.

One probable reason for this situation is that the type of growth habit which favors apomixis is apparently the opposite of that which promotes self-fertilization. Data presented in Chapter V (see Table 4) show that self-fertilization is predominant in annuals and in short-lived perennials, and is rare or absent in perennials with rhizomes or other effective means of vegetative reproduction. On the other hand, Gustafsson (1948a) has emphasized the fact that the sexual ancestors of agamic complexes are nearly all perennials, and many of them possess accessory methods of vegetative reproduction, such as rhizomes or stolons. This situation is probably explained by the fact that the change from cross- to self-fertilization can be accomplished by a simple genetic mechanism which does not necessarily affect fertility, while the acquisition of an agamospermous method of apomixis is usually associated with sexual sterility, either through interspecific hybridization or through genetic factors causing a disturbance of meiosis. So, just as in the case of polyploidy, the evolutionary line which is acquiring apomixis must pass through a bottleneck of partial sterility, and efficient vegetative means of growth and reproduction preadapt plants to these conditions. It is probably for this reason that, although apomixis would be expected to promote weedy tendencies, apomicts are not conspicuous among the weedy flora of cultivated fields and roadsides. The plants of such habitats are mostly annuals, and acquire through self-fertilization the constancy which helps them in colonization.

The third effect of apomixis is the limitation of genetic variability imposed on those plants which have adopted this method of reproduction. Over a short period of time, agamic complexes are capable of a rapid burst of evolution in terms of the production and establishment of new genotypes. But once an agamic complex has come to consist chiefly of apomicts, its evolutionary future is decidedly limited. If obligate apomixis has become predominant, new evolutionary progress is bound up with the distribution and potentialities of the remaining sexual species. If these species become much restricted geographically and ecologically, the evolutionary plasticity of the complex is lost, and it can no longer evolve in response to changing environments. Babcock and Stebbins (1938, pp. 61–62) have pointed out that aggressive, weedy tendencies are evident in those apomicts of *Crepis* related to the widespread sexual *C. acuminata,* while the apomicts related to the highly restricted sexual species *C. pleurocarpa* and *C. monticola* are themselves relictual types, showing little or no tendency to spread. An agamic complex with predominant obligate apomixis is a closed system which can produce little or no variation beyond that already present in the sum total of its sexual ancestors. As long as recombinations of these ancestral characteristics will yield gene combinations which are adapted to some available environment, evolution can continue, but when climatic changes or the evolution of more efficient competitors has started to encroach on the environments to which these genetic recombinations are suited, the agamic complex will gradually decline and die out.

In complexes like those of *Rubus, Poa,* and *Potentilla,* which contain chiefly facultative apomicts, the potentiality for new variation is independent of the fate of the sexual species. Such complexes have a longer lease on life, acquired by a favorably adjusted balance between apomictic and sexual reproduction (Gustafsson 1947b, pp. 173–178). Judging from their present distribution, the complexes of *Rubus, Potentilla,* and *Poa* are relatively old, since they are well represented in the temperate regions of both hemispheres and appear to have acquired their initial distribution along with the mid-Tertiary Holarctic flora (see Chapter XIV). On the other hand, most of the complexes with obligate apomixis show their relative youth by their restriction to a single hemisphere or to one hemisphere plus arctic-alpine regions elsewhere on the earth. Furthermore, the apomicts of these complexes with facultative apomixis have for the most part retained their aggressive tendencies, while in most complexes with obligate apomixis there are some groups of apomicts which appear as "conservative," relictual types, such as the *Crepis* apomicts mentioned above and certain forms of *Antennaria* and *Taraxacum* in Newfoundland and eastern Quebec (Fernald 1933).

Nevertheless, even in complexes with facultative apomixis, there is little evidence that they can give rise to anything except new recombinations of the genes present in the original sexual ancestors. There is no evidence that apomicts have ever been able to evolve a new genus or even a subgenus. In this sense, all agamic complexes are closed systems and evolutionary "blind alleys." It is true, as Gustafsson (1947b, p. 178) has maintained, that both sexual and apomictic groups are born, live their span upon the earth, and sooner or later die out. But other things being equal, the life expectancy of agamic complexes is shorter than that of sexual groups. Furthermore, while sexual species may, during the course of their existence, give rise to entirely new types by means of progressive mutation and gene recombination, agamic complexes are destined to produce only new variations on an old theme.

