Forty Years of Genecology

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I. The Scope and Concepts of Genecology

A. introduction

The term genecology was applied originally by Turesson (1923) to the study of the infraspecific variation of plants in relation to environment. Genecology was in this way established as a branch of ecology, comparable with and in various respects complementary to autecology and synecology, the former concerned with the environmental relations of individual species and the latter with those of plant communities. Turesson's early publications (1922a, 1922b, 1923, 1925, 1930) illustrate the synthesis of approaches — genetical, ecological and taxonomical —

which he accommodated within the discipline of genecology. The essential unity of these early researches lay in their concentration upon the species as "a genetically complex community, the distribution and the composition of which is largely determined by ecological factors and the genotypical constitution of the individuals . . ." (Turesson, 1923). Their aims, in brief, were to lay bare the patterns of infraspecific* ecological adaptation, and elucidate the mechanisms whereby this adaptation was achieved.

The separate identity of genecology depends upon the preservation of this combination of aims; like all synthetic disciplines, it breaks up into its components when purposes different from or more specific than those constituting the original frame of reference are introduced. Thus genecology merges into taxonomy when the primary aim is to systematize for classificatory purposes patterns of infraspecific variation; into genetics, when the mechanisms of variation and selection form the main targets of study; and into plant physiology when it is the physical responses of the organism to the environment which are of interest.

There seems still to be a need to preserve the identity of genecology in the original Turessonian sense, since for the understanding of an important phase of micro-evolution the synthesis is indispensable, in the same way that a synthesis — on a broader canvas — was essential in the development of the argument of "The Origin of Species". It is the purpose of this article to assess the present position of genecology and to attempt to distinguish a few of the general principles that appear to have emerged since the pioneer days. In doing this, facts and concepts have been drawn not only from researches which have been expressly oriented towards genecology, but also from related fields, where they contribute to the genecological synthesis in the broad sense.

B. SOME BASIC PROPOSITIONS

The basic propositions of Turessonian genecology may be summarized as follows: (1) Wide-ranging plant species show spatial variation in morphological and physiological characteristics; (2) much of this infraspecific variation can be correlated with habitat differences; (3) to the extent that ecologically-correlated variation is not simply due to plastic response to environment, it is attributable to the action of natural selection in moulding locally adapted populations from the pool of genetical variation available to the species as a whole. Turesson's own work, as exemplified particularly in the papers of 1922, 1925 and 1930, was devoted in large part to the substantiation of propositions (1) and (2), and to showing that ecologically-correlated inter-population variation was

* "Infraspecific variation" in this article means variation below the level of the average Linnaean species (See the discussion pages 165 to 167).

commonly genetically based rather than dependent upon the direct modification of individuals. The experimental methods employed — involving mostly sampling from wild populations and comparison under standard conditions of cultivation — have been reviewed and discussed many times, and need not be described further here. The results of Turesson's studies were satisfactorily conclusive. To them may now be added a mass of evidence accumulated subsequently by others, so that it may be accepted as an established fact that plant species in general do show genetically-based ecological differentiation.

If this be generally conceded, it cannot be said that there has been as satisfactory an agreement on the nature of the *patterns* of infraspecific ecological differentiation in the higher plants. Turesson's method of population sampling and comparative cultivation led him to the view that species commonly constituted a mosaic of populations each adapted to characteristic habitats, each habitat-form being more or less distinct — that is to say, separated by a variational discontinuity — from other (e.g. Turesson, 1936). This conclusion led in turn to the concept of the *ecotype*, now so firmly identified with Turesson's work that genecology itself has been called "the doctrine of the ecotype" (Faegri, 1937). Perhaps the most specific statement of the doctrine appears in Turesson's second paper (1922b): "The mass of genetically distinct forms which make up the Linnaean species do not distribute themselves indiscriminately over an area comprising different types of localities, but, on the contrary, are found in nature to be grouped into different types, each confined to a definite habitat. Further, these 'ecotypes' do not originate through sporadic variation preserved by chance isolation; they are, on the contrary, to be considered as products arising through the sorting and controlling effect of the habitat-factors upon the heterogeneous species-population."

According to Faegri (1937), Langlet (1934) was the first to point out that, since most of the major habitat factors vary spatially in a continuous and not "stepped" manner, graded rather than discontinuous variation is to be expected in a wide-ranging species as a consequence of adaptation to habitat. There can be no doubt that Turesson's methods, involving as they generally did sampling from rather remote populations occupying markedly different habitats, were not of a type likely to detect continuous spatial variation did it exist. More recent studies using adequate sampling methods have shown that adaptative variation may be either continuous or discontinuous, and it may now be said that the important questions concern not the existence of different patterns of variation but the forces acting within species to generate them, matters considered at length in Section II. Nevertheless, the lively discussion of the relative significance of continuous and discontinuous variation has

continued up to the present (Clausen, 1951; Clausen *et al.*, 1940, 1948; Faegri, 1937; Gregor, 1939, 1944, 1946a, b, 1956; Gregor and Watson, 1954, 1961; Langlet, 1959, 1963; Sinskaia, 1931), and the immediately succeeding paragraphs survey some of the background.

C. ECOTYPES OR ECOCLINES?

For reference to graded variation within populations or population systems of organisms the useful word *cline* is available, introduced by Huxley (1938) as an "auxiliary taxonomic concept". "Cline" unqualified implies simply the existence of a variational gradient; the prefix *eco-* indicates that the gradient can be correlated with an environmental variable.

The well known researches of Gregor and his associates on *Plantago maritima* (Gregor *et al.*, 1936, 1950; Gregor, 1938, 1939) revealed several types of graded inter-population variation, including some which was evidently ecologically correlated. In the discussion of his paper of 1938 and in his review of 1944, Gregor considered various genetical, ecological and taxonomical aspects of such variation, and subsequent work has confirmed the general validity of most of his conclusions. The cline concept is extensively used by Gregor in the recording of graded variation. Geographical clines (which may have an ecological basis where the variation is correlated with regional changes of climate) he refers to as *topoclines*; where the variation can be associated with the stages of an ecological sequence (which may never appear as an actual physical range of habitats to be encountered in a transect between two geographical points), it is referred to as an *ecocline*. Gregor emphasizes the need always to consider ecological variation in relation to the habitat range of species viewed as a continuum rather than as a complex of discrete non-overlapping environments; this leads him to the view that the ecotype must be imagined subjectively "as a certain range of variation on a genotypic gradient selectively developed in response to a climatic, edaphic, biotic, or for that matter any environmental gradient we may choose to examine". The *Plantago* data contain examples of quantitative characteristics — growth habit, scape length, spike density — which follow the environmental gradient waterlogged-mud drained "saltings". For reference purposes Gregor divided the populations into three ranges, predominantly decumbent, ascending, and erect, which he referred to as ecotypes. This treatment illustrates his attitude towards the use of the term ecotype: that it should be employed in a subjective sense to refer to "certain populations belonging to an ecocline". The definitions of certain terms concerned with infraspecific variation advocated by Gregor in 1939 were:

"*Cline*, any gradation in measurable characters.

Topocline, a cline following a geographical gradient.

Ecocline, a cline apparently correlated with an observable ecological gradient.

Topotype, a population in a geographical region possessing characters differing from those of another region. A topotype may be *extraclinal* if it does not fall within a geographical gradient in character expression, or *intraclinal* if it has reference to a particular range on a geographical gradient.

Ecotype, a particular range on an ecocline."

In Gregor's usage of this period, then, ecoclines, rather than ecotypes are to be regarded as representing the significant "ecological subcategories" of plant species.

The genecological work of the Carnegie group (Clausen *et al.*, 1940, 1948, Clausen and Hiesey, 1958a) reveals a notably different outlook upon infraspecific patterns of ecological differentiation. The study of variation in *Potentilla glandulosa* along a transect across central California recorded in the publication of 1940 suggested a comparatively simple pattern, the populations falling into morphologically distinguishable climatic ecotypes corresponding to the taxonomic subspecies *typica*, *reflexa*, *hanseni* and *nevadensis*. Although these are in a sense ecoclinal in that their distribution is related to a climatic gradient, they were interpreted by Clausen *et al.*, as population complexes replacing each other geographically in rather an abrupt manner, not at all comparable with the "ranges on ecoclines" envisaged by Gregor. An emphasis upon the distinctness of these major intraspecific groupings is a feature of the earlier publication; it also appears in that of 1948 devoted to the *Achillea millefolium* complex, although here a somewhat different situation is described. The populations sampled across the same California transect were regarded as belonging to eleven distinct climatic races ("or ecotypes"), four of the hexaploid *A. borealis* and the remainder of the tetraploid *A. lanulosa*. The races of *A. lanulosa* from the western slope of the Sierra Nevada are said to form "a graded altitudinal series that shows the close interrelationships between the physiological characteristics of the races and their environments"; they thus form an ecocline in the sense of Gregor. However, while for Gregor the ecotype is no more than an arbitrary section of an ecocline, the climatic race within *Achillea* is considered by Clausen *et al.* to be a coherent entity, distinct from others. It is described as follows: "Each climatic race consists of many local populations possessing in common those characteristics essential for survival in their particular environmental zone. Similarity in essential characteristics does not preclude individual variability. No

two populations are identical in composition, and they are composed of individuals scarcely two of which belong to the same biotype. Although the individuals and the populations vary, the races are statistically and reactionally distinct." (Clausen *et al.*, 1948, p. 122.)

The viewpoints of Gregor's and Clausen's school represent, in a sense, the poles of opinion in the period prior to 1950. Before reviewing more recent work, we will consider some methodological problems concerned in the analysis and interpretation of infraspecific diversification.

D. GENECOLOGICAL CATEGORIES

Turesson's view of the nature of infraspecific ecological differentiation led him eventually to treat the ecotype as a form of classificatory category, and to apply a nomenclatural system comparable with that of orthodox taxonomy. In this, the ecotypes were named according to their habitat predilections — *oecotypus alpinus*, *oecotypus arenarius* etc. (Turesson, 1925). There is undoubtedly a strong psychological compulsion to attempt to systematize knowledge of infraspecific ecological variation by this kind of classificatory approach, and the existence of orthodox taxonomy as a model encourages the direct transfer of methods. Yet it is now quite apparent that systems based upon the construction of discrete classes are inadequate to accommodate the diversity of genecological data, even if the additional flexibility of a hierarchical arrangement ("ecotypes within ecotypes") is permitted.

The view that "ecoclines represent the ecological subcategories" has been expressed by Gregor (1944). It is obvious that the "subcategory" envisaged here is different in kind from any orthodox taxonomic unit, since the basis of definition is not character correlation, within a real or imagined population, as it is for example with all the categories of nomenclatural taxonomy, but a selected trend of character variation viewed in relation to an extrinsic factor, either position on the earth's surface or ecological distribution. There is a sense in which an ecocline *can* be looked upon as a classificatory unit, when it denotes "a series of habitat populations showing genotypic gradation related to a particular environmental gradient" (Gregor, 1944); this usage would bring together a group of populations because of a particular relationship with each other in the same way that a group of populations may be classed together in a regional subspecies. The criteria for the grouping together are, however, obviously different: with the subspecies *similarity* is what is significant among the populations, with the ecocline, a particular pattern of *difference*. There are in any event good reasons for not thinking of ecoclines as classificatory units in the "group of populations" sense, the most compelling being that one and the same local population may contribute to different ecoclines. The essential fact about an eco-

cline is that it is a trend of variation within a major population, namely the species; in recording the infraspecific variation, what is important is to define the trends and the factors with which they are correlated, not to seek for nameable subcategories. If the concept of ecocline in this more abstract sense ("a variational trend", rather than "a group of populations") is accepted, then Gregor's definition of the ecotype as a range on an ecocline loses much of its meaning.

Indeed, it may be asked whether the concept of the ecotype has outworn its usefulness and whether it might not now be discarded with advantage. In a recent paper from Gregor's group (Gregor and Watson, 1961), it is concluded that a better understanding "could be achieved through the accumulation of records in which the emphasis has been transferred from the discrete ecotype to the trends of ecotypic differentiation". The reluctance of several authors to use the term ecotype in recent literature reflects a rather general agreement with this view (Heywood, 1959). Nevertheless, the abandonment of the term would be difficult, and indeed undesirable. As an appellation for a group of populations known to have features in common adaptive to a recognizable habitat it continues to have a respectable use. It only becomes disreputable in misuse, or when its use is taken to imply acceptance of over-simplified conceptions of the nature of infraspecific ecological variation.

Turesson's efforts to elucidate patterns of ecological adaptation in plant populations led him to propose genecological categories at and above the level of the average Linnaean species as well as below, namely the *ecospecies* and the *coenospecies*. The definitions of these categories and the evolution in their use since the time of their original suggestion have been reviewed and discussed several times (Gregor *et al.*, 1936; Turrill, 1938, 1946; Clausen *et al.*, 1939, 1940, 1948; Valentine, 1949; Baker, 1952; Heslop-Harrison, 1953b; Cain, 1954). It would be supererogatory to cover this ground again here; but it is important to pay some attention to the relationships between genecological and taxonomic interpretations of the species, since much of this article is concerned with infraspecific variation, in the broad sense.

Nomenclatural taxonomy in its present form depends upon the definition of classes in a hierarchial system, the classes at each level being based upon an assessment of overall resemblance in the range of features available for study. The basic unit, as defined by the "International Code of Botanical Nomenclature" (1956) is the *species*, which is to be named with a binary combination consisting of the name of the genus followed by the specific epithet. The principal tasks of the taxonomist concerned with formal nomenclatural taxonomy turn out to be identification and definition of variational units which may conveniently be

named as species, and the grouping of these units in a category system derived in all essentials from that of Linnaeus. However these activities may be embroidered — for example, by the attribution of lofty motives concerned with phylogeny — it is demonstrably true that they form the major part of taxonomic research.

Now it is a peculiarity of Linnaean-style classification that its requirements do themselves generate a "species concept" — one which has come to be accepted almost universally and usually unquestioningly by practising taxonomists (Heslop-Harrison, 1962, 1963). The properties required of a variational unit suitable for recognition as a named species are that its constituent individuals should show overall resemblance, in that any one should have more characteristics in common with any other than would either with an individual of another group; that it shows distinction from other groups of the same kind; and that it should have some degree of persistence in time. These are essentially the properties of the *morphological species* of Mayr (1942) and others.

Two of the practical consequences of attempting to apply universally a species concept of this general type are, firstly, that units of very varied biological character are defined as species in different groups in consequence of the diversity of genetic systems prevailing among plants, and, secondly, that in some groups where discrete variational units cannot be distinguished the taste of individual taxonomists becomes the sole determinant of what shall be ranked as species, so that chronic disagreement about nomenclatural treatments is practically inevitable.

In sexually reproducing, outbreeding groups, however, Linnaean-style taxonomy has met with reasonable success, and it has become apparent that this has been so because of the existence in these groups of variational units which do, in the main, conform satisfactorily in their properties with those required of the taxonomic species. These units constitute the *biological species* of Mayr (1942). Mayr's definition of biological species is as follows: "Species are groups of actually or potentially inter-breeding populations which are reproductively isolated from other such groups." As he has himself pointed out, this kind of definition contains criteria of two kinds: that concerned with reproductive isolation, and that of collectivity — "species are *groups*, etc." Partly in consequence of this duality, no basis is available for the objective definition of the biological species any more than existed for the Linnaean species: indeed it may be argued that the reasoning of Mayr and others simply provides the theoretical endorsement for the application of Linnaean style classificatory methods in sexual groups (Heslop-Harrison, 1955, 1963).

There are several uncertainties arising from Turesson's definitions and

usages of his own genecological units, some of which arose undoubtedly from linguistic difficulties. Turrill (1946) observes that in aiming at "an understanding of the Linnaean species from an ecological point of view", Turesson (1922b) was justified in his use of the term *ecospecies*, since species "as they are realized in nature" are ecologically delimited. The whole impression gained from reading Turesson's early writings is that he was looking upon ecospecies synthetically: as being composed of ecologically differentiated populations, the ecotypes, forming a mosaic throughout the distributional area. The second criterion of the biological species of Mayr, reproductive isolation, did not become part of the definition of the ecospecies until 1929, when Turesson referred to the ecospecies as "an amphimict population, the constituents of which in nature produce vital and fertile descendants with each other giving rise to less vital or more or less sterile descendants in nature, however, when crossed with constituents of any other population."

Baker (1952) has argued that whatever interpretation may be placed upon this definition, the most appropriate application for the term ecospecies is in reference to population systems that are isolated from each other by both ecological and genetical barriers. Ecotypes of the same ecospecies are, in contrast, assumed to be inter-fertile when brought into reproductive contact by the elimination of the eco-geographical isolation holding them apart in nature.

Leaning as it does upon a genetical criterion, this conception of the ecospecies would at first sight appear to be more useful from a gene-cological standpoint than the seemingly more arbitrary species concept of nomenclatural taxonomy based as it is largely upon comparative morphology. The genetical criterion cannot, however, be readily turned into a definitive test, since no general principles can be enunciated for recognizing barriers to crossing: all integrades exist between failure to interbreed due to ecological isolation and total intersterility (Heslop-Harrison, 1955). This limits the usefulness of the ecospecies concept in comparative genecology, since it cannot be assumed that the term will always connote the same thing. Situations in different genera can only be assessed one against the other when all the associated circumstances — breeding systems, nature and effectiveness of isolating mechanisms and the like — can be compared.

In the ensuing pages, the word species is used in the usual biological manner, permitting it to take up a meaning largely from the context (Heslop-Harrison, 1963). In general the meaning is that of "ecospecies" in a broadly Turessonian sense; in some instances this involves a direct conflict with nomenclatural taxonomic usage — as in the examples of "species pairs" like *Silene maritima* and *S. vulgaris* which stand in relation to each other much as ecotypes of one ecospecies.

E. GENECOLOGICAL TECHNIQUE

Phenotypic inter-population variation in a plant species may arise from three principal sources: (i) the direct plastic modification of individuals; (ii) genetical divergence in consequence of selection, and (iii) fortuitous genetical divergence resulting in various ways from sampling errors — e.g. drift in small populations, or the establishment of deviating colonies from small numbers of founders. The variation arising from (i) and (ii) may be expected to show correlation with habitat factors; (iii) will be random with respect to habitat. The essential problem of genecology is to devise ways to distinguish and study variation arising from (ii). For the sake of clarity, we will refer to this variation as *genecological differentiation*, following Harberd (1957). The problem of distinguishing genecological differentiation will be seen to have two parts; it requires the separation of adaptive from random inter-population variation, and the separation of the adaptive variation, in turn, into genetic and non-genetic components.

The difference between the requirements of genecological and taxonomic surveys is worthy of note. From the taxonomic viewpoint, all variation may be regarded as grist for the mill, except that the purist would reject the "modification" as a candidate for nomenclatural recognition. It is of no taxonomic significance whether two subspecies have diverged under selective pressures or merely in consequence of some fortuitous change in gene frequency in the course of an ancient migration; it is the difference that matters, not its source. In the genecological survey, on the other hand, information about regional variation is useless *per se*; it must have the support of other types of evidence before any evaluation of the adaptive differentiation of the species can be attempted.

This evidence can be sought in two general ways. The direct approach is to attempt to demonstrate adaptive responses experimentally, the aim being to discover whether or not populations in different parts of the species range do vary *inter se* in their ability to cope with diverse environmental variables, each being best equipped to deal with its own local circumstances. This essentially physiological approach to the investigation of genecological differentiation is discussed in Section III. The alternative, indirect, approach is to seek correlations between "plant type" and "habitat type". If these are consistently found, they may be taken to indicate adaptive divergence without any knowledge of the physiological meaning of the differences observed, since the only reasonable explanation for their existence is the differential effect of selection in the various habitats, save for the possibility of conditioning mentioned on p. 215.

In most genecological studies of the last forty years the intention has been to detect habitat-correlated, genetically-based variation, using population sampling methods of different kinds followed by comparative cultivation. Many have been open to criticism because the techniques adopted have hardly been adequate to permit the critical distinction between random and non-random variation. As Harberd (1957, 1958) and Wilkins (1959, 1960a) have pointed out in valuable critiques of genecological methodology, it may be extremely difficult — and in some cases, indeed, perhaps impossible — to make this distinction by the orthodox type of genecological trial.

Since the whole object of such trials is to seek for differences between populations and relate these to habitat, comparisons between populations taken singly and in groups are constantly required. Unless these comparisons can be placed upon a statistically and biologically sound basis valid conclusions cannot be drawn. In statistical terms, the exercise is to partition the genetical variance of the species in such a way that that part attributable to habitat type can be estimated and its significance evaluated. The ideal situation for analysis would be one where a species had encountered a mosaic of habitats while expanding its range, the selective influences in each habitat acting in turn upon the whole available pool of genetical variation. A comparison of between-habitat and within-habitat variances could then be expected to expose as significant those differences which were truly adaptive. All practical cases differ from the ideal one in some respect or other, and some so radically that analysis if not impossible can yield only dubious results. The example of regional subspecies illustrates the point. It may be possible to show that the area of one coincides with a climatic zone different from that of another; each can certainly be said to be "adapted" to its environment to the extent that it survives, but it cannot be said that all the morphological and physiological differences between them have necessarily been the outcome of differential selection in the two areas. As Wilkins (1959) has pointed out, the area of one may have been colonized by a small somewhat unrepresentative invasion from the other, so that adaptive differences rising secondarily in consequence of selection are confounded with the original chance differences between the colonists and the population from which they emerged. In this case evidence of genecological differentiation must be sought by the experimental demonstration of adaptation, using reciprocal transplant methods to test survival capacity or controlled environments to measure response to individual habitat factors.

This difficulty is part of a general one, arising from what Wilkins (1959) has termed "a general uncertainty about the variance found within a local population". Another aspect of this has been stressed by

Harberd (1957, 1958), namely the danger of attributing false significance to differences between populations in genecological trials in consequence of unsatisfactory sampling procedures. Harberd has been concerned with the particular case of a single genotype being incorporated several times in a sample because of the clonal spread of a parent plant to an unknown degree. By decreasing the within- population variance in a trial this can lead to the attribution of "spurious significance" to differences between populations. Both Harberd (1957) and Wilkins (1959) are driven to the conclusion that the within- population variance is not a particularly useful statistic in genecological studies, and that the value of a trial is most likely to be increased by increasing the number of populations sampled rather than the sample size. For a trial of given scale, the ultimate is a sample of one plant from each population; then, as Wilkins (1959) says, the variance would automatically be that within a purely statistical assemblage of unrelated individuals, and there would be no reason to expect any two such assemblages from the same geographical area to show non-adaptive differences.

A further source of confusion in genecological studies lies in the form of material collected for experimental garden or other investigation. The investigator in general has two choices: he can transfer mature living plants, or he can grow his material from seed. In the former case, he is sampling from a selected population; in the latter, he is sampling from a population which has descended from selected ancestors but has not itself suffered selection. The implications of this are sometimes overlooked. When populations occupy unlike habitats but are in sufficiently close proximity to permit gene exchange, differentiation will only proceed if selection pressure is high enough to out-balance gene flow (p. 204). In the extreme case, adaptation will be a generation-to-generation matter, with an essentially random dispersal of genotypes over the entire area each year and a subsequent stringent selection for adapted genotypes in each habitat "sub-population". In this case, to rely upon seed samples for the estimation of genotypic differences is to guarantee that they will not be found. Even when remote populations are being compared, a seed sampling method may not provide an adequate picture of what the actual surviving population in a given site is like. In the absence of disruptive gene-flow from other populations, recombination is unlikely to turn up radical deviants in any quantity, but where an adaptive response depends upon a nice balance of polygenes in an outbreeding population amodal types are certain to occur in each generation, normally destined to succumb in the wild unless they happen to be included in a seed packet. The aberrant individuals recorded in various studies on photoperiodic and other responses of ecotypes may have had

this origin. All this leads to the conclusion that the comparison of "seed-population" and "plant-population" variances would itself be worth while in genecological trials of perennial plants where technically possible — as it would be in periodicity studies on clonally divisible grasses and the like.

A word is necessary here concerning the other important distinction which has to be made in a genecological survey — between the genetical and non-genetical components of inter-population variation. The common practice is to attempt to eliminate the effects of direct environmental modification of individuals by cultivating population samples side by side in a standard garden. This method (which ante-dates genecology by at least a century) may be quite adequate to permit the kinds of distinction required, given an appropriate design of lay-out and analysis. In some circumstances, however, it may be unsatisfactory.

The most important deficiency of the method is that in eliminating environmentally imposed variation it may obscure genetically determined differences in the capacity to react adaptively *to* special environments. This is particularly dangerous where the aim is not merely to observe morphological differentiation but to test physiological responses. For example, consider the case of two genecologically differentiated populations, one with the capacity to react adaptively to intense sunlight, the other without. Tests made after side-by-side cultivation in a "neutral" environment under moderate illumination could fail altogether to reveal any difference in response to intense light. One might go so far as to say that an "ecotype" is never adapted to its special milieu when cultivated in an experimental garden; it merely carries the ability to become so adapted under the appropriate evocative environment. It may in cultivation show differences from plants from other habitats, but the differences need not relate at all closely to its true adaptive capacities. The work of Björkman and Holmgren (1963), described in detail in a later section, is exemplary in giving full attention to the matter of pre-conditioning.

Another deficiency of the comparative cultivation method lies in the possibility that the test environment while suppressing some environmentally induced characteristics may evoke others never expressed in the natural habitats. A sample from a phenotypically uniform natural population may turn out to be genotypically highly diverse when observed in a different environment, and this artificial enhancement of variance could prejudice attempts to detect and evaluate genecological differentiation. Numerous examples of this effect have now been recorded, particularly in connection with the environmental control of developmental periodicity; Sinskaia (1958) and Clausen and Hiesey (1958b) discuss some of its implications for genecology. It may be noted

that this exposure of latent genotypic variation has nothing to do with the *uniformity* of the test environment; it is simply that this environment increases the penetrance of certain genes compared with the native one. There is another even more subtle way in which the within-sample phenotypic variance may be increased, even under supposedly highly uniform controlled environments: this is when genotypes are carried so far out of their norms that developmental regulation is disrupted (Heslop-Harrison, 1959a). Here it is not a question of the exposure of genetical heterogeneity — the effect may be seen in what is effectively a pure line — but rather the amplification to a phenotypically obtrusive scale of developmental "noise".

Many of the limitations of the simple transplant technique are removed when methods of varied-environment or reciprocal transplanting are adopted. The classical example of this approach is the work of Clausen *et al.* (1940 *et seq.*) using transplant stations along a coastal plain to inland mountain transect in California — work which had a prototype, albeit an unsatisfactory one, in the experiments of Gaston Bonnier.

A further technical problem meriting consideration is the selection of characteristics for observation in a genecological study. Morphological characters are those most readily investigated; yet as Turesson pointed out repeatedly in his pioneer papers, it is the whole reaction of plant to habitat which is of adaptive importance, physiological responses being paramount. In a paper on recognizing adaptive variants, Wilkins (1960a) points out that as the only ultimate test of adaptation is survival in the given habitat all other kinds of evidence, including that derived from comparative cultivation, is bound to be circumstantial. The best form of such circumstantial evidence, he suggests, is that arising from the study of correlations between measurable habitat factors and plant characters. Frequently there will be no possible way of assessing the biological significance of the features measured, and although the existence of correlations may suggest they are adaptive, an element of uncertainty remains since it is always possible — and indeed for many morphological characteristics, probable — that what is observed is itself no more than a by-product of the physiological process basically concerned. Concentration upon morphological characters may in fact lead to incorrect conclusions about the "adaptedness" of populations if the characters themselves are neutral enough in respect to selection to vary randomly over the area sampled, particularly when the random variation is taken to indicate the *lack* of adaptation. Langlet (1963) has quoted as an example of this kind of reasoning Clausen's conclusion (1951) that since no correlation was detectable between latitude of origin and a small group of morphological features, no ecological clines are present in *Layia platyglossa*.

F. GENECOLOGICAL DIFFERENTIATION: SOME ILLUSTRATIVE EXAMPLES

Notwithstanding the technical difficulties mentioned in the foregoing paragraphs, a wealth of data now exists illustrating the patterns of habitat-correlated variation encountered in higher plant species. As a prelude to the discussion of evolutionary aspects of genecological differentiation in Section II, a number of examples will now be reviewed under headings defining the main types of situation known at present.

1. Major Ecological Races with Vicarious Distributions

The most fully studied example of a species containing distinct ecological races with practically exclusive areas is that of *Potentilla glandulosa*. In the most recent publication of the Carnegie group (Clausen and Hiesey, 1958a), this species is discussed again. The distinctness of the four "ecotypic" subspecies in the Californian area studied is maintained, but the additional data available reveal that each is itself heterogeneous.

TABLE I

Characteristics of the Ecotypic Subspecies of Potentilla glandu-losa *along the Central Californian Transect. [Data from Clausen and Hiesey, 1958a.]*

	typica	*reflexa*	*hansenii*	*nevadensis*
Distribution	Coast Ranges and lower Sierra Nevada	Low and middle altitudes of Sierra Nevada	Meadows, mid-altitudes of Sierra Nevada	High altitudes of Sierra Nevada
Habitat	Soft chaparral and open woods	Dryish, open timbered slopes	Moist meadows	Moist, sunny slopes
Climatic tolerance as experimentally determined	Coastal to middle altitudes	Coastal to middle altitudes	Middle and high altitudes (poor survival near coast)	Middle and high altitudes (poor survival near coast)
Seasonal periodicity at Stanford (alt. 30 m)	Winter- and summer-active	Winter-active or -dormant; summer-active	Winter-dormant summer-active	Winter-dormant summer-active
Internal variation	Wide, probably several "ecotypes"	Wide, probably several "ecotypes"	Wide, at least two "ecotypes"	Moderate, at least two "ecotypes"
Self-compatibility	Self-fertile	Self-fertile	Undetermined	Self-sterile

Table I, part of a comparative table given by Clausen and Hiesey, gives the essential information about distribution, ecology, periodicity and internal variation for the four subspecies.

The accounts given of the internal variation of the subspecies indicate that each is genecologically differentiated at a lower level. The pattern of this differentiation is related to local climate and microclimate as determined by aspect and altitude, and also to edaphic features. Subsp. *typica* is quite evidently extremely heterogeneous; according to Clausen and Hiesey, "Individuals within each local population differ in minor but distinguishable morphological and physiological characters. Neighbouring populations differ statistically in their average biotype composition even though they belong to the same ecotype. Populations from climatically distinct regions are to a greater degree divergent both morphologically and physiologically and represent ecotypes." Subsp. *reflexa* is also recorded as being heterogeneous, but seemingly to a lesser degree. Two distinct ecotypes are distinguished within it: one, inhabiting low level forest, being winter active and early flowering in cultivation, and the other, from higher level *Pinus ponderosa* forest, being winter dormant and late flowering. Subsp. *hanseni*, although occupying only a comparatively small total area, is one of the most variable of the four occurring in California. It is described by Clausen and Hiesey as constituting a link between the foothill and high altitude races of the subsp. *reflexa* and *nevadensis*. In morphological features and earliness, "with increasing altitude . . . *hanseni* tends more and more to resemble *nevadensis.*" Moreover, the same trend is present in life form — "The forms of *hanseni* are generally hemicryptophytes . . . the *hanseni* populations from lower altitudes, however, develop short woody crowns similar to the chamaephytes of *reflexa*, whereas those from higher altitudes are more rhizomatous, as in *nevadensis.*" These observations certainly seem to show that a system of clines does exist in *hanseni*, but later in the same account the authors appear to deny that this is so. Subsp. *nevadensis*, from the highest altitudinal belt, appears to reveal the narrowest range of variation, but even so, genecological differentiation is present. Two climatic ecotypes are described, one alpine and the other sub-alpine, differing morphologically and in periodicity.

Clausen and Hiesey relate the distinctness of the four central Californian subspecies of *P. glandulosa* to the sharply differentiated climatic zones across the transect from the Pacific to the Sierra Nevada. They remark that north and south of the area investigated in detail the pattern of zonation becomes obscured; then, "the rather well defined subspecies found in central California break down into other combinations of characters." Within the area where the subspecies are well distinguished, inter-gradation between them is said to be minimal, and

where it occurs Clausen and Hiesey interpret it as evidence of hybridization.

Another example of a Californian species with vicarious, ecologically specialized subspecies is that of *Gilia capitata*. *G. capitata* is a polytypic species with a natural range extending from central California to British Columbia. Following an intensive study of population samples from various parts of the range, both as acquired in the wild and in comparative cultivation, Grant (1950, 1952, 1954) has concluded that eight recognizable entities worthy of taxonomic recognition as subspecies are present. Except for subsp. *abrotanifolia* and *pedemontana* which have overlapping ranges, these subspecies replace each other geographically in a pattern related to both the north-south climatic gradient of the Pacific coast and the east-west gradient from the coast towards the interior. Grant recognizes two basic types within the complex, subsp. *capitata*, a plant of rocky hillsides, and the two subspecies *chamissonis* and *staminea*, plants of sand dunes or sand plains. These may have had a common parentage in subsp. *abrotanifolia*. With subsp. *tomentosa*, subsp. *capitata* forms a pair of ecotypic vicariads, *tomentosa* maritime and *capitata* inland; similarly subsp. *chamissonis* and *staminea* can be looked upon as a pair of ecotypes, one coastal, the other inland. The remaining races may have arisen through introgressive hybridization between the primary subspecies. Their success, according to Grant, has resulted because "ecological opportunities" were available to hybrid types. Their populations are thus also ecologically differentiated. As with *Potentilla glandulosa*, the overall pattern outlined by Grant for *Gilia capitata* is one of comparatively stable ecological races extending over very considerable areas. Within the subspecies, however, he describes several examples of "inter-colonial" variation, in some cases extending to such characters as seed germination and flowering time. The possibility of clinal variation in the character of glandulosity in subsp. *capitata* is also considered. Grant does not attribute ecological significance to this local variation, but it is possible that more intensive study might show its adaptive character.

In the shrubby California genus *Ceanothus*, Nobs (1963) describes "species equivalent to ecotypes" in the section Cerastes. They are accepted as taxonomic species because of their morphological distinctness, and "the genetic basis of their differentiation and subsequent stabilization . . . revolves primarily on the coherence of the genotypes balanced against the selective pressures of the natural environments". All are completely interfertile in experimental crossings. In the area north of San Francisco Bay, where eleven of these "species" occur, the majority "are geographically separated, and coincide in distribution with changes in ecological habitats, especially with soil type". In general, where the

species do meet, their ecological limitations severely inhibit natural hybridization.

Not all of the ecologically-correlated variation within the section Cerastes is accounted for by this sub-division. While some of the narrowly ranging species seem reasonably uniform, *Ceanothus gloriosus* shows further differentiation into maritime and inland races, also given taxonomic recognition, as varieties. *C. cuneatus* has "developed numerous recognizable forms", and "the aggregations of characters that typify each form follow essentially a clinal transition which coincides with a gradual ecological gradient . . .".

The common feature of the three examples from the Californian flora outlined in the preceding paragraphs is that vicarious ecological races are seemingly present, distinct from each other in morphological and physiological characteristics. The ecological races are all evidently themselves heterogeneous to a greater or lesser degree, showing local variation which is probably both adaptive and non-adaptive. The fact that the situations in the three genera have been given different taxonomic treatment is confusing but irrelevant; it merely indicates that in polytypic species complexes the taste of the individual worker tends to be the arbiter so far as nomenclature is concerned.

2. *Ecological Races with Interdigitating or Mosaic Distributions*

There are now several well-documented examples of ecologically differentiated races which do not possess vicarious areas but overlap geographically, each occupying its own characteristic type of habitat within the common area. Again, varying taxonomic treatments tend to obscure the essential similarity of many cases. By the criterion of free gene exchange in experimental crosses sympatric ecological races may merit inclusion in one and the same ecospecies, but their nomenclatural treatment normally depends upon their degree of morphological differentiation. If this is conspicuous and consistent they will, quite justifiably, be generally named as species; otherwise they may be classified as subspecies, or may even escape taxonomic recognition altogether.

The example of the *Ranunculus lappaceus* group in south-eastern Australia is one of the most remarkable yet described (Briggs, 1962). Seven named species occur in the 5 000–6 000-ft altitude zone of the Kosciusko plateau. All are closely similar in karyotype, and are recorded as being freely interfertile; they may thus be regarded as being part of the same ecospecies. The different races show very narrow ranges of ecological tolerance, and, since the characteristic habitats are scattered throughout the area, they have a mosaic distribution.

The faithfulness of the races to their particular habitat is evidently extremely strong. The situation is illustrated by *R. millanii* and *R. dis-*

sectifolius, the former characteristic of fen communities and shallow depressions in grassland areas subject to intermittent flooding and the latter of wet grassland, was less than $\frac{1}{2}$ m in width; the two forms were entirely restricted to their characteristic habitats, and hybrids were encountered only in the ecotone. Reciprocal transplant experiments were carried out with these two forms; *millani* showed only moderate growth in the *dissectifolius* habitat, and *dissectifolius* failed altogether to survive in the *millani* habitat.

Briggs considers that the identity of the different races is maintained by their ecological specialization, which is sufficiently strong to ensure that hybrid derivatives have no chance of success in the wild except in ecotones, which tend in general to be narrow. This seems to be true also of several taxonomic "species pairs" in the European flora such as *Silene maritima* and *S. vulgaris*, *Melandrium rubrum* and *M. album*, and *Geum rivale* and *G. urbanum*. The common features here are that the entities concerned in each pair are distinguished from each other by several consistent differentiae: they are freely interfertile in experimental crossings, they have distinct ecological tolerances, and they do not hybridize freely in the wild except where ecotones occur or where there has been habitat disturbance. In addition, the total geographical ranges although overlapping are not coincident, and with some there is evidence that the distinctness has persisted since early post-glacial times (Turrill, 1946).

Obviously all of the examples quoted so far are interpretable as cases where two or more races have differentiated allopatrically in both morphological and physiological properties, and have then acquired sympatric ranges by migration, their integrity being preserved subsequently in the common area by strong ecological specialization. There are several essentially similar cases where ecological races have been given taxonomic recognition as subspecies because the differentiae are fewer, or less distinctive, than would normally be required of taxonomic species. The subspecies of *Dactylorchis incarnata* in the British Isles constitute habitat races showing morphological differentiation principally in floral characteristics (Heslop-Harrison, 1953a, 1956). The differentiae are maintained in cultivation, and are associated with phenological and other physiological differences. Populations referable to the various subspecies often occur in close proximity without loss of identity, and occasionally even intermingled where there are rapid alternations in habitat. Thus in one locality plants referable to *pulchella* and *coccinea* occurred together in a field traversed by an old herringbone drainage system. The hollows of this carried a wet-soil vegetation forming a continuation of a lake-side fen. On the drier mineral soil of the ridges, 85% of the plants were *coccinea*; in the hollows, 96% were

pulchella. In this situation the habitats, although adjoining, were distinct. In others studied, particularly in the East Anglian fens where human intervention has blurred ecological boundaries, many nondescript, intermediate habitats exist. In these the *D. incarnata* populations are heterogeneous, and the character combinations typifying the named subspecies are often broken up. The probable role of floral characters in contributing to the reproductive isolation of the ecological races of *D. incarnata* (Heslop-Harrison, 1958) is mentioned in a later section (p. 212).

The pattern of ecological differentiation in *D. incarnata* is one of distinct yet intermingled races; in other species of the genus a bolder regional differentiation is evident, reminiscent of that described by the Carnegie group in *Potentilla glandulosa*. The aggregate *D. maculata* consists of two ecospecies, *D. fuchsii* and *D. maculata*, the former diploid and the latter tetraploid, which show different ecological tolerances throughout the European range (Heslop-Harrison, 1951). Each of these in turn contains regional subspecies of an ecotypic nature. *D. fuchsii*, for example, is represented in the British Isles by three forms, distinct enough to have been acknowledged taxonomically as subspecies, *fuchsii*, *hebridensis* and *okellyi*. Subsp. *fuchsii* is wide-ranging, occurring in meadows and open woodland on neutral or moderately basic soils; subsp. *hebridensis* replaces subsp. *fuchsii* along the western seaboard in regions of extreme oceanic climate from Cornwall, through western Ireland and the Hebrides to Sutherland, while subsp. *okellyi* is restricted to areas of karst-like limestone in Ireland and north-western Scotland (Heslop-Harrison, 1953a, 1958). The subspecies are distinguished by several correlated morphological features, maintained in cultivation, and also to some extent by phenology. They have the aspect of distinct races which have attained their present distributions independently, but again this can be no more than a subjective judgment.

In some recorded examples of genecological differentiation, the evidence is inadequate to attempt any kind of distinction between possible monotopic or polytopic origins. Thus Habeck (1958) has studied the variation in seedlings from seed samples of *Thuya occidentalis* from twenty-nine sites within the distributional area in Wisconsin. The sampling sites were classified into "typical lowland swamps" and "well drained uplands". Marked differences in response to three conditions of soil moisture were observed in cultivation, and Habeck concluded that two distinct ecotypes, one adapted to the upland conditions and the other to the lowland, co-exist in Wisconsin throughout the species area. Nothing in the recorded data serves to establish whether two races different in origin are involved, or whether the ecotypes have evolved polytopically in response to local selective pressures.

The same kind of difficulty arises in interpreting ecological races con-

fined to certain extreme soil types occurring locally in otherwise normal terrain, as for example over outcrops of serpentine rocks, or on the spoil heaps derived from lead and other mineral workings. The sudden changes of vegetation encountered with the transition from non-serpentine to serpentine soils is well documented for many parts of the world (Whittaker, 1954; Walker, 1954). Frequently this is seen in a complete disappearance of intolerant species. In some cases, a taxonomic species is replaced abruptly by another, very closely related one; in others, edaphic races tolerating serpentine conditions occur which are not sufficiently well differentiated morphologically to have merited taxonomic recognition (Kruckeberg, 1954).