APOMIXIS AND PLANT BREEDING

The fact that apomixis occurs in a number of economically valuable crop plants has rendered a more than academic interest to studies of this phenomenon. The most important apomictic crop plants are the various species of *Citrus,* but apomixis is known or suspected in other cultivated fruits, such as the mango (H. J. Webber 1931, Juliano and Cuevas 1932, Juliano 1934, 1937), the mangosteen (Sprecher 1919, Horn 1940), and blackberries (see above). It occurs in the rubber-bearing plant guayule (*Parthenium argentatum,* see above), as well as in species of *Taraxacum* related to another rubber plant, *T. kok-saghyz.* Among forage grasses, it is conspicuous in *Poa pratensis* and apparently also in *Paspalum* (Burton 1948), while it occurs in some groups of ornamental shrubs, particularly *Malus* (crabapples, Dermen 1936b) and *Eugenia* (Pijl 1934, Johnson 1936). It is obvious that breeding programs on such groups must be conducted differently from those on sexual plants, and plant breeders who are planning a program on some group unknown cytogenetically, particularly if it belongs to the Gramineae, the Rosaceae, or the Compositae, should include among their preliminary explorations studies designed to determine whether or not apomixis is present.

As is evident from the discussion in this chapter, the presence or absence of apomixis in a group cannot be determined simply by castration experiments or by a few casually conducted experiments of emasculation and cross-pollination to determine whether or not hybrids can be obtained. A large proportion of apomicts are pseudogamous and need pollination for the successful production of seed just as much as do sexual species. Furthermore, many apomicts, being facultative, can yield occasional hybrids when pollinated by a different species, so that the production of hybrids in small numbers is insufficient indication that no apomixis is present.

Positive evidence for the presence or absence of apomixis can be obtained only from laborious and time-consuming studies of megaspore, embryo sac, and embryo development. But properly conducted breeding tests on a sufficiently large scale should in most groups provide reasonably decisive indirect evidence. If emasculation is possible, this should be carried out on a large scale, and the stigmas of the emasculated flowers should be pollinated with either a foreign species pollen or, preferably, with pollen from a different genotype bearing a dominant marker gene, as was done by Burton (1948) in *Paspalum*. If cross-pollinations of this type repeatedly yield a consistent percentage of strictly maternal individuals, apomixis can be suspected. If the flowers and anthers of the species are so small that emasculation is impracticable, the pollen should at least be examined through the microscope to see whether it stains well, and stained dissections of the styles and the stigmas of flowers bagged at anthesis should be examined for growing pollen tubes. If this is found, and if the resulting progeny are uniform, self-fertilization rather than apomixis is to be suspected; since, as mentioned in the preceding section, these two processes do not usually occur in the same group.

In groups known to be apomictic, the degree of apomixis should be determined by appropriate progeny tests (Powers and Rollins 1945), since facultative apomicts can be treated entirely differently from obligate ones. Fortunately, all the economically important groups mentioned above are, so far as is known, facultatively apomictic, and interspecific hybrids have been obtained in many of them. If any economic group is found to contain mostly obligate apomicts, the genus should be explored for sexual species, and pollen from these should be employed for breeding whenever possible. Even in groups containing mostly facultative apomicts, the sexual species may contain a supply of genes for disease resistance and other valuable properties which can by no means be ignored. Obviously, a study of the method of inheritance of apomixis in such groups is one of the next essential steps, so that estimates can be made of the extent to which apomixis will be recovered in the progeny of hybrids.

Selection and progeny testing in apomictic groups must obviously be conducted on an entirely different basis from that in sexual ones. Tinney and Aamodt (1940) in *Poa pratensis* and Rollins, Catcheside, and Gerstel (1947) in *Parthenium argentatum* have made some suggestions as to how this can be done. In *Poa,* the genetic constancy of seed produced by apomixis makes possible the testing of some varieties without the time-consuming process of establishing numerous clonal divisions from a single plant. Selection of new strains could be made from the occasional sexual plants found in most strains. In *Parthenium,* variety testing could be carried out as in *Poa.* But here there is a particularly useful source of new genetic variability, namely, the 36-chromosome "haploids" which occasionally develop from reduced eggs of normally apomictic 72-chromosome plants. These haploids inherit from their mothers the tendency to produce chiefly unreduced gametes; therefore, when pollinated by 72-chromosome plants they produce some offspring with this number of chromosomes. Since genetic segregation has occurred both in the production of the egg which gave rise to the haploid plant and in the pollen grains which fertilize its eggs, considerable genetic variation can be expected among the progeny of haploids pollinated by diploids. But each individual of this variant progeny will breed true through apomixis. This ingenious scheme for obtaining both the variability needed for selection and the constancy needed for testing, increase, and commercial use of a variety may be applicable only to guayule and to a few other apomictic species with similar properties. Nevertheless, there is little doubt that intensive studies of the fundamental nature of apomixis in other groups of economically important plants will be a valuable and perhaps essential prelude to the breeding of improved varieties in them.