These edaphic ecotypes are usually quite sharply demarcated physiologically from neighbouring populations on normal soils, reflecting the abrupt change in habitat. Kruckeberg's study of 1950 is of special interest, since he included observations on two species already extensively studied genecologically, *Gilia capitata* (Grant, 1950; see p. 175) and *Achillea borealis* (Clausen *et al.*, 1948). Within the subspecies *capitata* of *Gilia capitata*, considered by Grant to constitute a reasonably homogeneous race with a distribution related primarily to regional climate, Kruckeberg detected local populations adapted to serpentine soils and meriting recognition as edaphic ecotypes. Similarly, in the inner Coast Range-Sierran foothill race of *Achillea borealis* subsp. *californica*, regarded by Clausen *et al.* as a climatic ecotype, serpentine tolerant and intolerant edaphic ecotypes were distinguished. Kruckeberg (1954) comments on the *Achillea* situation as follows: "There are thus edaphic subdivisions within climatic ones in this species, i.e. ecotypes within ecotypes. Moreover, since the geographical area covered by the foothill climatic ecotype is very diverse lithologically and therefore is a mosaic of different soil types, additional edaphic ecotypes may well be expected. The superimposition of ecotype on ecotype at least suggests that there exists a much more complex genotypical response to habitat than is implied in consideration of single environmental factors."

The differentiation of serpentine tolerant races in wide-ranging species has its parallel in miniature in the emergence of local populations tolerant of the toxic soils formed on the spoil heaps from lead mines and other mineral workings (Bradshaw, 1952). Wilkins (1960a, b) has initiated the study of lead tolerant populations of *Festuca ovina* in Britain. Three "types" were distinguished, in respect to tolerance, one (wide-ranging) intolerant, and two others, restricted to lead-containing soils, of medium and high tolerance respectively when tested for rooting in lead nitrate solutions. Tolerance was not associated with any morphological features, so Wilkins has been reluctant to talk of "lead soil ecotypes". Evidently there is nothing comparable to a homogeneous race

involved, the pattern of lead tolerance being superimposed upon all other systems of adaptive and non-adaptive variation within *Festuca ovina*.

3. Clinal Variation

Some of the most informative examples of infraspecific ecoclines have been described in woody species. Thus the variation of the Scots pine, *Pinus sylvestris*, throughout its European range has been the subject of much illuminating research and some controversy (Langlet, 1934, 1936, 1959, 1963; Wright and Baldwin, 1957). In his earlier work, Langlet described clines spanning almost 25° of latitude, involving several morphological and physiological features such as leaf length, hardiness, dormancy period and shoot extension rate. The 1938 international test involving fifty-two provenances provides some particularly striking evidence. In the trial grown near Stockholm, Langlet recorded the percentage of dry matter in the needles of 2–4 year seedlings in the late autumn. This particular measure showed a close relationship with the length of the growing season, assessed as the number of days with an average temperature of 6° C or more, in the native habitats. A still closer relationship was apparent between dry matter content and the length of the first day of the year with an average temperature of greater than 6° C. The scatter diagram is reproduced in Fig. 1a: the regression is curvilinear, and r exceeds $+0.98$ (Langlet, 1959). The clinal nature of the variation is quite beyond challenge.

The trial reported upon by Wright and Baldwin (1957) involved forty-six of the fifty-two provenances tested by Langlet, but their treatment and conclusions were radically different. The material was grown in New Hampshire, at a latitude of 43° N, some 14° south of Stockholm. According to Wright and Baldwin, the evidence suggested that the variation in Scots pine is discontinuous, and they grouped the sampled populations into a number of regional ecotypes. Some of these — in the northern part of the range — occupied latitudinal belts, and bore a clinal relationship to each other; others further south coincided with no particular latitudinal or climatic zones. This treatment has been heavily criticized by Langlet (1959), who pointed out that the method of grouping the different samples geographically and comparing regional means for the various characters observed would necessarily obscure variational continuity. His own re-plotting of the height data for 17-year trees grown in New Hampshire in relation to day length is reproduced in Fig. 1b. There is a remarkable correspondence between the distribution shown in this figure and that shown in Fig. 1a; as Langlet remarks, Wright and Baldwin do seem very satisfactorily to have demonstrated continuous variability in Scots pine, in spite of their own conclusion to the contrary.

The clines in pine revealed by the studies of Langlet and others include examples of latitudinally correlated variation in characteristics which are essentially associated with developmental periodicity. Presumably they reflect the varying response to photoperiod through which adaptation to length of growing season at different latitudes has been attained. Other similar examples, including the "photoperiodic ecotypes" of Vaartaja (1959), are discussed in Section III.
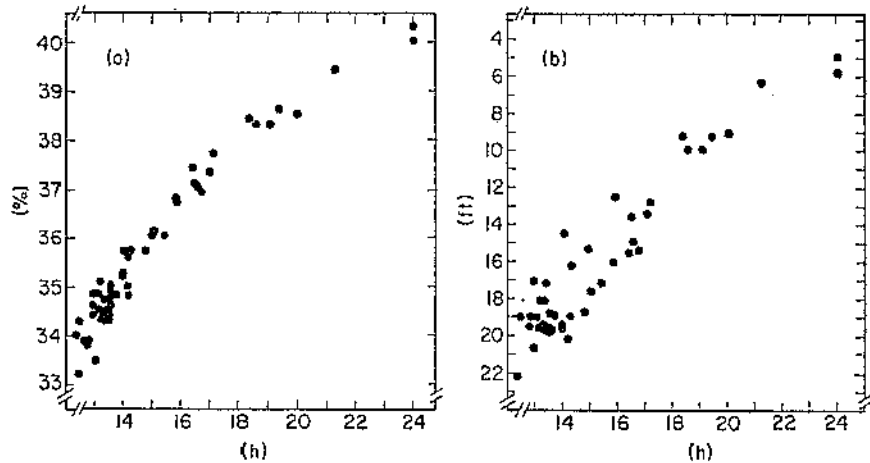

Fig. 1. (a) Relationship between dry matter content and the length of daylight of the first day in the year with an average normal temperature of +6° C at the native habitats of fifty-two provenances of *Pinus sylvestris* grown at Stockholm. (From Langlet, 1959.) (b) Relationship between tree height at 17 years and the length of daylight of the first day in the year with an average normal temperature of +6° C at the native habitats of forty-six provenances of *P. sylvestris* grown in New Hampshire, U.S.A. (Data of Wright and Baldwin, 1957, re-plotted by Langlet, 1959.)

In view of the abundant evidence that the periodicity of growth in forest trees is closely related to the length of the growing season in the habitat of origin, a report by Daubenmire (1950) indicating that cambial activity in *Pinus ponderosa* is not related to latitude or altitude of origin is of some interest. Forty-one trees, originating from populations spanning 14° of latitude and occurring up to an altitude of 7 200 ft were studied in cultivation together in northern Idaho. Considerable variation in the duration of cambial activity was observed within the samples from the various populations, but there was no meaningful pattern of variation between the populations, and certainly no obvious relationship with latitude. This observation stands in some contrast with that of Weidman (1939), who grouped the same material into four regional races on the basis of needle number, length and anatomy, and growth rate and hardiness. The data given by Weidman also provide some evidence of clinal variation related both to latitude and altitude.

G   C.E.R.

Since the earlier work of Gregor and his collaborators on *Plantago maritima*, ecoclinal variation has been described in several herbaceous species. Böcher's investigations of *Prunella vulgaris* (1945, 1949) have involved comparative cultivation of large numbers of population samples from throughout the species range, both in standard and varied environments. He considers that units worthy of being termed ecotypes occur within the species, the principal ones being associated with montane-boreal habitats, and with dry, medium dry, wet and shaded soils in lowland habitats. However, "in *P. vulgaris* there is continuous variation, for which reason the ecotypes . . . represent the most frequent character combinations in the different types of habitat. A large number of biotypes or races may not be conformable to the ecotype system, because in respect of one or more characters they do not agree with the ideal combination (the most characteristic features of the ecotypes)." Böcher refers to the ecotypes within *P. vulgaris* as theoretical concepts, since they are, essentially, "composed of ranges within a whole series of continuous or almost continuous character gradients or clines." His position is thus very close to that of Gregor.

Böcher and co-workers have also given evidence of ecoclinal variation in *Plantago coronopus* (Böcher *et al.*, 1953, 1955). The diploid complex represented by *P. coronopus* L. and *P. macrorhiza* Poir. forms a very variable series of populations around the Atlantic and Mediterranean seaboards of Europe. Comparison of population samples from throughout the range in cultivation led to the conclusion that the adaptive trends were best expressed "as through a number of clines running from the north to the south in Europe. Strains of southern origin deviate from those from the north by often being of greater size, with more ascending leaves and scapes, wider leaf-rhachis and longer spikes. They further seem to be more resistant to drought". Dwarf races occurring in the north-west on exposed rocks and cliffs were considered to constitute a race distinct enough to be called an ecotype, which, however, differed from another similar ecotype on sea cliffs in southern Scandinavia.

Like *P. maritima*, *P. coronopus* shows great local variation in Europe, and it is likely that major clinal trends suspected by Böcher *et al.* overlie local patterns of ecotypic and ecoclinal variation comparable to those described by Gregor for the former species in the British Isles (Dodds, 1953).

Studies on the phenotypic variation of wild populations have often revealed very distinct clinal trends related to climatic gradients (e.g. *Alnus glutinosa*, McVean, 1953; *Melampyrum pratense*, Smith, 1963), and although much of the observed variation may well be in consequence of plastic modification, there seems little doubt that some will be genotypically based. Indeed, the view of Stebbins (1950) that "it is likely that most species with a continuous range that included more

than one latitudinal or altitudinal climatic belt will be found to possess clines for the physiological characteristics adapting them to the conditions prevailing in different parts of their range" has now been fully justified.

A special type of clinal variation occurs in polymorphic species when successive populations show progressive change in the proportion of the morphs (Huxley, 1955). Such ratio clines frequently reflect directly the distribution of allelic genes, and several examples have now been described. Thus Harland (1946) detected a cline in *Ricinus communis* in Peru in the proportional representation of genes for stem bloom (glaucousness, or waxiness). Bloom is determined by a pair of alleles, *B–b*. The castor bean is not native to Peru, but it is naturalized as a weed, as well as being in cultivation, up to considerable altitudes. Passing inland from Lima to an altitude of 7 764 ft the proportion of plants bearing bloom increases from $0 \cdot 15\%$ to 100%. In experimental cultivation in the Lima district, homozygous *B* type plants were found to be sterile in the winter, whilst *bb* plants fruited throughout the cold season, although at a diminished rate. The winter sterility of *BB* plants Harland attributed to the cold and fog of this season in Lima; the increase of such plants with increasing elevation inland is associated with an increase in the amount of sunlight and the diminution of fog. In what way glaucousness is physiologically disadvantageous in the Lima climate is not apparent. It may be that bloom is simply a superficial expression of some unknown more profound physiological condition, or, as Harland suggests, selection has been for some closely linked gene of physiological significance.

Parallels to Harland's *Ricinus* case occur in several species of *Eucalyptus* in Tasmania, where clines in the incidence of glaucousness have been described by Barber (1955) and Barber and Jackson (1957). The glaucousness of leaves and stems is considered to be under oligogenic control, and the clines, detected by field inspection, are taken by Barber to represent changes in the allelic frequencies at one or more loci controlling wax development. In three species, *E. gigantea*, *E. gunnii* and *E. coccifera*, parallel clines were observed in a transect passing from altitudes of *c.* 2 500 ft to 4 000 ft in north central Tasmania. In *E. gigantea* which has the lowest altitudinal range, glaucousness is dominant in the lowest populations; thereafter to 3 500 ft glaucous types are absent, when they reappear to achieve a frequency of 60% at 3 750 ft. In *E. gunnii* and *E. coccifera* a simpler clinal pattern appears, with non-glaucous plants at lower elevations giving place quite rapidly to glaucous ones with increasing altitude. In *E. gunnii* there is an additional cline in glaucousness of juvenile foliage which is said not to be in step with that in the adult-type foliage. Although the clines described by Barber are described as involving changes in proportion of glaucous and non-glaucous genotypes, he also indicates that growth conditions affect

expressivity, low temperatures promoting the formation of wax when the genotype allows it. The correlation he deems most significant is that with temperature along the altitudinal transect, increasing frost being correlated with increasing glaucousness. Again, the physiological significance of glaucousness in relation to the factor which is presumed to be selective is not apparent.

Two ratio clines have been described in the corn field weed, *Spergula arvensis*, by New (1958, 1959). The characters concerned were the papillation of the seed coat, and the incidence of pubescence on stems and leaves. The inheritance of the seed coat character was found to be dependent upon a pair of alleles, there being no dominance. The inheritance of hairiness was less simple, but no dominance was found, and New concluded that since two classes "medium hairy" and "densely hairy" were usually distinguishable in field populations, the phenotypic ratio must represent gene frequencies. There is no genetic association between the two characters. Sampling and scoring were done directly in the field. In both characters clines were detected passing across the British Isles from NNW-SSE, the proportions of densely hairy and of non-papillate plants increasing towards NNW. Superimposed upon these regional clines, local clines in the same characters were found related to altitude, the proportion of non-papillate and of dense-hairy plants increasing with elevation. New carried out experiments under controlled environments to determine whether the characters were associated with any obvious selective factor. The direction of the geographical clines in the British Isles is also that of a gradient from a warmer, somewhat drier climate towards a cooler, wetter one, and it is therefore of interest that New found non-papillate, densely hairy plants intolerant of high temperatures and low humidity, suggesting that they would be at a selective disadvantage in the SSW of the country. Non-papillate plants also show a lower fertility at high temperatures and low humidities, and their seeds germinate better at low temperatures than high. All of this certainly suggests that the clines are selectively maintained by climate — those related to altitude as well as the larger geographical ones. Again, the physiological basis of the observed differences in reactions of the different genotypes is not clear; as New points out, there is even a certain perversity in the hairy types being less resistant to low humidities, when pubescence is often considered to be an adaptation to reduce water loss.

4. Small Scale Genecological Differentiation

Local patterns of genecological differentiation have now been studied in several genera. Bradshaw (1959, 1960) has investigated the common grass species, *Agrostis tenuis*, over a small area of central Wales. Thirty-

three colonies were sampled, and the samples were compared in standard and varied environments. Substantial differences were observed in morphological and physiological features under standard cultivation. The differences are considered by Bradshaw to be adaptive, and he concludes that it is "the environment, even its local variations, which determines the pattern of differentiation. So where there are sharp changes in environment . . . there are sharp correlated changes in the populations. Where there are gradual changes in the environment . . . the population changes are equally graded. Where in such gradients there are sudden local variations . . . there are sudden population changes". Evidently *A. tenuis* shows a mixture of continuous and discontinuous variation on a very local scale, and Bradshaw declines to identify any of the populations as ecotypes, or even to apply the concept of clines.

The picture sketched by Gregor and Watson (1954) for variation in *Lolium perenne* in Britain shows some similarity with that described for *Agrostis tenuis* by Bradshaw. In their later investigation of local genecological variation in *Plantago lanceolata* (Gregor and Watson, 1961), sample size was restricted in favour of number of populations sampled, in sites scattered throughout a mosaic of different habitats mainly within an area of 70 × 30 miles in southern Scotland. The sites were grouped into three broad classes: A, species-rich pasture; B, species-poor, lightly grazed vegetation, and C, ungrazed vegetation dominated by *Molinia caerulea*. In cultivation under standard conditions, the plantain samples showed average leaf lengths increasing progressively from habitat type A to habitat type C, the differences between the groups being statistically significant. There is thus a "dispersed" ecocline in the characteristic, in so far as the three habitat types, A, B and C, can be regarded as forming an ecological gradient in this small geographical area. This study also included an assessment of the role of developmental plasticity in the adaptation of the plantains to minor variations between the habitats.

A study of small-scale genecological differentiation by Harberd (1961b) is of particular interest since no fewer than thirteen taxa were investigated simultaneously. The sampling was carried out within one broadly defined type of community, *Agrostis-Festuca* grassland, and within a comparatively small geographical area. A total of eighty sites were selected in a series ranging from "flushed" to "leached", and five circular turves c. 7 cm in diameter were taken from each; the plants were grown on from ramets present in the turves. One to ten characteristics were scored in the different species. Using the within-site variance as the error term, an analysis of variance showed that more than 70% of the characters scored differed significantly between the popula-

tions. These differences need not, of course, be related to habitat differences within the eighty sites. To test for genecological differentiation, Harberd grouped the sites into seven variants of the *Agrostis-Festuca* community, in the series flushed → leached. Differences significant at the 1% level between the grouped samples were found in only four species characteristics. In *Carex caryophyllea*, leaf length differed significantly between the groups, and this character showed a relationship with the position of the site in the series, shorter leaves coming from the more flushed sites. In *Poa trivialis*, a trend in flowering time was associated with the site-group series, flowering being later in the flushed sites. In *Festuca rubra* and *F. ovina*, differences were observed which did not relate satisfactorily to the habitat series. In *F. rubra*, Harberd considers the observed difference could have arisen from reduplication of genotypes between the sampling sites; he offers no explanation for the anomalous result with *F. ovina*. Flowering time in *Cerastium vulgatum* was found to be correlated significantly with the position of the site in the ecological series, although the character did not reach significance in the site-group comparison. This investigation provides a convincing demonstration of the value of extensive sampling methods in genecology, since the design of the programme permitted a clear distinction to be made between fortuitous inter-population variation and that which is likely to be of genecological significance.

Ehrendorfer (1953), in a study on a geographical scale similar to that of Harberd, detected genecological differentiation within an essentially continuous population of *Galium pumilum*. The plant community was *Arrhenatherum* meadowland, within which various facies could be recognized according to aspect, exposure and soil moisture. The ten sampling sites could be placed in four groups, from warm, dry, open to cool, moist, shaded. The incidence of hairiness was found to vary markedly between the groups, the proportion of hairy individuals in the samples falling progressively from 55 in the driest habitat to 19 in the dampest. Since hairiness is determined by a single dominant gene, this is an example of ratio ecocline. Observations made in the field showed that flowering was earlier on the average in the drier sites. Although the differences in this feature between the sample sites were likely to have been determined in part by direct environmental effects, Ehrendorfer found some association between hairiness and precocity, suggesting that some of the variation between sites in flowering time was genetically based.

Although many of the published studies of genecological differentiation in the Californian flora have emphasized the large scale, regional patterns, there have been examples of investigations on a more local scale, and some have offered comparative data. Thus Grant's analysis of

the variation of *Gilia achilleaefolia* (1954) provides an interesting contrast with his study of *G. capitata*, discussed above. *G. achilleaefolia* shows very great local variation from colony to colony throughout its range. According to Grant, the local variants "do not group themselves into broad geographical assemblages, as in most species including the related *G. capitata*, but the broader subdivision in the species is rather along ecological lines. The large-flowered races with dense heads occupy sunny hillsides in grassland and oak savannah; the small flowered races with loose cymes occur in the shade of oak woodland or redwood forest; and there are numerous transitional forms in the semi-shade of open oak woods". The situation here described is comparable with that encountered by Bradshaw in *Agrostis tenuis*, the pattern of differentiation following closely upon local ecology so that sometimes continuous and sometimes discontinuous variation is encountered.

Cook's study (1962) of *Eschscholzia californica*, the Californian poppy, is of interest since it combined a regional survey of thirty-one populations dispersed throughout the Californian range with a local survey over a 35 mile transect. Some of the data concerning population variation appear to be based upon samples from the wild, so that there is no guarantee that all variation recorded is genotypic; but in so far as it concerned floral characteristics the probability is that direct environmental influence accounted for little. Longevity was assessed in samples under comparative cultivation. Each of the floral characteristics examined was found to vary gradually, sometimes independently and sometimes in a parallel manner; no discontinuities were encountered suggesting the existence of regional races. Some of the clines observed could be related in a general way to major ecological gradients, but the evidence presented does not suggest that all necessarily do so. From the local study, it was concluded that much of the variation, particularly in such features as developmental periodicity, is closely related to habitat conditions, so that neighbouring populations may differ abruptly if the habitats are strongly differentiated, or intergrade, in a clinal manner, when the habitats themselves intergrade.

G. GENECOLOGICAL DIFFERENTIATION: SOME GENERALIZATIONS

The foregoing examples illustrate most of the principal kinds of genecological differentiation known in higher plant species. The interpretation of the different patterns must necessarily depend upon an appreciation of the evolutionary situation each represents, and this in turn must be based upon some understanding of the nature of the response of plant populations to selection and the role of genetic systems in determining that response, matters discussed in Section II. So far as the observational evidence is concerned the following generalizations may be made.

(a) The geographical distributional pattern of a species is a determinant of the pattern of genecological differentiation. Where an area is continuous, spanning, say, an appreciable range of latitude, clinal variation is likely to be found, particularly in long-lived species of stable communities; if there are discontinuities, regional races with distinct ecological tolerances may be encountered.

(b) The total ecological range of a species is significant. In a species restricted to the modulations of a particular kind of habitat, any ecological variation will tend to be clinal. If a species spans a range of discrete habitats which are themselves sufficiently distinct, ecological races of the nature of the ecotypes may be found, even when the habitats are contiguous.

(c) Systems of continuous and discontinuous variation may be combined at the same and at different levels. Thus:

(i) A species may show differentiation into major ecological races associated with different types of habitat within its area, and within one or more of the races there may at the same time be ecoclinal variation adaptive to smoothly varying climatic factors.

(ii) Local variation of an "ecotypic" kind may occur within the framework of a grand system of clinal variation extending throughout the species area.

(iii) Conversely, within major ecological races local adaptive clines may be found.

(iv) Hierarchical patterns of both ecotypes and ecoclines may exist: thus a regional ecological race may itself be composed of a system of more local ecotypes, and within a major ecocline local systems of clinal adaptation may be present.

(v) In widely ranging species, clinal variation adaptive to different factors may occur, giving in the extreme case, patterns of "intersecting clines".

The existence of complexities such as those listed under (c) above means that the results of any particular genecological study will tend to be related to the scale on which it is conceived. Thus the minutae that engage Bradshaw (1959, 1960) in his investigation of *Agrostis tenuis* in a small area of central Wales would pass largely unnoticed in a study on the geographical scale of that of Clausen *et al.* of *Potentilla glandulosa* (1940). This is not to suggest that identical methods would reveal corresponding variational patterns in these two particular species, but merely to point out that the results so far obtained with them are not capable of direct comparison. We shall see that much can be deduced about the probable patterns of genecological differentiation within a species from a knowledge of its genetic system, distribution and general ecology, and it would seem an essential now to take these factors into

consideration in the design of genecological investigations so as to determine the scale and nature of the sampling programmes to be adopted to produce information of value in comparative studies.

H. GENETIC BASIS OF ECOTYPIC DIFFERENCES

It is a commonplace of descriptive genecology that ecotypes tend to differ in characteristics such as growth habit and dimensions of organs which show continuous variation within populations. Moreover, the gradation between ecoclinally related populations in these features and in others such as developmental periodicity is itself usually found to be continuous, or so finely stepped as to be effectively so when the modulating effects of the environment are superimposed. These two observations are best explained by the hypothesis that ecotypic differences are mostly polygenically controlled (Mather, 1943).

Discussing in 1953 the genetical structure of natural populations Mather noted that the direct evidence of polygenic systems mediating continuous variation was not abundant, most likely because the experimental demonstration of their presence is difficult. Among plant examples he quoted the species of *Layia* and *Madia* mentioned by Clausen *et al.* (1940), and the same authors' comments on the ecotypic variation of *Achillea borealis* (Hiesey *et al.*, 1942).

The analysis now available of the genetics of the races of *Potentilla glandulosa* from the more recent work of the Carnegie group (Clausen and Hiesey, 1958) provides much the fullest evidence of the genetic basis of ecotypic differences. Most of the differential features are controlled multifactorially; but the number of loci concerned is seemingly not especially high.

In the study, crosses were made between individuals of the subspecies *typica* (Californian coast), *reflexa* (Sierran foothills) and *nevadensis* (subalpine form and alpine form). The most fully analysed crosses were between *typica* and the *alpine* form of *nevadensis*, and between *reflexa* and the subalpine form of *nevadensis*. In the first of these, large F_1 and F_2 populations were studied in a standard garden, and in the second, F_1, F_2 and F_3 populations were grown in the standard garden and in addition cloned F_2 individuals were compared at three transplant stations at different altitudes on the Californian transect. Up to nineteen characters were observed simultaneously in the experiments, and the huge body of data was processed by a punched card technique. Estimates of the minimum number of genes associated with the character differences observed between the different races were based upon comparisons of F_2 frequency distributions with binomial distributions. These estimates for nineteen characters are summarized in Table II, from the original of Clausen and Hiesey. For the whole complex of differential features

G2   C.E.R.

observed in the ecotypes studied, they estimate that about 100 or more loci may be concerned. "Considered in terms of the complex array of observed recombinations that can be accounted for in the F_2 and F_3 combinations", they comment, "this number seems to be remarkably small. Thus with a rather limited number of basic genetic building blocks, the diploid species *Potentilla glandulosa* apparently has been able to evolve an extensive array of ecological races fitted to diverse environments."

TABLE II

Estimate of Minimum Number of Genes Governing the Inheritance of 19 Characters in Two Inter-ecotypic Hybrids of Potentilla glandulosa. [*From Clausen and Hiesey 1958a.*]

Character, and action of genes	Estimated no. of gene pairs
1. *Orientation of petals:* 2 erecting, 1 reflexing	3
2. *Petal notch:* 1 producing notch, 2 inhibiting	3
3. *Petal colour:* 2 whitening, 2 producing yellow, 1 bleaching	5
4. *Petal width:* 4 widening, 1 complementary, 1 narrowing	6
5. *Petal length:* 4 multiples	*ca.* 4
(plus possible inhibitors)	
6. *Sepal length:* 3 or 4 multiples for lengthening, 1 for shortening, 1 complementary	*ca.* 5
7. *Akene weights:* 5 multiples for increasing, 1 for decreasing	*ca.* 6
8. *Akene colour:* 4 multiples of equal effect	4
9. *Branching, angle of*	*ca.* 2
(also genes for strict to flexuous branching)	
10. *Inflorescence, density of*	*ca.* 1
(plus modifiers)	
11. *Crown height*	*ca.* 3
(also genes for presence or absence of rhizomes and for thickness of rhizomes, to which crown height is related)	
12. *Anthocyanin:* 4 multiples (1 expressed only at Timberline), 1 complementary	5
13. *Glandular pubescence:* 5 multiples, in series of decreasing strength	5
14. *Leaf length:* transgressive segregation; many patterns of expression in contrasting environments; possibly different sets of multiples activated	*ca.* 10-20
15. *Leaflet number in bracts*	*ca.* 1
(plus modifiers)	
16. *Stem length:* transgressive segregation, 5 to 6 multiples plus inhibitory and complementary genes; many patterns of expression in contrasting environments	*ca.* 10–20
17. *Winter dormancy:* 3 multiples of equal effect	3
18. *Frost susceptibility:* slight transgression toward resistance	*ca.* 4
19. *Earliness of flowering:* strongly transgressive; many patterns of altitudinal expression; possibly different sets of genes activated	many

The comparison of the performance of cloned F_2 individuals from the *reflexa* × subalpine *nevadensis* cross at the different transplant stations revealed notable differences in the effect of environment upon gene expression. Clausen and Hiesey refer to "qualitative" characters, mostly expressed in the flowers, which although subject to some modification at the different stations are yet relatively stable, and to "quantitative" characters modifiable by environment to the extent that genic differences may be totally masked. These modifiable characteristics mostly relate to growth properties and developmental periodicity. In stem growth, a high correlation ($r = 0.48$) was observed between performance at Stanford (30 m altitude) and at Mather (1400 m), and a lower one ($r = 0.12$) between Stanford and Timberline (3050 m). In respect to flowering time, the F_2 progeny showed scarcely any significant correlation between the stations, although at each the order of flowering between the different individuals was consistent from year to year. It may be surmised that both penetrance and expressivity of the genes segregating in the F_2 of the *reflexa* × subalpine *nevadensis* cross vary in the environments of the three transplant stations, but Clausen and Hiesey comment that the genic systems controlling the quantitative characters have proved too complex for any satisfactorily comprehensive interpretation of the effects of the diverse environments on gene expression.

Another feature of great interest in the work of the Carnegie group is the analysis of the correlations between the characters distinguishing the ecological races in F_2 progeny of inter-racial crosses, (Clausen and Hiesey, 1958a, 1960). These are expressed diagrammatically in Figs. 2a and 2b for the two fully analysed crosses, *typica* × alpine *nevadensis* and *reflexa* × subalpine *nevadensis*. In the first of these crosses, of the 91 possible combinations of the 14 characters, 67 showed some degree of association. In the second, the 12 characters permitted 66 combinations, of which 38 were significantly correlated.

Correlations of the type observed could conceivably arise at a physiological level, and it may well be that some of those illustrated in Fig. 2 do represent different expressions of single basic growth processes. However, Clausen and Hiesey consider that evidence points to some form of genetical association between the characters, which they refer to as coherence. The chromosome number of *P. glandulosa* is low ($n = 7$), and they attribute the coherence of racial characters to the high probability that, with so small a number, some at least of the genes governing any pair of quantitatively varying, polygenically governed characters will be linked. They have shown very convincingly that the coherent constellations of characters studied are either themselves concerned with survival in the habitats of the different ecological races, or cohere also with unobserved physiological properties which determine survival.
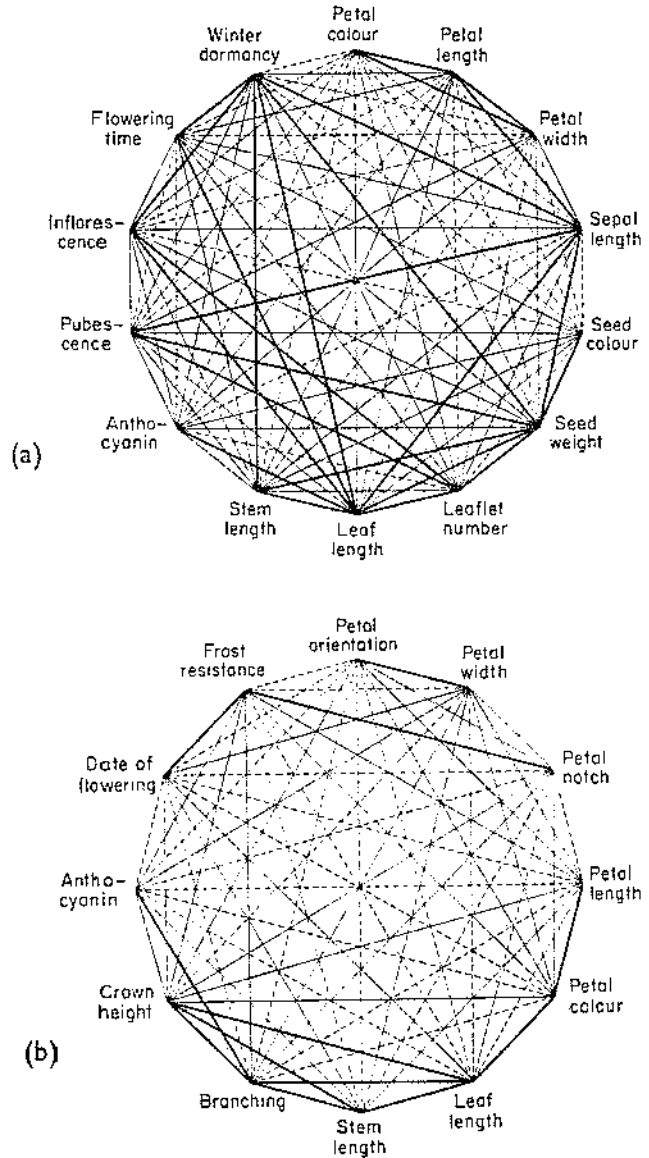
FIG. 2. (a) Statistical correlations between pairs of characters in 992 F_2 progeny of *Potentilla glandulosa* subsp. *nevadensis* × *P. glandulosa* subsp. *typica*. (b) Statistical correlations between pairs of characters in 570 F_2 progeny of *Potentilla glandulosa* subsp. *nevadensis* (subalpine form) × *P. glandulosa* subsp. *reflexa* (foothill form). In each figure, a heavy line indicates $r = 0.25-0.80$, a light line, $r = 0.09-0.25$ and a broken line, $r = 0.00-0.09$ (insignificant). (From Clausen and Hiesey, 1958.)

The evidence for one cross, *reflexa* × subalpine *nevadensis*, is given in Table III. The F_2 progeny carrying the highest proportion of *nevadensis*

TABLE III

Percentages of Long-period Survivors at Three Transplant Stations, Stanford (warm temperate; altitude 30 m), Mather (subalpine, 1400 m) and Timberline (alpine, 3 000 m) among Three Classes of F_2 Progeny of the Cross Potentilla glandulosa subsp. nevadensis (subalpine form) × P. glandulosa subsp. reflexa (foothill form). The clones were classified according to an index based upon 12 phenotypic characters in which the parental populations differed. Long-period survivors are ramets of clones that survived over 5 years at Stanford and 9 years at Mather and Timberline. [From Clausen and Hiesey 1958.]

Characterization of index classes	Percentage of long-period survivors			No. of clones
	Stanford	Mather	Timberline	
Most *nevadensis*-like	17·8	49·5	75·6	90
Intermediate	77·0	71·5	34·3	330
Most *reflexa*-like	70·8	76·5	13·5	89

features survive best in the subalpine habitat, and those with *reflexa* characters are most viable in the natural foothill environment of this race.

The existence of these closely knit systems of character correlation in the ecotypic races of *P. glandulosa* has reinforced the view of Clausen and Hiesey that they are distinct, non-intergrading, units, Thus, "combined with natural selection, moderate genetic cohesion within the characters of a race tends to ensure its perpetuation as an evolutionary entity. When morphological characters are included in the coherence systems, morphologically distinct ecotypic subspecies may result, as in *Potentilla glandulosa*" (Clausen and Hiesey, 1958). Evidently they consider that the genetic cohesion together with the sharp differentiation of the habitats on the central Californian transect preserve the identities of the races, a situation that would be most readily reconciled with a monotopic rather than a polytopic origin of each. The point is reverted to in a later section (p. 212).

II. EVOLUTIONARY ASPECTS OF GENECOLOGICAL DIFFERENTIATION

A. INTRODUCTION: THE ORIGIN, STORAGE AND RELEASE OF VARIATION

Turesson's definition of the ecotype (1925) as the product "arising through the sorting and controlling effects of the habitat factors upon

the heterogeneous species population" shows that he looked upon adaptation to habitat as the outcome of selection; but, as Baker (1953) has pointed out, he and other pioneer workers were handicapped by imperfect conceptions of the nature of the variability of plant populations, and were accordingly unable to formulate at all clearly how selection was likely to operate in bringing about the differentiation of habitat races. At least in his earlier papers Turesson wrote as if he looked upon the typical plant species as consisting of a generalized population plus specialized "radiations" from it, the ecotypes. The generalized population was rich in "biotypes" (defined by Faegri, 1937, as groups of individuals with identical genetical constitution), while the ecotypes were "biotype depleted". This conception was opposed by Faegri (1937), who objected to the idea that biotypes pre-adapted for alpine or other extreme conditions could survive in an undifferentiated lowland population awaiting, as it were, their opportunity to invade a mountain habitat, and argued further that if specialization necessitated genetical impoverishment ecotypes would be populations ultimately destined to become extinct rather than to be the starting points of new species.

Much of the early difficulty lay in the impression that genetical variation in plant populations must necessarily be largely overt. The species consisted of biotypes (sometimes referred to as though they constituted something like self-propagating pure lines, even in outbreeding species); and the biotypes were the units which were selected or rejected in the course of adaptation to habitat. Without some appreciation of the subtle ways the ebb and flow of variation is governed in plant populations no other standpoint was possible. Current understanding of the way genetical variation may be generated, recombined, exposed, conserved, concealed and lost in the course of sexual reproduction may be dated from two principal publications — Darlington's "Evolution of Genetic Systems" of 1939, and Mather's paper on polygenic inheritance and natural selection of 1943. More recent discussions of these processes in higher plant populations are given in Stebbins' "Variation and Evolution in Plants" of 1950, and in review papers by Baker (1953, 1959), Stebbins (1957, 1958) and Grant (1958).

In general, adaptive changes in a population must depend upon the accumulation of minor genic changes, mutations, under the directive action of selection. As Mather (1943) has shown, a compromise will always be involved between fitness for the environment as it exists, and the flexibility which will permit further adaptive change.

Fitness is best served by the production of progeny optimal for the immediate circumstances; flexibility by the continuous generation of variants some of which may be optimal for environments only to be encountered in the future, or elsewhere on the earth's surface. The raw

material for variation is genic change; the devices through which variability is regulated in populations constitute collectively the genetic system (Darlington, 1939). The three principal components of the genetic system may be identified as: (a) the chromosomal system, which establishes the rate of gene segregation and recombination; (b) the breeding system, which governs the level of hybridity; and (c) the intrinsic and extrinsic factors determining in interaction the sizes of breeding groups. We will consider the first two components here; the third is discussed in a later section (p. 204).

Darlington (1939) has referred to the "sum of the haploid number of chromosomes and of the average chiasma frequency of all the chromosomes in a meiotic cell" as the recombination index. A high index must determine a rapid rate of gene segregation and recombination, and so a rapid flow of variation from the concealed to the overt form and back again; a low index must in contrast establish a slow rate of turn-over of variation. In terms of the fitness-flexibility compromise, a high index gives flexibility, at the expense of the continuous destruction of any gene combinations giving fitness in the prevailing milieu, while a low index preserves any existing state of fitness at the sacrifice of future adaptive potential.

The balance between homozygosity and heterozygosity in a population is established by the prevailing system of breeding; in higher plants, that is to say, by the various properties determining the habitual mode of pollination. Cross-pollination may be promoted by sex differences, dichogamy, heterostyly, and incompatibility mechanisms including certation phenomena; and self-pollination may be imposed by cleistogamy or mechanical adaptation of the flower ensuring direct transfer of pollen from anther to stigma. In many plants mixed breeding is the rule, either, as Mather (1943) has pointed out, because of the inefficiency of a cross-pollinating mechanism, or because of the existence of a genetically determined system enforcing a regulated ratio of self- to cross-pollination. Such regulated systems must be subject to selection, but retrospectively, like other components of the genetic system.

Heterozygosity is a necessary prior condition for recombination and for the release of concealed genetic variation; cross-pollination thus acts like a high recombination index to promote variability. Self-pollination by raising the level of homozygosity restricts recombination and checks the flow of variation, in the extreme case leaving it eventually distributed among homozygous pure lines. Cross-pollination and high recombination index are complementary in promoting the flow of variability, but low recombination index and selfing constitute alternative means to one and the same end, namely the enhancement of genetic stability over a succession of generations.

One aspect of the function of the genetic system is the regulation of the phenotypic expression of genetic variation. Latent variation may be carried in the heterozygotes of a diploid population in the form of recessive genes, which will reach expression only with the segregation of homozygotes. Where phenotypic characters are governed by several genes each with small individual effects other possibilities for the concealment of genetic variation exist. Mather (1943) has shown how with such polygenic systems a constant phenotypic frequency distribution in a population can be maintained by selection with the simultaneous preservation of a high level of genotypic variation. Because a given phenotypic expression can be determined by several polygene combinations, the selectively favoured group in each generation may be essentially uniform in adaptive characters, but will always transmit genetic diversity to their progeny. Moreover, isolated populations may attain phenotypic similarity under similar selective pressures by the assembly of different polygene complexes each in a more or less homozygous state; between them they will then preserve a reservoir of genetic variation which will be tapped only when they pass back into breeding contact.

In governing the flow of variability in a population, the genetic system necessarily affects the potentialities for response to selection; it is thus one of the major factors to be taken into account in seeking to understand the origin of adaptive variation in plant species. Baker (1953, 1959) has considered the effects of differences in reproductive methods on race formation, but he acknowledges that it would be equally possible to "examine the consequences of the formation of certain kinds of race upon breeding behaviour of the plants". Indeed it is barely justifiable to separate intrinsic and extrinsic aspects, for they are always in interaction. The genetic system in the short run may determine the pattern of response to the environment, but environmental selection acting in a retrospective mode will determine what kinds of genetic system will prevail in the ultimate survivors in any particular ecological situation. Nevertheless, however tangled may be the chain of cause and effect, patterns of infraspecific variation will inevitably show some relationship with genetic systems and the extrinsic factors impinging upon them.

B. MODES OF SELECTION

Mather (1953) has termed the three basic modes of selection stabilizing, directional and disruptive. Under stabilizing selection the mean of the phenotypic distribution is favoured at the expense of the extremes; with directional selection, one extreme is favoured; and with disruptive selection both extremes. It is obvious that in one and the

same population selective forces could act in a stabilizing way on some phenotypic features and, simultaneously, in a directional or disruptive way on others. Moreover, multipolar disruptive selection could be imagined in which more than two expressions are simultaneously favoured.

In considering how these selective situations are realized in populations of higher plants, some sense of the kinds of compromise involved in long and short term adaptation is necessary. A plant population which survives in a given habitat must do so in the face of various inimical secular factors and against the predation and competition of other organisms. Since survival depends upon a variety of properties (some, like the needs to maintain gas exchanges and yet control water loss, even antagonistic) a degree of compromise on the physiological level must always be involved.

The success of that achieved by any given phenotype could be measured by various criteria, but so far as the persistence of the population is concerned reproductive performance is obviously a principal one. In the relative sense in which the concept of adaptation is commonly applied, we might say that a population is well adapted to its habitat when it succeeds at least in maintaining its numbers through successive generations.

If this is achieved over an interval of time in an outbreeding population without phenotypic change it may be supposed that the selective forces at work are acting in a stabilizing way to eliminate phenotypes deviating from what is evidently an adaptive mode. The extent of restriction of the phenotypic distribution provides a measure of the intensity of selection. Stringent selection must involve the loss of genetic variation, but as we have seen where polygenic systems are concerned some will always be conserved in a cryptic state.

Now a further element of compromise is involved in relation to environmental change. Plant habitats are subject to regular cyclical changes of different periods; to random fluctuations, again of different periods; and to long term trends of change. Plant populations may be accommodated to these changes in various ways. Taking first the nondirectional changes, a relationship of the first importance is between the duration of the life span and the period of the cycle or fluctuation. If the life span is such as to exceed the period of cyclical change, or the average period of some habitually fluctuating environmental variable, it must be supposed that a level of physiological adaptation has been achieved which permits the effects to be absorbed. The patterns of developmental periodicity seen in perennials, discussed more fully in a later section (p. 227 *et seq*.), represent physiological solutions to the problem of accomodating annual variation in climate. Forest flora must also preserve

a capacity to tolerate fluctuating climatic change of longer periods, such as the "sun-spot" cycle recorded in the annuals rings of the redwoods, and the irregular variations in winter temperatures and precipitation that have been a feature of temperate latitudes in post-glacial times (Manley, 1954).

Either because the periods favourable to growth are too short, or because the amplitude of variability of environmental factors is beyond tolerance, some habitats will not permit the survival of perennials. However, adaptation to ephemeral habitats or to severe cyclical or fluctuating changes can be attained by curtailment of the life cycle. The annual habit represents a satisfactory solution to the problem of exploiting temporary habitats, or of surviving in a climate where there is extreme but regular seasonal variation in vital habitat factors such as temperature and rainfall. By fitting in with the major cycle of change the annual avoids the requirement for adaptations giving tolerance to the adverse season, which can be safely weathered in the seed; it is left then to face the longer and shorter period fluctuations. The methods available to achieve this are of three general kinds. The "annual" cycle can be distorted to accommodate irregular longer cycles; this response is seen in species of arid regions with sporadic rainfall, where the amount of precipitation is itself a determinant of germination time. Or the developmental plasticity of the individuals may be such that the phenotypes produced each year are adapted to match the conditions of that year. Or, finally, the average phenotypes may possess an amplitude of tolerance great enough to accommodate year-to-year fluctuations in climate during the growing season.

The ephemeral habit is an adequate solution to survival in habitats subject to severe and irregular disturbance. It commonly combines the ability to suppress growth altogether during unfavourable periods, a property which we may term avoidance, with adaptive developmental plasticity and a high amplitude of individual tolerance.

These different kinds of physiological adaptation to change necessarily bear some relationship to community structure and stability. The long-lived perennial habit is that characteristic of the stable climax community such as forest or permanent grassland. In the case of forest, the moderating and controlling effects of the dominants themselves on soil and microclimate constitute a damping factor stabilizing the environment still further for tree seedlings and the herbaceous members of the community. So far as the tree species are concerned, this is, of course, an aspect of the "independence of environment" designated by Huxley (1942) as one of the marks of evolutionary progress. The annual habit must necessarily be associated with a less uniformly favourable environment and accordingly with communities of a less stable kind,

while the ephemeral habit, representing as it does mere opportunism, must be associated with the most labile of all kinds of community.

These relationships between life-span, non-directional environmental change and community type have important implications for the operation of selection. In the stable community, it is obvious that selection will tend to act rather consistently in a stabilizing mode. In the less stable communities of fluctuating environments selective pressures are, in contrast, likely to be erratic — with the annual, because of year to year climatic and other variations, and with the ephemeral because of the seasonal changes themselves and other more catastrophic events. What is to be considered the "optimum" will depend on the period of time over which the selective influences are integrated.

The time scale of change in relation to longevity is again of paramount significance where longer-term, directional, environmental change is concerned. A long-lived perennial will be exposed during its life-time to various environmental fluctuations. If the habitat is truly stable, the average experience of each generation will be the same. If there is a trend of some kind, the change will emerge as a progressive shift of the average. The effect of selection will be to favour those phenotypes conforming in each generation to a gradually changing optimum. A model situation may be seen in forest migrations of the post-glacial. Climatic changes meant the shift of climatic belts latitudinally. During the quaternary in the northern hemisphere the changes were slow enough to allow the major forest communities of long-lived species to migrate in step. The migrations took place through the replacement of one species by another in consequence of climatic selection, but, simultaneously, intraspecific selection achieved the necessary adjustments of developmental periodicity to fit the forest dominants to their new latitudes.

The situation of short-lived species, with their diverse patterns of physiological adaptation to short-term environmental fluctuations, differs in that the generation time is not sufficient to ensure an automatic averaging over several cycles of change. Yet the average condition may be changing progressively; and survival of the population must depend upon the ability not only to accommodate the fluctuations but to shift in step with the average. If this is to occur, the response to selection must be regulated in such a way that the transient influences are without effect in producing short term changes in genetical structure — which would involve a sort of evolutionary "hunting" like that of a cybernetic system adjusted so as to give excessive feed-back — while the long-term trends are met by progressive, smooth adjustment of the average phenotype.

All of the foregoing considerations involve aspects of Mather's fitness-flexibility compromise, and we may now examine how the different

situations may be met. The conditions of the stable community, with strong centripetal selection towards a progressively but slowly changing optimum, favour the free release of variation; by this means a perennial with high reproductive capacity can purchase long-term evolutionary advantage at the cost of a great sacrifice of progeny. In terms of the genetic system, this means high recombination index combined with cross-pollination. In temporary habitats, or where environmental fluctuations are beyond the tolerance range of plants of a perennial habit, the advantage will lie with the production of large, relatively uniform populations through successive short generations, and a genetic stability permitting the preservation of any adaptive peak achieved without excessive segregation and without too rapid a response to selective influences of a transient nature. This implies a genetic system parsimonious in the phenotypic release of variability, which means a low recombination index, or inbreeding, or, in the extreme case, apomixis.

These various relationships are summarized in Table IV. Most have been documented and exemplified by Stebbins (1950, 1957, 1958) and Grant (1958), and some have been discussed by Baker (1953). It may be noted that some of the conclusions of Thoday (1953) in a discussion of the components of fitness seem to be at variance.

Evolutionary change arising *sui generis* has been ignored in the foregoing discussion. As the history, for example, of the tropical rain forests

TABLE IV

Relationship between Some Components of the Genetic System and Longevity, Community Type, Physiological Features and Variation Pattern

Free gene recombination resulting from a high recombination index and outbreeding.	*Restricted gene recombination* resulting from a low recombination index or inbreeding.
Associated with:	*Associated with:*
(a) Protracted life span of individuals reaching maturity.	(a) Short life span of individuals.
(b) High and selective seedling mortality; dispersal capacity moderate to poor.	(b) Low seedling mortality during colonization of suitable habitats; efficient seed dispersal.
(c) Membership of closed climax communities in stable or but slowly changing habitats.	(c) Membership of impermanent communities in ephemeral, fluctuating or shifting habitats.
(d) High range of physiological tolerance in the adult, frequently dependent upon precisely adjusted developmental rhythms but not necessarily associated with phenotypic plasticity.	(d) Avoidance of adverse conditions in the seed state, with or without an associated capacity for adaptive plastic response to environmental stress.
(e) Continuous, clinal variation.	(e) Discontinuous variation.

reveals, a long-maintained, favourable environment with no marked trend of secular change does not mean evolutionary stagnation. This is presumably because there must always be ways in which an organism can steal a march on others even, as it were, in Utopia. Stabilizing selection must favour the "optimum" phenotype from the phenotypes available in each generation, but given a continued release of genotypic variation in phenotypic form some recombinants may attain new and better optima in respect to the capacity for exploiting the very same environment. A trend of change may thus be initiated within the community; and in so far as a change in one species produces a new environment for others it may be supposed that the pattern of selective forces will be in continuous flux.

A final matter meriting consideration in the context of this section concerns selection in the course of migration. There can be little doubt that the genecological differentiation observable in north temperate species is the product of evolutionary change during or following immediately upon fairly recent species migrations of a major scale. In general terms, it is possible to homologize the progressive change in the character of the environment that a species is likely to meet at the periphery of an expanding area with a temporal environmental trend experienced in one locality. Indeed, for the short-lived species of temporary or fluctuating habitats there would seem to be no essential difference between the two situations; the problems of matching an existing environment with enough fit genotypes, while at the same time generating sufficient diversity to permit colonization of slightly different ones, remains the same. With the perennial pre-adapted for the stable, closed community there are some significant differences. The principal one is that in the van of a migration centripetal selection is eased to the extent that dispersal is into an open community. The case is analogous to that in which a population is in a phase of rapid increase of numbers: variation may be expected to rise (Mather, 1953). Moreover, the "optimum" phenotype of the open marginal community may not be that of the main closed community, so the phenotypic distribution of the colonists may not only reveal a higher variance but a different mean. The exact implications of this situation have not hitherto been worked out, although it may be supposed that the effect will mainly be transient since the progressive closing of the community may be expected to restore the original balance of selective forces. The matter is considered again in a later section (p. 209).

C. VERSATILE REPRODUCTIVE SYSTEMS

Obligate self-pollination, by putting an end to recombination, must in the long run jeopardize the survival of a species; it might therefore be

interpreted as an evolutionary cul-de-sac (Darlington, 1939). It seems probable, however, that autogamy is rarely complete, and many species appear to benefit from an ability to interpolate outbreeding episodes between long periods of selfing, the condition Fryxell (1959) has called cyclical autogamy. The outbreeding episodes result in immediate increase in the level of heterozygosity, leading to the segregation of new recombinant genotypes in future generations. In offering new pabulum for selection, this facilitates further ecological adaption. The restoration of the autogamous habit rapidly reduces heterozygosity again, but the opportunity is available for the fixation of new adapted variants as pure lines.

The sporadic release of variation in this manner is well-known both in wild and cultivated autogams. The control must necessarily be an external one, and several environmental factors, alone or in consort, may be concerned. Environmental control of cleistogamy has been known since Darwin's day, and Uphof (1938) has listed many examples. Cleistogamy is effective in promoting self-pollination, but it is not necessarily an adaption to this end, since it can also serve as a device permitting reproduction under circumstances adverse enough to preclude normal pollination (Stebbins, 1957). In many described examples, the norm of a species is chasmogamy and outbreeding, cleistogamy resulting from unfavourable conditions of soil or moisture supply (e.g. *Stipa leucotricha*, Brown, 1952). Of more interest from the evolutionary point of view are cases where the norm is self-pollination, cross-pollination being the rarer alternative. In the facultatively cleistogamous grass *Bromus carinatus*, Harlan (1945a, b) found that chasmogamous panicles were formed only under the most favourable growth conditions. Most wild stands sampled in California and Arizona consisted of one or a few practically homozygous lines, but highly heterozygous hybrids were occasionally produced in consequence of chasmogamy and outbreeding. These hybrids Harlan considered could act as the progenitors of "race swarms" from which new, uniform populations might be derived.

A similar variation pattern to that described in *Bromus carinatus* typifies many of the short-lived tropical and sub-tropical Andropogoneae, and environmentally governed facultative inbreeding mechanisms have been observed in these also. *Bothriochloa decipiens*, reported by Blake (1944) as commonly cleistogamous in the wild, possesses an adaptation ensuring the discharge of pollen within the flower. This takes the form of a glume pit which prevents the emergence of the single anther and ensures its dehiscence in contact with the stigmas if the glumes do not open at anthesis (Heslop-Harrison, 1961). The extension of the stem determines whether or not the inflorescence is exserted, and so the possibility of chasmogamy; this is subject to control by photo-

period and temperature. In another grass of the Andropogoneae, *Rottboellia exaltata*, both the incidence of cleistogamy and the total production of pollen are affected by the photoperiodic regime in which plants are grown (Heslop-Harrison, 1959b). The tendency towards self-pollination in these grasses is certainly to be associated with the occupancy of habitats of limited permanency in areas of forest. It is of some interest that they can be brought into a state permitting outbreeding by environmental factors, for their ecological habit may demand not only the ability to build up large homogeneous populations when a favourable habitat is available, but also to achieve, rather regularly, enough recombination to permit the colonization of new habitats suddenly made accessible by local catastrophic change in the forest cover. *Rottboellia exaltata* shows great geographic variation, sometimes on a very local scale (Hubbard, personal communication), and it would be informative to know to what extent this is ecologically correlated.

The matter of ecological adaptation in apomictic complexes merits comment. Obligate apomixis, by suspending entirely the capacity for recombination, must, like obligate inbreeding, presage ultimate extinction once the circumstances for which a lineage is adapted cease to be available. Yet many major apomictic complexes have achieved considerable ecological success, and have done so by what is essentially genecological differentiation (Turesson, 1943, 1956; Nygren, 1951; Clausen, 1954). This must mean that some capacity for attaining recombination remains, and it is probable that in all successful apomictic complexes some sexual potential is retained. This could be through the survival of some sexual races acting as progenitors of apomicts, or through the ability of mainly apomictic lineages to produce some progeny by sexual processes (Gustafsson, 1947; Stebbins, 1950). Haskell (1953, 1959), has convincingly demonstrated quantitative variation in ecologically significant characteristics like flowering time in the progeny of the pseudogamous, largely diplosporous apomict *Rubus nitidioides*, and has shown a response to selection. The parental clone is highly heterozygous, and Haskell suggests that the limited and irregular segregation observed might be explained by recombination during oogenesis (autosegregation). With aposporous apomicts, complete sexual competence may be preserved, so that the progeny are partly sexual and partly clonal. Apospory is very widespread in grasses of the Paniceae, Andropogoneae and related groups (Brown and Emery, 1958), and it may be surmised that it is commonly facultative. In *Dichanthium aristatum* of the Andropogoneae, the balance between sexuality and apospory is subject to environmental control (Knox and Heslop-Harrison, 1963), and there is evidence that it varies from population to population in the wild (Knox, personal communication).

It is apparent that a combination of sexuality and apomixis could be specially advantageous in some ecological circumstances through offering simultaneously the ability to attain a high level of recombination and the capacity to reproduce *en masse* any well adapted genotypes that may emerge (Heslop-Harrison, 1959c). In allowing the immediate fixation of an adapted genotype whatever its level of heterozygosity the system has advantages over cyclical autogamy, where genetic stability is only achieved with an approach to homozygosity.

A closely comparable situation exists where a species is capable of efficient vegetative reproduction. A successful genotype, in achieving vigorous growth, is immediately at a competitive advantage irrespective of its reproductive performance through seed. If propagation is through stolonifery or other direct vegetative means the dispersal capacity may be limited, but an aggressive clone may be expected to spread within the physical limits of the site to produce a highly homogeneous stand (Harberd, 1961a).

It is significant that these versatile reproductive systems are commonly found in species — notably the perennial grasses — occupying habitats of moderate permanency but of some ecological diversity. In successional terms, they are neither ephemeral pioneers, nor yet necessarily components of climax vegetation. The fact accords well with the theoretical advantages to be expected from the special properties of their reproductive systems.

D. ISOLATION AND GENECOLOGICAL DIFFERENTIATION

The relationships set out in Table IV are obviously of great importance for the interpretation of patterns of genecological differentiation in plant species, particularly in connection with the much-debated matter of ecoclinal as contrasted with ecotypic variation. We see that, in general, the group of circumstances set out in the left-hand column of the table will tend to favour continuity and so an ecoclinal type of variation, while those in the right-hand column will favour discontinuity and so a pattern of variation interpretable in terms of discrete ecotypes.

Table IV does not, however, account for all the agencies which may act to generate variational discontinuity within a species, because it does not cover those factors which impinge upon the operation of the genetic system through their effect on the extent of breeding groups. In the obligate self-pollinator, the breeding groups constitute individuals. In cross-pollinators, the size of the breeding group may be affected by the ecological habit of the species, which establishes the density of individuals and the potential geographical range; by the nature of the terrain, which controls the continuity of distribution; by the dispersal

range of pollen and propagules, and by influences governing reproductive periodicity.

At the one extreme are "colonial" species, occurring in panmictic populations perhaps numerically large but isolated spatially from others. This pattern is necessarily imposed on a species when suitable habitats are widely scattered in comparison with the average dispersal range of pollen and propagules. At the other extreme are species which tend to form continuous wide-ranging communities. Within these, the probability of any two individuals mating depends largely upon their spatial separation, and it may not be feasible to define breeding populations lesser in extent than each major distributional area, as is commonly true with widely distributed forest trees. However, it is possible to overestimate the extent of what might be termed "simultaneous" panmixis in these species. The fact that individual pollen grains can be carried great distances may be of limited significance, since the chance of fusion between gametes of remote provenance is determined by the proportion of foreign and local pollen in the atmosphere, and in a closed community the latter is always bound to predominate overwhelmingly. The effective pollination range may thus be quite small. Colwell (1951) found that extremely little of the pollen of *Pinus coulteri* released at a height of 12 ft was carried more than 150 ft even downwind; and Bateman (1947), following gene flow rather than pollen movement directly, found that with maize a distance of 60 ft was enough to reduce crossing to 1%. Moreover, the phenological gradients in continuous wide-ranging populations of potentially inter-fertile individuals become major barriers to long-range crossing, since they limit the distance over which a grain released at any one point is likely to encounter a receptive stigma. Latitudinal adjustment to photoperiod will thus contribute to limiting panmixis. The conclusion must be that in a continuously dispersed, wind-pollinated species the average area within which there is an appreciable chance of two individuals mating will normally be quite small in relation to the total range. What is important is that pathways for slow, continuous gene migration *do* exist, uninterrupted by barriers, through large parts of the species area.

Most distributional patterns lie between these extremes, with local concentrations of individuals separated by thinly inhabited belts corresponding to topographical barriers or zones of unsuitable ecology. In terms of gene flow, whether such a situation resembles one or other extreme depends again upon the average dispersal ranges of pollen and propagules. With insect pollination, ecological limitation of the vectors may be so strong as effectively to exclude gene exchange between neighbouring concentrations of individuals; "genetic mobility" (Darlington, 1939) may then largely become a function of seed dispersion. On the

other hand, the effectiveness of wind-pollination and seed dispersal together may be such as to reduce substantially the isolating effect of local discontinuities, even when the distribution pattern is as fragmented, as in a coastal species like *Plantago maritima* (Gregor, 1946a).

Any form of spatial isolation which is effective in restricting gene flow between two populations of a species will act to facilitate the independent response of the populations to local selective influences. Isolation must therefore always favour the establishment of discontinuities in the variational range of adaptive characters where the separate populations occupy dissimilar habitats. This will be true whatever the intrinsic properties of the genetic system, provided only that there is some release of genetic variation for selection to act upon.

By establishing that the distributional pattern will be one of numerous more or less isolated populations, the ecological predilections of species with the "colonial" type of distribution mentioned above themselves create the conditions for ready fractionation into discrete ecotypes adapted for the minor modulations of the characteristic habitat. Even in the case of outbreeding species with tendencies to form continuous stable communities and to show clinal variation, the occurrence of a topographical barrier imposing some degree of reproductive isolation will favour the appearance of variational discontinuity, producing regional ecological races, or "stepped" ecoclines (Gregor, 1944).

These propositions concerning the role of spatial isolation as a determinant of discontinuity can, of course, be traced back to Darwin and Wagner, and they form a well established part of genecological lore. There is, however, the important question as to whether or not spatial isolation is a *sine qua non* for the development of variational discontinuity. The view of many contemporary evolutionists is that it is, and that divergence in geographical isolation must necessarily precede the evolution of the genetically determined bars to crossing that mark the final step of speciation. This opinion has been especially canvassed by animal systematists (e.g. Mayr, 1942, 1947, 1959; Cain, 1954). There is now, however, excellent evidence from the experimental work of Thoday (1959), Thoday and Boam (1959) and Thoday and Gibson (1962) to show that disruptive selection as defined by Mather (1953, 1955) can produce what is effectively a racial divergence in the face of a very high level of intercrossing.

Thoday's experiments were carried out with *Drosophila melanogaster*, but the results have immediate interest for the plant situation. One experiment (Thoday and Gibson, 1962) began with eighty flies of each sex from a wild strain. From each sex the eight flies with the highest sternopleural chaeta number and the eight with the lowest were selected. The thirty-two flies were permitted to mate at random during a period

of 24 h, after which the eight high and the eight low chaeta number females were separated. From their progeny, the eight low and eight high flies of each sex were selected and mated at random, and the process was repeated in each generation. By the fourth generation of selection, almost all the high flies selected came from the progeny of high females and almost all the low flies from the progeny of low females. By the twelfth generation, the distribution curves did not even overlap. In this experiment, mating was not enforced in any particular pattern, and initially it must have been entirely at random. As the experiment progressed, reproductive isolation developed, limiting the formation of hybrids between the high and low modes. In an earlier experiment (Thoday and Boam, 1959) mating was enforced between low and high lines so as to ensure the *maximum* amount of gene flow; significant divergence still occurred in consequence of the disruptive selection. Thoday and Boam remark that the two sub-populations in this experiment are "in a formal sense, in the same relative situations as would be two parts of a population in a mosaic environment consisting of two distinct habitats arranged, for example, as a chequerboard. In such a situation a population could in principle develop two different forms, one adapted to each of the component environments even if there were forced (50%) gene-flow between the two forms (ecotypes)".

It will be recognized that with higher plants there could be several forms of the basic disruptive-selection situation. For example, the dissimilar habitats could intermingle in the mosaic fashion envisaged by Thoday, or they could interdigitate, or they could occupy distinct provinces within the potential breeding area of the population. Again, the selective pressures in the habitats could differ in intensity, so that a wide range of phenotypes might survive in one and a very narrow range in the other.

Taking an extreme case, it might be that the dispersal capacity of a species was such that throughout an area where two habitats, A and B, occurred, seeding was essentially random. Selection in each generation would then establish that phenotypes appropriate to the conditions of habitat A survived there and were eliminated from B, and that those adapted to B similarly persisted in B and were eliminated from A. The breeding population would then be effectively dimorphic, although still panmictic. The parallel with Thoday's (1962) experimental situation is close though not exact, since the dimorphic *Drosophila* breeding population was derived by selecting the extremes from the total population, whilst in the plant case the morphs are selected from the sample of seeds happening to reach each of the two habitats. Nevertheless, it is evident enough that if Thoday's results can be extrapolated at all they mean that the occupants of each habitat in successive generations should pro-

gressively give rise to higher and higher proportions of phenotypes adapted to the same habitat. In other words, ecotypes should evolve, even in the face of the cross breeding.

Some additional factors need to be taken into account. Obviously the intensity of the disruptive selection will be a paramount factor in determining the rate of differentiation. This probably means that this kind of response is only likely to occur at any significant rate where extreme habitats are encountered; and it is noteworthy that some of the best examples of clear-cut ecotypic differentiation are found in habitats where selection is patently intense. The most familiar situation is the asymmetrical one, where a generally favourable habitat adjoins or is interpenetrated by another distinctly less favourable: a coastal belt of extreme conditions adjacent to an equable hinterland, or an area of serpentine soil in an otherwise edaphically normal region. The response here should be such as to produce a specialized but narrow group of phenotypes (at least so far as the adaptive characteristics are concerned), while permitting the survival of a much wider range in the adjoining less demanding environment. There is, of course, no reason to expect divergence in non-adaptive characteristics.

It is to be noted that once divergence has been initiated other circumstances will subsequently develop to encourage it. Thus there will necessarily be a movement away from randomness so far as seed dispersal is concerned, since each surviving individual is likely to seed more intensively its own immediate neighbourhood and so its own appropriate habitat than more remote parts of the alternative habitat. In so far as its adaptive characteristics are heritable, this will ensure that a higher proportion of adapted than non-adapted seedlings arise in each habitat. The same will apply with respect to pollen dispersal; mere contiguity in the individual habitats will guarantee some assortative mating. In consequence, a higher proportion of recombinants giving more extreme phenotypes will be generated, so allowing a progressive directional change towards better and better adaptation. In a habitat where selection is intense the product would ultimately be an assemblage of biotypes lying outside of the original distributional range altogether.

The situation discussed above in which disruptive selective pressures arise within a population because of its occupancy of a heterogeneous environment represents a special case, since it is envisaged that the population is capable of at least surviving in all of the diverse habitats *ab initio*. This cannot always be true. A capacity for phenotypic plastic adaptation may be important in permitting the invasion of some types of unusual habitat (p. 213), but beyond any extended tolerance range which this may provide, immigration into an environment offering novel and perhaps intense selective pressures will demand new geneti-

cally adapted recombinants, perhaps not immediately available. This must very frequently be the situation during the migration of a plant species into new territory, and it is one of a good deal more than theoretical interest considering that the north temperate floras have undergone massive oscillatory migrations during glacial and post-glacial times.

It may be that the circumstance mentioned above (p. 201) is significant under these conditions, namely that during a period of migration a free release of genetic variation might be favoured in the van. This would arise if the intraspecific competition were heavy enough under the conditions of a closed community to restrict very severely the range of phenotypes reaching reproductive maturity in the territory already occupied. In a thinly colonized marginal zone, some of the intense selective factors active in the closed community would be relaxed, with the consequent survival of new phenotypes. To the extent that these carried new gene combinations, they might be expected to enhance the segregation range in the pioneer belt. This availability of fresh recombinants would necessarily favour migration into novel habitats and the establishment of adapted races there, provided only that any adaptive gene complexes assembled were not immediately broken up by contamination from elsewhere. Mayr's (1954) argument that peripheral populations would be inhibited from adapting successfully to new environments by the disruptive effect of gene migration from the interior of the species range has been contested by Thoday and Boam (1959), who on the basis of the experiments described above state that there is no reason in principle why a locally adapted population should not be formed even if one-way gene flow were so great that all progeny were hybrids. Evidently this particular facet of genecological differentiation would merit more observational and experimental study.

There is another factor that is likely to be significant in promoting the differentiation of plant populations under disruptive selection, namely the effect of the immediate environment on phenology. In the British Ecological Society's series of transplant experiments, summarized by Marsden-Jones and Turrill (1938), some effect of soil type on date of flowering was observed in half of the species tested. Thus in 1932 a sample of *Plantago major* cultivated on "clay" reached maximum flowering by 19 June, but a corresponding sample of plants of the same parentage cultivated on "sand" in an adjacent plot did not reach a flowering peak until 15 July. Aspect may similarly produce phenological differences. Thus Mitra (personal account) working at Saskatchewan found up to a fortnight delay in the flowering of *Stipa* species on the north as compared with the south faces of an artificial east-west mound of 10° slope. Ehrendorfer, in the study mentioned of *Galium pumilum* (p. 186) (1953) observed distinct differences over the small area studied in

flowering time; plants in the drier, open sites regularly reached anthesis before those in the moister, shadier localities. Here, of course, the possibility of some genetical differentiation for flowering time in the population is not excluded, but the circumstances as discussed by Ehrendorfer do suggest that the environmental control of phenology may have imposed some restriction on free gene exchange between the sub-populations even during the initial differentiation.

The implication of observations such as these is that the mere occupancy of a heterogeneous habitat can fragment a plant population into partly isolated breeding groups by breaking down the synchroneity of flowering. Since each distinct habitat will have its own particular effect, the sub-populations in each will have a characteristic flowering period. The plants in each type of habitat will thus remain panmictic, but will be genetically isolated from others in different habitats to the extent that the flowering periods fail to overlap. This is an irrefutable example of ecological isolation, not to be discounted on the basis of any of the arguments of Mayr (1947).

E. MONOTOPIC AND POLYTOPIC ORIGIN AND THE RETENTION OF RACIAL IDENTITY

A distinction can be drawn at least on theoretical grounds between mosaic patterns of ecological races where each race has had a monotopic origin, and the superficially similar patterns which have arisen through the polytopic origin of like ecotypes in response to corresponding selective factors in different parts of a species range. It is to be expected that races that have had single independent origins will normally be distinguished by several correlated differentiae, both adaptive and non-adaptive. On the other hand, only the adaptive characteristics are likely to be shared in common between the various populations of an ecotype which has originated polytopically, and the populations may differ among themselves in respect to non-adaptive features. A classical case of presumed polytopic origin is that of the sand-dune ecotype of *Hieracium umbellatum* described by Turesson (1922b). This occurs in sand-dune habitats widely scattered around the periphery of the species area in Sweden. The different populations share in common various adaptive features such as a capacity for rapid shoot regeneration, but they differ in minor leaf characteristics, each showing a resemblance in these characteristics with neighbouring inland populations.

The inhomogeneity of ecotypic populations of polytopic origin is likely to be evident also in the genetic basis of their adaptation. Since similar phenotypes can be established by different combinations of polygenes, there is no reason to suppose that identical selective pressures in remote sites will necessarily fix the same group of genotypes. In con-

trast, if the various sites have been colonized by a single race the populations may be expected to be genetically homogeneous except in so far as secondary differentiation has progressed. Clausen (1951) reported a study of prostrate maritime populations of *Layia platyglossa* of the Californian coast in which an attempt was made to discover whether the complex had had a monotopic or a polytopic origin. Representatives of two phenotypically similar populations 140 miles apart were intercrossed, and a large F_2 family was raised. The adaptive characteristics — prostrate habit, succulence and late flowering — appeared uniformly in the F_1, and showed no F_2 segregation. The F_2 was, however, variable in respect to other characters such as density of internodes and number of disk and ray florets. This result certainly suggests that the genetical basis of the adaptive characteristics is identical in the remote populations, yet the occurrence of some F_2 segregation does indicate heterogeneity. Clausen concluded that the maritime race does in fact, represent a single and rather ancient evolutionary entity. If so, the dissimilarities between the populations in non-adaptive characteristics must have arisen through secondary differentiation.

Where two or more races, originally allopatric, have attained coincident or overlapping ranges by secondary migration it must be supposed that there are factors operative preventing miscegenation. The sequence is, of course, that widely accepted as being usually involved in speciation (Mayr, 1942): divergence in geographic isolation, followed by the emergence of some form of reproductive isolation, followed in turn by further migration to produce overlapping distributions. It is not within the scope of the present paper to discuss the broader problems of isolating mechanisms and speciation, but some consideration of the factors acting to preserve the identity of sympatric ecological races is merited.

Ecological specialization may itself form the most potent such factor. Where a predilection for highly distinctive habitats has been evolved, this must impose spatial isolation to the extent that the habitats themselves are dispersed geographically. Beyond this, the fact that each race has attained an adaptive peak for its particular habitat will mean that recombinants will be at a disadvantage in competition with their parents and uncontaminated progeny: they will become the victims of stabilizing selection in each habitat. While the pattern of selective forces remains unchanged, hybridization will be disfavoured.

Many of the described cases of isolation imposed by strong habitat specialization concern pairs or groups of entities sufficiently distinct in morphology and distribution to have merited recognition as taxonomic species (p. 187). Well-documented examples are *Quercus ilicifolia* and *Q. marilandica* (Stebbins *et al.*, 1947) and *Silene vulgaris* and *S. maritima* (Marsden-Jones and Turrill, 1957). With both of these pairs hybridiza-

tion does occur where the parents grow in close proximity, but the hybrids, being ill-adapted to the available habitats, fail to survive in the wild. The limitations of hybrids to intermediate habitats or ecotones has been excellently demonstrated by Briggs (1962) for the Ranunculi of the *lappaceus* group (p. 176). Here there seems no doubt that the restriction of gene flow depends almost entirely upon selective elimination of hybrids, even though the characteristic habitats may alternate over distances of only a few metres.

The same principle is evident on a larger scale with the ecotypic subspecies of *Potentilla glandulosa*. Clausen and Hiesey (1958a) comment on the situation as follows: "Undoubtedly, at the edges of the distribution of the four subspecies of *P. glandulosa* a certain amount of hybridization is constantly taking place. Natural selection, however, limits the extent of genic infusion among the subspecies. In regions where equilibrium has thus been reached, the subspecies are able to maintain their identity." There are other factors acting to limit gene exchange between the *P. glandulosa* subspecies; *reflexa* and *hanseni*, for example, differ in flowering time by as much as a month. Moreover, all of the subspecies except *nevadensis* are self-compatible and thus probably extensively inbred (Baker, 1953). Nevertheless, the importance of ecological isolation in preserving their independence is beyond question.

The significance of isolation dependent upon the flower fidelity of pollinators in entomophilous groups has been emphasized especially by Grant (1949). Minor differences in floral characteristics among ecological races of genecologically differentiated species may contribute to maintaining isolation through this so-called ethological means. The specialization of pollinators certainly forms an effective isolating mechanism with the two species of *Melandrium*, *M. rubrum* and *M. album* (Baker, 1947). The ecotypic subspecies of *Dactylorchis incarnata* (p. 178) are barely distinguishable in vegetative features, and are yet sharply differentiated in flower colour and patterning (Heslop-Harrison, 1956). There is no direct evidence, but the possibility is open that this provides some measure of ethological isolation and has facilitated the independent migration of these races through north-western Europe (Heslop-Harrison, 1958).

Ecological isolation and isolation dependent upon the behaviour of pollen vectors both arise from genetical properties of the populations concerned, and all intermediates exist between these comparatively mild barriers and the ultimate disharmony which results in hybrid sterility or inviability. Ecological and to a lesser extent ethological isolation differ, however, from isolating mechanisms dependent upon partial or complete intersterility in not being irremoveable once established. This means that evolutionary fluidity is preserved; to extend

Mather's phrase, fitness for existing environments is not acquired at the cost of a narrow specialization which sacrifices the flexibility offered by a large gene pool. The change of circumstance which renders the original close adaptation to previously existing habitats valueless may simultaneously permit the survival of hybrid derivatives that otherwise would have been eliminated in favour of the strictly adapted types. What Anderson (1949) picturesquely calls "hybridization of the habitat" may entail a new release of genetic variation, and a new starting point for adaptive differentiation (Anderson, 1949, 1953).

F. PLASTICITY, GENETIC ASSIMILATION AND CONDITIONING

In consequence of their growth by apical meristems, higher plants possess high potential phenotypic plasticity. The continuous serial production of fresh organs means that a capacity to respond developmentally to environmental influences is present throughout life, not, as in the higher animal, only during an early embryonic period.

It is apparent that these responses may or may not be adaptive. Thoday (1953) has suggested the term "developmental flexibility" for the truly adaptive property of generating phenotypes functioning satisfactorily in a range of environments. Mere morphological plasticity is not necessarily evidence of developmental flexibility. For example, the passive response to a factor establishing, say, a particular growth form, does not necessarily mean that a plant is better adapted for the environment in which that factor is present than it would be if it produced some other growth form under the same conditions. Nevertheless, there is good reason to suppose that the plasticity of higher plants does often have adaptive values, within certain limits.

It has long been supposed that the wind forms of plants are adaptive, and direct supporting evidence for this view is now available from the work of Whitehead and Luti (1962) and Whitehead (1962, 1963a, b). In maize and sunflower, exposure to wind speeds approximating those found in mountain regions induced anatomical and morphological changes which were demonstrably advantageous with respect to overall water economy. The phenotype became more xeromorphic, and the change was harmoniously related to the incidence of the adverse conditions. Whitehead points out that neither species is notably plastic, yet there is no doubt that they are equipped with a developmental flexibility which must extend their potential ecological tolerance ranges quite substantially.

The work of Björkman and Holmgren (1963), discussed at length in a later section (p. 224 *et seq.*), provides some evidence of the adaptive value of variation in leaf morphology and physiology caused by differing levels of insolation. As part of these experiments, leaves of the different

ecotypes of *Solidago* were conditioned to various levels of irradiation. Plants of the "sun" ecotype showed adaptive change, the photosynthetic rate at light saturation being higher following growth in high light intensities. Plants from the "shade" ecotype were incapable of adapting to the highest light intensity used, and the leaves were in fact damaged.

Björkman and Holmgren's observations on *Solidago virgaurea* suggest very clearly that the range of developmental flexibility in this species is somewhat limited. In respect to the capacity for adapting to different light environments, it would seem that the genotypes tested would not be flexible enough to span more than a part of the observed tolerance range of the species; the breadth of this evidently depends upon the differentiation of ecotypes. There are, however, cases of species which seem to be capable of colonizing unusual habitats either by producing modified phenotypes (developmental flexibility) or by evolving ecotypes (genecological differentiation). Turesson (1922b) mentions the example of the forma *nana* of *Succisa pratensis*. This is an extreme dwarf form, attaining a stature of no more than 8·5 cm, occurring in the upper part of salt marshes around the coast of Scania. Samples transplanted from various populations differed in their behaviour under cultivation. All increased in height to some extent, but some populations proved to contain individuals fully capable of achieving the stature of plants from inland populations, whilst others were composed exclusively of hereditary dwarfs.

Examples like *Succisa pratensis* f. *nana* raise the general problem of the relative values of developmental flexibility and genecological differentiation as devices permitting the extension of ecological range. It is obvious that some direct phenotypic adaptability will always be of value in buffering a plant against minor modulations of environment, either spatial or chronological. Why should tolerance not be extended indefinitely in this manner? Since the evidence shows that genecological differentiation is the "preferred" means of adapting to extreme habitats, it follows that there must be inherent disadvantages in direct phenotypic modification. Turesson's own conclusion (1922b) probably covers the essential point: "The question may be made clearer by the assumption that the same characteristics which in one form of the species (the resulting modification) requires the exposure to an environmental factor of high intensity in order to become developed, may in another form (the hereditary variation) result as a response to a very much lower intensity of this factor. . . . It is conceivable that the habitat responsible for the development of the characteristic in question may at the same time act as a limiting factor upon general development in the case of the modification, while no such limiting action results in the hereditary variation because of the promptness with which it responds to this same habitat

factor." In short, the physiological economy of producing directly an adapted form is of selective value.

Turesson's argument may be linked with that advanced by Waddington (1953a), concerning the "genetic assimilation" of acquired characteristics, the so-called Baldwin effect. According to this, if there is variability in a population in the capacity to react to a particular environment by the production of a modified phenotype which is at a selective advantage in that environment, then the reacting genotypes will necessarily be favoured. Successive generations of selection for the capacity to react to the effective stimuli may be expected to lower the intensity of stimulation required to produce a given phenotype, and ultimately to bring about an approach to a state where the favoured phenotype is produced spontaneously. The feasibility of this kind of genetic assimilation has been demonstrated in a well-known experiment of Waddington (1953b) with *Drosophila*, the characteristic being a wing venation defect induced in the normal genotype by a high-temperature shock during pupation. In the line selected for ready expression of the defect, flies appeared in the 14th generation which revealed it without temperature treatment.

Given that there *is* advantage of the kind envisaged by Turesson in the direct rather than the enforced production of adapted phenotypes, and given further that genetic variability exists in a population in the capacity to respond to the effective environmental factors, then it seems inevitable that some form of genetic assimilation will occur. The significance for genecological differentiation is evident. The ability to exploit an unusual habitat in consequence of inherent developmental flexibility will, as it were, provide a species with a beach-head. To the extent that more facile phenotypic adaptation to the new environment is favoured, genes contributing to this will accumulate in the immigrant sub-population, and so the threshold at which the specialized form appears will be lowered. Since the intensity of selection will decrease as this process progresses, the adjustment will be asymptotic, and finality will never be reached. This means that some adaptation will always depend upon developmental flexibility, and it is significant in this connection that, on transplantation to neutral environments, individuals of ecotypic populations adapted to extreme environments invariably regress in some degree towards the norm of the species.

Waddington's principle of genetic assimilation offers a plausible interpretation of one form of quasi-Lamarckian response to habitat. The possibility of other, more direct, mechanisms is, of course, still to be kept open. Durrant's experiments on environmental conditioning in flax (1958, 1962) seem to show unequivocally that one major group of habitat factors, namely soil nutrients, can induce heritable changes in pheno-

type. In one experiment, eight combinations of nitrogen, phosphorus and potassium fertilizer treatments were given to a parental generation, and effects on weight of progeny were observed for four generations under uniform soil conditions. In the second generation, the descendants of plants receiving NK but not P weighed only one-third of those receiving PK. The "genotrophs" or conditioned forms differed in morphological features other than gross production, and revealed various physiological peculiarities. Durrant has referred to them as being adapted to different environments, and it is evident from his data that their performance does not always bear the same relationship to the "normal" under diverse conditions of cultivation. in the open and in greenhouses. It is not apparent, however, that the effect of conditioning in flax is necessarily to produce a genotroph better adapted to the soil environment inducing the change.

The possibility that environmental conditioning in flax might depend upon the behaviour of cytoplasmic determinants was considered by Durrant (1958), but later abandoned (1962). The suggestion was that under the inducing conditions the relative multiplication rate of nuclear genes and plasmagenes might be affected, so establishing a new nuclear-cytoplasmic relationship. Should this new relationship constitute a stable equilibrium, the condition might be propagated through successive generations. Essentially the same suggestion had previously been made by Crosby (1956) as a theoretical basis for the inheritance of acquired adaptations. A model system is described by Crosby in which a plant is presumed to be adapted to a mild environment with a low concentration of a plasmagene favouring resistance to low temperatures. Under cooler conditions, growth rate and so cell division rate is reduced. If it be assumed that the rate of reproduction of the plasmagenes concerned with cold resistance is not reduced proportionately, then their concentration will increase in the cell, so progressively enhancing cold tolerance. If the conditioned state is transmitted through the reproductive cells, then progeny will be better equipped to survive in the cooler environment.

Crosby emphasizes that acquired adaptation of this kind is most likely to be found in generalized characteristics like growth and vigour; it is in these features that Durrant's genotrophs differ most from their parental strains. The response as envisaged by Crosby and Durrant may be looked upon as a sort of physiological adjustment of phenotype to environment akin to that involved in the conditioning of individuals during growth, but having a transmitted element providing for the partial pre-adaptation of progeny. Certainly there is no need to discount this possibility on any physiological grounds. It is well known that induced states such as those arising from vernalization and photo-

periodic treatment may be transmitted through many cell generations without decay, and may, furthermore, be amplified and transmitted to other plants by grafting. Indeed, having regard to this, what is remarkable is the efficiency of the mechanism which acts in the commonality of cases to restore reproductive cells to a basal, undifferentiated and unconditioned state. That occasionally this restoration should be incomplete so that some proportion of a parental experience is transmitted to progeny seems not at all unreasonable.

Durrant's experiments illustrate one kind of transmission of acquired characteristics; evidently it would be profitable now to reconsider the possibility that some habitat-correlated variation may be due to direct conditioning and subsequent transmission of the conditioned state to progeny. It is interesting to note that there is no *a priori* reason to expect conditioning invariably to produce adapted phenotypes, except in so far as a principle like that of Crosby might be involved. This opens the possibility of there being *non-adaptive*, habitat correlated variation. However, there is as yet no direct evidence of such a phenomenon, and in the succeeding discussion of the physiological aspects of genecological differentiation it will not be taken into consideration.

III. PHYSIOLOGICAL ASPECTS OF GENECOLOGICAL DIFFERENTIATION

A. INTRODUCTION

The detection of genecological differentiation within a species generally depends in the first instance upon the observation of habitat-correlated variation in morphological features. As we have seen (p. 168) it is presumed that if populations in one type of habitat are regularly found to differ from those in another in any characteristics whatever, those differences (or others unobserved genetically or developmentally correlated with them) must have adaptive significance, because the only plausible cause of the divergence, discounting the kind of conditioning mentioned in the foregoing section, is the differential effect of selection in the two environments.

This argument depends not in the least upon any physiological interpretation of the differences. Yet it is difficult to arrest genecological investigation at the point where presumed adaptive differences have merely been identified, for the question of their actual survival value in the habitats concerned then obtrudes itself. An important matter to clear up is the level at which answers to questions of this type would be deemed acceptable. Consider the case of two "ecotypes" A and B, from two habitats, *a* and *b*. In habitat *a*, A performs better than B as assessed by some arbitrary measure such as dry matter accumulation, and in

habitat b, the position is reversed. An experimental demonstration of this fact would provide one type of explanation for the occurrence of each ecotype in its characteristic habitat. It might be considered unsatisfactory, (a) because it does not follow that the measure selected is that of primary significance for survival when the two are in competition (some other factor, for example, the powers of seed dispersal, may be more important in these conditions), and (b) because the experiment does not reveal which factor or complex of factors in the habitats was responsible for the difference in dry matter production, nor which physiological mechanism in the plants themselves was responding differentially in the two ecotypes. To proceed further with the problems under (a) would demand an assessment of more estimates of performance, each posing its own set of questions under (b). To pursue the queries under (b) would require a factor by factor analysis of the habitats, and a function by function study of the plants. The difficulty under (a) might be met in part by comparing the relative fitness of ecotypes directly in competition in the different habitats, the performance measure adopted being simply survival. Other things being equal, the expectation is that the habitat "sieve" will once more sort them out appropriately. An ecotype Derby of this kind would not, of course, represent a recapitulation of the evolutionary processes which led to ecotypic differentiation, since at no time in the course of evolution would the end products of differentiation in specialized habitats come together in direct competition in any one habitat. In the ideal situation, nevertheless, it might be expected to provide direct evidence to support the original circumstantial case for the ecotypic differences being adaptive. It is this kind of evidence that is sought in reciprocal transplant experiments, and in varied environment experiments such as those conducted by Clausen *et al.* (1940, 1948). Given this reassurance about the adaptive value of the ecotypic characteristics acting in consort, questions of the (b) type still arise, namely: In what way are they adaptive physiologically speaking? If answers on this level are really required, there is no escape from the need to trace direct causal connections between environment and plant responses. For the higher plant, habitat factors are commonly regarded as being of three general kinds, climatic, edaphic and biotic; yet it is an ecological platitude that survival is determined by the simultaneous effect of all, the environment being "holocoenotic" (Cain, 1944). What possibility is there, then, of linking "character" or "response" with "factor", when the ontogeny and physiology of the plant are expressions of the reaction between the entire genotype and the entire complex of environmental influences? In the generality of cases the answer to this must be, very little; particularly when the habitat differences are small and multidimensional. Then

truly will the terminus have been reached. Fortunately, however, when it *is* difference between habitats which is under consideration, the situation may be simpler, because very often it is possible to identify the major determinants. "Adaptation" is still likely to be a holistic process, but it is feasible to measure plant responses to the major environmental variables singly and in interaction in various simple patterns, and obviously this can be done in a comparative manner with populations of different provenances.

It needs no emphasis that this type of study only becomes useful as a basis for extrapolation to the natural situation when the conditions of the experiments themselves can be related in some meaningful manner to those in nature. Merely to match the list of morphological differentiae observed between ecotypically differentiated populations with another of physiological differentiae demonstrated under some experimental condition or the other is obviously not enough. It is only when a functional difference can be shown to be associated with a differentially acting environmental factor that we are beginning to approach the understanding of a causal sequence. Yet even here it may still not be possible to say with assurance that the selective agent and the specific function upon which it impinges have been identified. The possibility remains that the "real" target of selection is an associated or secondary response, or a function for which the one studied acts as a governor or time-keeper.

B. EDAPHIC ADAPTATION

There is no particular reason for supposing that the adaptation of plants to their rooting media will involve processes or principles different from those governing adaptation to the sub-aerial environment, but it so happens that there are examples of clear-cut patterns of adaptation to soil type which should permit a more precise kind of analysis than can be given to most examples of adaptation to climate or biotic influence.

Such a case is the tolerance of grass populations to soils contaminated with heavy metals, briefly described in a foregoing section (Bradshaw, 1952; Wilkins, 1957, 1960a, b). Wilkins compares this example to industrial melanism in moths: in both situations the selective factor can be identified precisely and its impact can be shown to be severe. In the case of *Festuca ovina*, lead is highly toxic to normal plants, yet on mine spoil heaps in the British Isles tolerant populations occur on soils containing up to 4% lead. Using an assay method based upon the measurement of extension growth in the roots of tillers grown in glass tubes in culture solutions under standard environments Wilkins (1957, 1960b) has obtained evidence suggesting that three types are present in the species: intolerant, medium tolerant and highly tolerant. The tolerant

plants are restricted entirely to lead-containing soils, and the intolerant ones to lead-free soils. Genetically the property of tolerance was found to be completely dominant, and although a full analysis has not been possible yet, it is conceivable that the tolerant genotypes may differ from the normal in substitutions at single loci. In a field trial no morphological features could be shown to be correlated with tolerance, and for that reason Wilkins has been reluctant to look upon the tolerant populations as constituting an ecotype. Whatever terminology is used, however, it is evident that this is an example of genecological differentiation in the broad sense, and rather an important one in that the selective factor has been identified with some assurance and related to a physiological property which should, in principle at least, be open to precise measurement.

The examples of ecological races adapted to serpentine soils also discussed in an earlier section are in some respects comparable. Kruckeberg (1954) states that a major criterion for serpentine tolerance must be the capacity for growth on soils of low calcium levels. A direct comparison of the tolerances of serpentine and non-serpentine races of *Phacelia californica* to calcium deficiency revealed a very clear difference; the normal soil race showed no growth in un-supplemented serpentine soil, the growth being equalized with supplements equivalent to 2 tons of gypsum per acre. NPK treatments greatly benefited the tolerant race on serpentine soil, but were without effect on the normal soil race on this medium. The suggestion of Walker (1954) that serpentine races might benefit from a capacity to accumulate calcium in preference to other cations was also verified with the *Phacelia* races. At each of three soil-calcium levels the tolerant race absorbed greater amounts of calcium and lesser amounts of magnesium, as revealed by tissue analysis. A similar distinction between serpentine and non-serpentine races in tolerance of calcium-deficient soils was observed in twelve other species of annual and perennial herbs, although no serpentine ecotypes were observed among the grasses tested.

Although there seems little doubt that the major adaptation shown by the serpentine races is their capacity to tolerate calcium deficiency, Kruckeberg points to the fact that serpentine ecotypes may show other adaptive characteristics. These include in particular the capacity to tolerate the exposure and sometimes drought which may also characterise the serpentine habitat. He concludes "that serpentine plants are physiologically adapted to the open characteristics of serpentine communities as well as to the special soil conditions, and that the physiological adaptations of serpentine plants may have some degree of morphological expression". This multidimensional adaptation of some serpentine races offers a pretty example for consideration in relation to

the general problem of ecotype evolution. The adaptation of these races must be to the whole environment of the serpentine, yet the dominant factor in this, according to Kruckeberg, is the calcium deficiency. Selection pressure has presumably been greatest therefore for the property of accumulating calcium preferentially; when this was acquired, the invading populations would become exposed to selection for tolerance to the other conditions in which the serpentine habitat differs less radically from the normal. The inter-locking nature of the various factors becomes apparent when it is appreciated that certain peculiarities of the serpentine habitat arise just because some species — including shade-forming trees — are excluded from it by their intolerance of calcium deficiency. A single major factor is here seen to generate a complex of selective pressures secondarily.

The demonstration of adaptive properties in races occurring on extreme soil types raises the further question of whether adaptation has been bought at the cost of the ability to survive in normal soils. In the case of lead tolerant fescue races, Wilkins (1960b) records a higher mortality among tolerant biotypes in cultivation under conditions of low competition. This observation does indeed suggest that selection for the ability to endure high lead concentrations in the soil has led to the plants' becoming dependent in some way on lead-rich soils, possibly, as Wilkins suggests, even by establishing a requirement for lead itself. Kruckeberg's observations (1954) on serpentine endemic *species* seem to show that their exclusion from normal soils is entirely in consequence of competition. In culture on calcium-replenished soils free from the suppressive effects of weedy annuals, serpentine endemic *Streptanthus* species thrived; subject to competition, survival was poor. It is perhaps not justifiable to argue directly from this to the case of serpentine ecotypes, and it may be that the adaptation of these has involved some sacrifice. McMillan (1956a) records that a "strain" of *Agrostis hallii* from a serpentine soil performed very substantially better, as judged by height and dry weight production, when cultured on serpentine soil than when grown on a control soil; this may indicate that here adaptation has involved specialization. But the example of *Achillea borealis*, in which some biotypes from normal soils are recorded by Kruckeberg (1950) as showing tolerance to serpentine conditions, proves that the capacity to survive on calcium-deficient soil does not necessarily put a plant to selective disadvantage in an otherwise unadapted population on a normal soil.

The two cases of edaphic adaptation discussed above relating to the tolerance of heavy metals and serpentine soils are unusual in that the selective factors are obviously severe and the circumstances in which they are encountered rather rare. It is obviously important to know

whether genetic adaptation occurs when species encounter less distinctive soil types. The best evidence so far available, that it does is that given by Snaydon and Bradshaw (1961) for *Festuca ovina*. In this study, samples from populations growing on soils with free $CaCO_3$ (pH 7·8–8·9) and on soils low in calcium (1·5–6·8 m.e. per 100g Ca; pH 4·3–4·6) were examined for their response to calcium in culture solution at levels of 5, 10, 20, 75 and 150 p.p.m. An analysis of variance showed that the within-type × treatment interaction was insignificant, justifying the placing of the populations in two groups, "calcareous" and "acidic". The growth of the two types, as assessed by dry weight production, is related to Ca level in Fig. 3. The striking features are the outstandingly
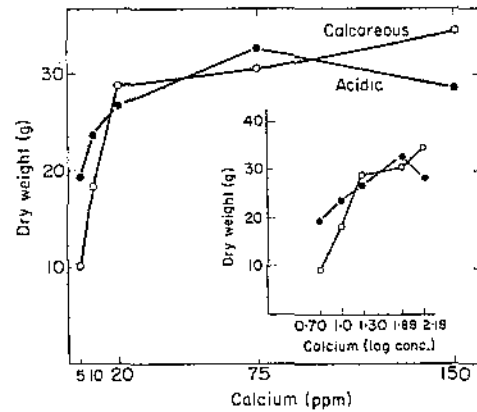

FIG. 3. The growth of *Festuca ovina* of "calcareous" and "acidic" types at various calcium levels. (From Snaydon and Bradshaw, 1961.)

better performance of the acidic type at low calcium levels and its poorer performance at the higher level. Plant analysis in an experiment in which genotypes from two contrasting populations were compared indicated a three times better calcium uptake at low calcium levels by plants adapted to acidic soils. At equivalent dry weights, plants from acidic and calcareous soils contained equivalent amounts of calcium, showing that the success of the plants from acidic habitats when grown in low-calcium solutions was not attributable to a lower *requirement* for the element.

Snaydon and Bradshaw point out that the response to calcium is not likely to be the only factor differentiating plant populations from widely different soils, but their results certainly suggest that the wide edaphic tolerance of *Festuca ovina* has been achieved by the differentiation of races physiologically adapted to different levels of soil calcium, so that calcium availability must have been a major selective factor.

C. ADAPTATION TO SOIL MOISTURE STRESS

In spite of the wide interest in the water relations of plants there have been few experimental studies of ecotypic adaptation to different levels of soil moisture. McKell *et al.* (1960) have compared two races of *Dactylis glomerata*, recognized taxonomically as the geographic subspecies *lusitanica* and *judaica*, for their performance under differing conditions of soil moisture stress. Subsp. *lusitanica* is known from the coastal area of central Portugal, where it occurs in a mild coastal climate, while *judaica*
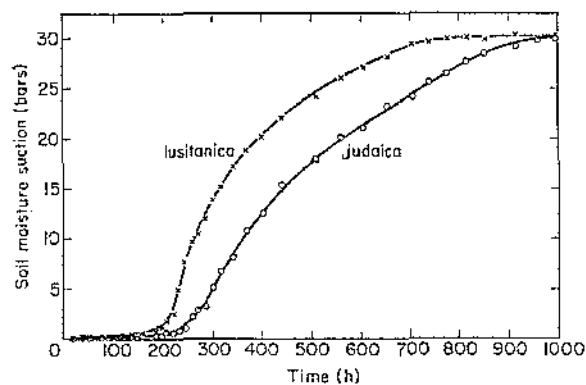

FIG. 4. Rate of water use by two ecotypic subspecies of *Dactylis glomerata*, subsp. *judaica* and *lusitanica*. (From McKell, Perrier and Stebbins, 1960.)

(probably the arid ecotype of Boyko and Tadmor, 1954) occurs in Israel and perhaps neighbouring countries in a dry Mediterranean climate (Stebbins and Zohary, 1959). Plants were grown in pairs in a sandy clay soil in cans. After growth under favourable moisture conditions for three months, they were clipped back and transferred to growth cabinets where they experienced a daylength of 14 h with a light intensity of 1300 fc, with a temperature of $18° \pm 1°C$. and $45\%_0 \pm 5\%_0$ R.H. A conditioning period of 1 month was allowed, after which the plants were clipped again and the observations begun. The cans were saturated initially and then allowed to dry out, the soil moisture being monitored continually by observing the electrical resistance of buried gypsum plugs. A difference in soil water utilization was observed between *lusitanica* and *judaica* on a per-plant basis, as shown in Fig. 4. Subsp. *judaica* showed a higher rate of leaf elongation and reached a greater cumulative mean leaf-blade length during the experimental period. On the other hand, *lusitanica* produced a greater final weight of foliage; evidently cell elongation is inhibited by water deficiency before dry-weight accumulation is curtailed.

McKell *et al.* note that subsp. *judaica* characteristically passes into a state of summer dormancy. This presumably forms its principal means of surviving the main period of moisture stress in its native habitat, rather than any direct adaptations to water deficiency. During the actual growth period the main physiological feature suggesting adaptation to soil moisture stress was the lower rate of water use; otherwise the overall responses were not very different from those of subsp. *lusitanica*.

D. ADAPTATION TO LIGHT INTENSITY

A conspicuous form of environmentally correlated morphological variation in higher plants is that apparent in leaves according to the intensity of illumination. Differences between sun and shade leaves of the same genotype are a direct consequence of the morphogenetic effects of light, and it is widely supposed that the characteristic features are in some way adaptive, although the direct evidence is slight (Wassink *et al.*, 1956). In consequence of plasticity, the sun and shade grown individuals of some species may reveal substantial phenotypic differences in leaf size and texture, but, as shown by Turesson (1922b) with *Lysimachia vulgaris*, such differences disappear on cultivation in standard environments. Heritable differences in leaf form between populations of a species from open and shaded habitats have, however, been frequently demonstrated, and this may be regarded as an example of genecological differentiation.

Although it is the variation in the light environment which is commonly most conspicuous, "sun" and "shade" habitats do inevitably differ also in other correlated factors, notably in temperature and humidity. There is therefore the familiar difficulty of identifying the effective selective factors, and again it must be supposed that several responses have been selected for simultaneously in the course of adaptation. Nevertheless, there is good reason for concentrating upon light as a major measureable differential factor in studying the adaptation of sun and shade ecotypes, particularly since the role of light in the economy of the plant is reasonably well understood.

An excellent study of photosynthesis efficiency in sun and shade ecotypes of *Solidago virgaurea* has recently been carried out by Björkman and Holmgren (1963). The sampled populations were from two shaded habitats, oak and beech forest, and two open habitats, dry open meadow at 105 m altitude and alpine heath at 600 m. Ten plants were selected from each environment and propagated to provide two pairs of individuals of each genotype. One pair from each clone was cultivated at low light intensity, 3×10^4 erg/sec/cm^2 and one pair at high, 15×10^4 erg/sec/cm^2. Other conditions were identical: photoperiod 16 h, temperature during light period $20 \cdot 0 \pm 0 \cdot 3°$ C and during dark $10 \cdot 0 \pm 0 \cdot 3°$ C. Air

humidity was maintained at 70 ± 5% R.H. After 4 to 8 weeks of pre-
liminary growth, photosynthesis measurements were made and ana-
tomical differences investigated. Mature rosette leaves were detached
and irradiated in temperature regulated, humidity controlled cells with
light from a xenon arc source. Photosynthesis was measured by monitor-
ing the utilization of CO_2 with an infrared absorptiometer. Two expres-
sions of photosynthetic activity are of importance in a comparison of
this nature: (a) the relationship between photosynthetic rate and light
intensity at low light levels (a satisfactory measure being the initial
slope of the rate-intensity curve), and (b) the photosynthetic rate at
saturation light intensity. Comparisons between three clones from each
of the four habitats are given in Table V, which is re-arranged from the
data of Björkman and Holmgren. The two population groups differ

TABLE V

(A) "Photochemical Capacity" (measured as initial slope of the
rate-intensity curves) for Plants of Three Clones from each of Four
Localities, Two Exposed and Two Shaded, of Solidago virgaurea,
Grown at Low Light Intensity. (B) Photosynthetic Rate at Light
Saturation in Plants from the Same Clones Grown at a High
Intensity

	Shaded habitats			Exposed habitats	
	A	B		A	B
Locality 1			Locality 3		
clone a	3·10	18·9	clone a	2·40	31·8
clone b	2·98	18·6	clone b	2·17	17·3
clone c	2·58	15·2	clone c	2·27	27·6
Locality 2			Locality 4		
clone a	2·90	18·6	clone a	2·26	24·6
clone b	3·04	17·0	clone b	2·34	23·8
clone c	2·98	19·2	clone c	2·44	27·8

Mean values for A: shaded, 2·93±0·08; exposed 2·31±0·04
Mean values for B: shaded, 17·9±0·6; exposed, 25·5±2·0
[Data from Björkman and Holmgren, 1963]

markedly in respect to both measures. The shade ecotypes are evidently
capable of a more efficient use of weak light than those from open habi-
tats, while those from open habitats can utilise intense light more effi-
ciently. It is important to note that the pre-conditioning of the plants
was such as to ensure a full degree of individual adaptation to low light
in the comparison of efficiency at low intensity, and to high light in the
comparison of rate at saturation intensity. Undoubtedly, therefore, the
differences are genetically based.

Other comparisons of importance made by Björkman and Holmgren are summarized in Table VI. The first observations (A) indicate that the exposed-habitat clones have a marked ability to adapt to the efficient use of strong light, when grown in strong light, lacked by those from shade habitats. The second (B) show that the photochemical response of the clones from open habitats is not affected by light intensity during cultivation, while culture under high light intensity does reduce the initial slope of the rate-intensity curve in clones from shade habitats.

TABLE VI

(A) *Ratios of Photosynthetic Rates at Light Saturation of Plants of Different Clones of* Solidago virgaurea *Grown in Strong Light and in Weak Light.* (B) *Ratios of "Photochemical Capacity" in Plants from the Same Clones Grown in Strong Light and in Weak Light*

	Shaded habitats		Exposed habitats		
	A	B		A	B
Locality 1			Locality 3		
clone a	0·95	0·63	clone a	1·86	1·12
clone b	0·92	0·63	clone b	1·65	0·98
clone c	1·04	0·67	clone c	1·59	1·06
Locality 2			Locality 4		
clone a	0·88	0·65	clone a	2·14	1·11
clone b	0·86	0·66	clone b	1·59	0·94
clone c	1·19	0·61	clone c	2·19	1·00

Mean values for A: shaded, $0·97\pm0·05$; exposed, $1·84\pm0·11$
Mean values for B: shaded, $0·64\pm0·01$; exposed, $1·04\pm0·03$
[Data from Björkman and Holmgren, 1963]

According to Björkman and Holmgren, chloroplasts of plants from shade clones grown in strong light are partly destroyed.

The results of this investigation seem to indicate unequivocally that the sun and shade races of *Solidago virgaurea* do differ in their photosynthetic properties in an adaptive manner. Whatever other selective forces may act upon populations entering these two types of habitat, it is evident that light intensity is of great — probably paramount — importance. The results suggest, moreover, that in this species at least the direct adaptability of the photosynthetic system is too low to permit a single genotype to perform adequately in both open and shaded habitats. It would obviously be informative to compare in this respect the behaviour of a species thought to be more plastic, such, for example, as the *Lysimachia vulgaris* studied by Turesson.

As part of a general investigation of the climatic races of *Mimulus cardinalis*, the Carnegie group (Hiesey *et al.*, 1959, 1960, 1961; Milner *et*

al., 1962) have been examining photosynthetic efficiency in various artificial environments. As reported so far, the work is principally of interest as a study in comparative physiology, since it is not always clear in what way the differences observed can be associated with adaptation to habitat. Two examples of responses observed in experiment which may be related to ecotypic adaptation have, however, been recorded (Hiesey *et al.*, 1960, p. 317). A clone from a high-altitude Yosemite population revealed a saturating light intensity for photosynthesis 1·5 times higher than one from a sea level habitat at Los Trancos; it is suggested that this may be related to a difference in average light intensity in the two habitats. Furthermore, the Yosemite plants were found to make less effective use of high CO_2 concentrations, photosynthesising at optimum temperatures and at light saturation, than plants from Los Trancos, and the possibility is mentioned that this may be concerned with the 15% reduction in CO_2 in the atmosphere at the altitude of the Yosemite race compared with that at sea level. Evidence concerning the effects of pre-conditioning comparable with that available for *Solidago virgaurea* seems not yet to have been obtained, but the first of these observations, so far as it goes, does suggest a similar pattern of racial adaptation to variation in available light to that demonstrated in *Solidago* by Björkman and Holmgren.

E. ADAPTATION TO CLIMATE

It is evident from the pattern of variation in many of the wide-ranging species discussed in Section I that infraspecific differentiation must frequently be dominated by the selective effects of regional climates. The analysis of these effects is beset with formidable difficulties. Those arising from the multifactorial nature of climatic differences have already been mentioned. In addition there is the complication that a diversity of solutions is available to plant populations for adaptation to climatic differences. In the example of habitat adaptation just reviewed, one pervasive environmental factor can be identified as probably having had the dominant selective influence; survival depends absolutely upon the capacity to adapt to it. Where habitats differ in a multiplicity of seasonally varying climatic factors at one and the same time, adaptation in several features may be required to permit survival, while continued existence may equally well be ensured by more than one pattern of response.

Undoubtedly the most powerful means available to the higher plant for adaptation to regionally varying climates is the ability to adjust the developmental cycle. This property is of the greatest significance when a species spans a range of climates differing in the pattern of incidence of unfavourable seasons — hot and dry, or cold. To survive adverse condi-

tions in a suitably protected state of dormancy can obviously be to close to an ideal solution, necessitating the minimum of direct adaptive adjustments of the normal processes of growth and nutrition by ensuring that they progress during the most favourable period of the year.

The adjustment of developmental periodicity to the particular requirements of a local climate is a matter of time-keeping, and it may be supposed that where survival depends on re-timing, selective pressures will develop to bring this about. Since seasonal variations in temperature and daylength provide the most reliable clocks in the plant environment, thermal and photoperiodic responses will thus necessarily become a target for selection, and variation in these responses is therefore to be expected in widely ranging species. We may speak of "photoperiodic" or "thermoperiodic" races or ecotypes in these species, but the adaptation is not of course to the photoperiod or thermoperiod in the sense that these factors are themselves selective; it is that adaptation to local climate has been achieved by the modification of photoperiodic or thermoperiodic reactions. This kind of adjustment by itself may not be adequate to ensure success if more or less inimical conditions prevail even during the most favourable period of the year. Survival may then require the acquisition of characteristics more directly adaptive, as well as the adjustment of periodicity.

As might be expected, the best analysed examples of climatic control of developmental periodicity have concerned bred strains of economic plants, particularly the cereals and biennial root crops. Among perennial species, forage grasses have been extensively investigated, and the work of Cooper (1951, 1952) on *Lolium* and Ryle (1963a, b) and Ryle and Langer (1963a, b) on *Phleum* is particularly relevant to the problem of analysing the environmental control of developmental cycles in ecotypes. The work of Wareing (1950a, b, 1951, 1953, 1954) on the photoperiodic responses of woody species is similarly of great genecological significance.

For the perennial plant of the temperate regions, it is established that temperature and photoperiod — separately or in conjunction — may affect the duration of bud dormancy, the period of leaf formation and stem extension growth, the timing of flowering and fruiting, the cessation of stem extension, and the onset of leaf-fall and resting bud formation. Response to temperature may be immediate, or inductive, as in the case of vernalization; and the reaction may be to the diurnal as well as the annual cycle of temperature change. Photoperiodic effects are mostly inductive. The usual physiological classification of species into "long day", "short day", "day intermediate" and "day neutral" with regard to flower initiation has little direct ecological significance since the important factor in nature is the response to the yearly cycle of daylength

change, not the behaviour under a fixed photoperiod. Valuable reviews of temperature and daylength effects in which ecological aspects are taken into consideration are those of Wareing (1956) and Chouard (1960).

Ecotypic variation in temperature responses has been studied experimentally in several species. Part of the current programme of the Carnegie group (Hiesey *et al.*, 1959, 1960, 1961; Milner *et al.*, 1962) is concerned with this aspect of racial differentiation, in *Mimulus cardinalis*. In an earlier study, Hiesey (1953) has investigated the thermal responses of the aggregate species *Achillea millefolium*. The reactions of cloned material of three races originally grown from seed under standard garden conditions were followed under different combinations of day and night temperature in growth chambers. The races were a diploid maritime one, corresponding to the taxonomic subspecies *arenicola* from a cool Californian coastal region, an interior valley diploid race native to the hot San Joaquin Valley of California, and a high montane race referable to *Achillea lanulosa* subsp. *typica* from an altitude of 8 700 ft in the Sierra Nevada. It may be noted that, strictly, this last race must be regarded as belonging to a separate ecospecies from the first two, having a tetraploid chromosome number, but much of the interest of the study arises from its inclusion. The responses of the races may be summarized as follows:

Coastal. Good growth and flowering was attained in night temperatures of 6° C in combination with 20° C or 30° C days; growth and flowering were inhibited with night temperatures of 17° C.

Interior valley. Good growth was attained with 6° or 17° C night temperature, while performance was slightly better with day temperatures of 20° C than with 30° C. Flowering was delayed somewhat when 6° C nights were combined with 20° C days.

Sierra Nevada. Growth was favoured by 6° C nights compared with 17° C, and apparently by 30° C day temperatures compared with 20° C. Flowering was stimulated by low night temperatures.

Hiesey relates these responses to the climates in the regions of origin. The coastal race, occurring in a region of low night temperatures, is clearly intolerant of 17° C nights, although capable of standing warmer days than the average in its native area. The San Joaquin valley race gives evidence of adaptation in its capacity for survival and satisfactory growth in all combinations of day and night temperature, consonant, according to Hiesey, with "the great amplitude of seasonal temperature variation in its native habitat and its all-year activity". The Sierran race evinces rapid development towards flowering with cool nights and warm days, again showing adaptation to climate in its place of origin, where during the growing season the average minimum temperatures range between 5° C and 9° C and the average maximum from 19° C to

24° C. The rapid development of the Sierran race compared with that from the Californian coast can be related to the much shorter growing season. Hiesey encountered marked variation between individuals in this study, but comments that the differences between the races overshadowed the within-race variation.

Clinal variation in the chilling requirements for bud break in *Acer rubrum* has been demonstrated by Perry and Wang Chi Wu (1960). The red maple has an extremely wide latitude range in North America, from southern Florida to Canada. In the northern part of the range, the frost-free season is less than 100 days, and in the southern no frosts are experienced at all. Chilling responses were studied by Perry and Wang Chi Wu in progenies reared from seed samples collected at eleven stations spanning the greater part of the latitudinal range. Plants raised from parents from southern Florida showed no chilling requirement, and bud break was in fact delayed by chilling treatments. Progeny from parents from the northern part of New York State mostly failed to break dormancy without vernalization, and where growth did occur it was abnormal. Plants from intermediate latitudes showed intermediate reactions. Among the samples grown without chilling at Gainesville, Florida, a strong correlation ($r = 0.96$) was observed between date of bud-break and the duration of the frost-free season at the site of origin.

This study reveals clear evidence of a clinal variation in the red maple in dormancy periods and in response to chilling. The experiments so far reported are not, however, adequate to elucidate fully the relationship between latitude, dormancy period and cold requirement. This would require an analysis of the responses of the populations from the different latitudes to a range of treatments, along the lines marked out in Olmsted's full study of dormancy in the sugar maple (1951).

Ecotypic variation in respect to chilling requirement for the induction of flowering has been demonstrated by Ketellapper (1960) in *Phalaris tuberosa*. Plants were grown from samples of caryopses collected from twelve localities throughout the Mediterranean range. Flowering time under a greenhouse temperature of 17–19° C without effective previous vernalization was observed, and also flowering time following chilling at 4° C at the three-leaved stage for periods of 0, 2, 4, 6 and 8 weeks, with subsequent growth in the greenhouse. A high inverse correlation ($r = -0.94$) was found between the percentage of plants flowering without cold treatment in each sample of *c.* 75 and the weeks of cold treatment required for full induction to flower. The duration of cold treatment required for full induction was also found to be highly correlated ($r = -0.95$) with the average temperature of the coldest month in the locality of origin. Ketellapper is, however, dubious as to the exact role of the cold requirement as a regulating factor for flowering time in the

wild. Under field conditions at Canberra, Australia, the time of flowering was found to bear no very close relationship to the vernalization requirement of the different races, suggesting that in this locality other factors — perhaps spring temperatures and photoperiod — may be determinative. He suggests that an interaction of vernalization temperature, spring temperature and daylength may determine the developmental period in the native areas of the races tested. Nevertheless, that genetical variation in cold requirement does exist and that this can be related to one important climatic parameter does suggest that the vernalization response has been subjected to differential selection in various parts of the natural range.

The role of photoperiodic responses in the adaptation of species of the grasslands of North America to the climates encountered in various parts of their range has been the subject of several studies in the last twenty years. The work of Olmsted (1944a, b) on *Bouteloua curtipendula* remains one of the most satisfactory analyses. *B. curtipendula* has a wide latitudinal range, extending from Mexico in the south to southern Saskatchewan in the north. Olmsted's study was based upon seed samples derived from twelve sites spanning 17° of latitude. Comparisons were made of growth and flowering periodicity under daylengths of 9, 13, 16 and 20 hours and under natural daylength at Chicago. A considerable amount of variation appeared within the samples, but regularities in their behaviour could be distinguished and related to provenance. The periods from germination to first flowering under the various photo-

TABLE VII

Number of Days until first Flowering after Germination on 11 April 1942 of 12 Strains of Bouteloua curtipendula *under Different Photoperiods. [Data of Olmsted, 1944a.]*

Source of seed	Latitude °N	9 h	13 h	Photoperiod 16 h	20 h	Nat. day (Chicago)
North Dakota	46½	—	—	73	69	55
Nebraska	42½	109	—	95	81	73
Nebraska	41½	—	—	95	95	95
Nebraska	40	—	123	123	109	81
Kansas	39½	—	—	109	109	109
Kansas	39	—	109	123	109	109
Oklahoma	37	—	—	95	123	123
Oklahoma	35½	—	73	—	123	109
New Mexico	32½	—	81	—	123	109
Arizona	32	—	95	—	—	—
Texas	29½	—	81	—	—	—
Texas	29½	55	81	95	—	—

periods recorded by Olmsted are shown in Table VII, the strains being ordered according to latitude of origin. The plants of the most southerly origin show a short-day type of reaction, and those from the northern sites are evidently accelerated in development towards flowering by long days. The Oklahoma and New Mexico samples show diversity in response, perhaps as Olmsted suggests because they contain both long-day and day-intermediate genotypes. In respect to vegetative development, the different races revealed a consistent pattern of response: with increasing latitude of origin, growth was increasingly suppressed under the shorter photoperiod. No internode elongation occurred in the primary axis of plants originating north of $39° N$ latitude in 9-h days, and none in plants originating north of $41\frac{1}{2}° N$ in 13-h days. Plants from southern latitudes elongated in all photoperiods.

The study of geographical variation in photoperiodic response in *Andropogon scoparius* (*Schizachyrium scoparium*) by Olmsted's pupil Larsen (1947) revealed a pattern of responses broadly similar to that observed in *Bouteloua*. In a comparison of samples from twelve stations spanning a latitudinal range of $21°$, plants from northern origins were found to be accelerated towards flowering by long days; in the case of *Andropogon scoparius*, however, the southern strains behaved as day-intermediate plants. Again short photoperiods marked suppressed growth in plants from northern localities.

While Olmsted's and Larsen's results were obtained under experimental conditions which cannot be compared directly with any natural situations, they do indicate quite clearly that the differentiation of races adapted to different lengths of growing season in the central grasslands of North America has involved the adjustment of photoperiodic response. The transplant experiments of McMillan (1956a, b, 1959) indicate that several other grass species show similar kinds of ecotypic variation, periodicity being adapted to the south to north decrease in the frost-free growing season and to a similar east to west gradient determined by decreasing precipitation during the later part of the summer.

Photoperiodic adaptation has also been demonstrated in tree species which span wide latitudinal ranges. Vaartaja (1954, 1959) found variation in the responses of northern and southern races in several tree species tested for growth rate and onset of dormancy under various photoperiods. Samples were grown from seed derived from native stands, and the seedlings were exposed to natural daylight for 11 h extended by artificial light to give photoperiods of 12, 14, 16 and 18 h. An example of Vaartaja's results is given in Table VIII, where the fresh weights of the tops of plants of *Betula papyrifera* from two localities, $17°$ of latitude apart, grown for 15 weeks under various photoperiods are

compared. Evidently a critical daylength exists for the northern race between 14 and 16 h below which growth is practically suppressed. The southern race, on the other hand, although depressed in growth by 12-h days, is still reasonably active in the shorter days. Similar responses (although none so extreme) were found in most of the sixteen other species tested; the general rule was that the northern races showed growth inhibition in longer photoperiods than those from southern sources. Vaartaja's results are also of interest in the light they throw upon the photoperiodic control of dormancy in the trees tested. In some species, continued apical growth in the northern races only proceeded under very long days; anything less than 16 h led to early dormancy. In

TABLE VIII

Fresh Weight of Tops (in mg) of Seedlings of Betula papyrifera *from Two Localities, Northwest Territories, Latitude 69° N, and Pennsylvania, Latitude 42° N, Grown for 15 weeks under Different Photoperiods.* [*Data of Vaartaja, 1959.*]

| Latitude °N | Photoperiod | | | |
	12 h	14 h	16 h	18 h
69	2	8	155	372
42	93	110	133	209

contrast, the southern races continued growth at much shorter photoperiods. Photoperiodic control of extension growth in some of the species of *Pinus* tested prevailed for only a matter of 14 weeks after germination; thereafter resting buds were formed regardless of treatment.

Although most of the published studies on the environmental control of developmental periodicity in ecotypes have stressed the role of one variable — temperature or photoperiod — there seems little doubt that in nature the two will always interact. As mentioned in an earlier paragraph, all phases of the developmental cycle, vegetative and reproductive, may be subject to environmental regulation; in addition, innate timing mechanisms may operate to control the length of certain phases or to determine when sensitivity to environmental control is developed. Given that the genetic control of these different regulatory mechanisms is such as to permit continuous quantitative variation (which implies that it should be polygenic) it is apparent that an appropriate response can be built up for almost any conceivable annual climatic pattern in which some period favourable for plant growth occurs. Moreover, the same kind of behaviour may evolve utilizing different combinations of mechanisms; thus a given phenological pattern may depend in one

species on a vernalization response, and in another upon spring photo-
period. This kind of variation could account for the exceptions to the
general rules observed in the studies of Vaartaja (1959) and McMillan
(1959).

We may take as a final example of a comprehensive investigation of
climatic adaptation the study of *Oxyria digyna* by Mooney and Billings
(1961). This work has combined a thorough study of the physiology of
natural populations with the imaginative use of controlled environment
cabinets, with the aim of elucidating the adaptive significance of inter-
population differences. *O. digyna* in North America occurs in the arctic
tundra as far north as 83° N, and as far south as the mountains of Ari-
zona. The populations can be ranked into two primary groups largely on
the presence or absence of rhizomes, the rhizomatous forms occurring in
the northern part of the range, and the non-rhizomatous from Alberta
southwards. Mooney and Billings studied populations from fifteen
localities throughout the North American range, and representatives of
several of these were examined under controlled environment conditions.
The principal comparison was between performances of plants of differ-
ent provenance in two environments simulating "arctic" and "alpine"
conditons respectively. The "arctic" chamber provided growing season
conditions comparable with those of the Alaskan Arctic Coastal Plain at
71° N, with constant light and alternating 12-h thermoperiods of 55° F
and 35° F. The "alpine" chamber simulated conditions in the Medicine
Bow Mountains in Wyoming, with a 15-h photoperiod and alternating
12-h thermoperiods of 65° F day and 40° F night. Growth and develop-
ment were followed under the contrasting conditions, and plants were
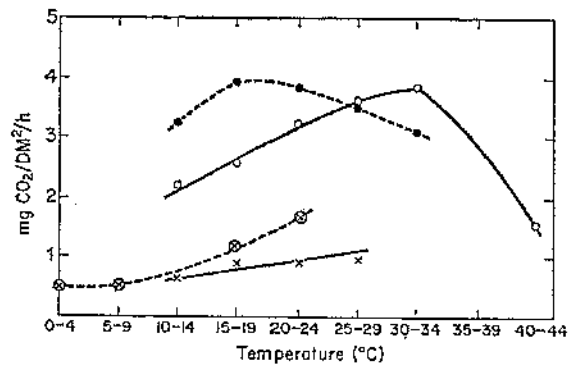

FIG. 5. Average photosynthetic and respiration rates of a southern alpine population
group of *Oxyria digyna* [latitudes 41° 20′ N, 38° 42′ N and 48° 40′ N] and of a northern
population group [65° 28′ N and 69° 50′ N] at different temperatures. Plants grown
initially in the "arctic" chamber, and measurements made in a closed system using an
infra-red gas analyser. From Mooney and Billings (1961). ● photosynthetic rates,
northern group;   ○ photosynthetic rates, southern group;   ⊗ respiration rates,
northern group;   × respiration rates, southern group.

extracted from the chambers as required for the measurement of photosynthesis and respiration.

From the many data presented by Mooney and Billings, a selection may be considered to illustrate some of their principal conclusions.

(a) Plants of northern populations have a higher photosynthetic rate at lower temperatures and attain a maximum rate at lower temperatures than do plants of the southern alpine populations, and,

(b) plants of northern populations have higher respiration rates at all temperatures than do plants of the southern alpine populations.

The evidence is contained in Fig. 5, showing pooled results from three southern alpine and two arctic population samples. The alpine group shows a temperature optimum for photosynthesis at the light intensity used of 30–40° C, and the arctic group, an optimum around 15–19° C, the maximum rates achieved being much the same. The respiration rate of the northern group is not only generally higher but shows a steeper rise with temperature than that for the southern group, indicating a lower temperature compensating point for the arctic populations.

(c) High-elevation, low-latitude plants attain photosynthetic light saturation at a higher light intensity than do low-elevation, high-latitude plants. This is evident from Fig. 6, in which rate intensity curves for a southern alpine and a northern population are compared at 20° C. It is notable that the southern, high-altitude population did not achieve complete light saturation even at 5 200 f.c, whilst the arctic population is saturated at 2 000 f.c.

(d) There is a clinal increase in the photoperiodic requirement for flowering from southern to northern populations. Data illustrating this for four populations from different latitudes are summarized in Table
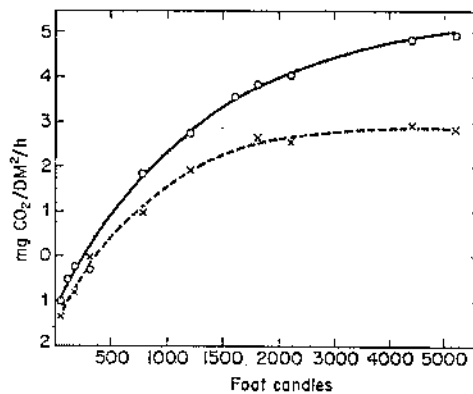

FIG. 6. Photosynthetic light curves at 20° C for a southern alpine population of *Oxyria digyna* [latitude 39° 40′ N] and a northern population [61° 23′ N]. From Mooney and Billings, 1961. ——————— southern alpine population; – – – – – northern population.

IX. It is evident that in response to photoperiod the latitudinal variation follows the same pattern as that discussed above for various grass and tree species.

TABLE IX

Phenology of Oxyria digyna *Plants from Four Populations in the "Arctic" and "Alpine" Growth Chambers. [Data of Mooney and Billings, 1961.]*

| Latitude of population | Percentage flowering after: | | | | | |
| | 4 weeks | | 8 weeks | | 16 weeks | |
	Arctic	Alpine	Arctic	Alpine	Arctic	Alpine
38° 42′ N	20	60	80	100	100	100
41° 20′ N	30	30	100	80	100	100
48° 42′ N	10	0	90	20	100	50
69° 50′ N	30	0	100	0	100	0

(e) The northern populations are substantially less tolerant of high temperatures than are the southern ones. This is illustrated by the summer death rate curves of the northern and southern populations compared in Fig. 7.

In discussing the general performance of plants from the different populations, Mooney and Billings conclude that the evidence indicates a close adjustment to the specific *light* climate of the habitat through adaptations in growth and flowering response, perennating bud formation,
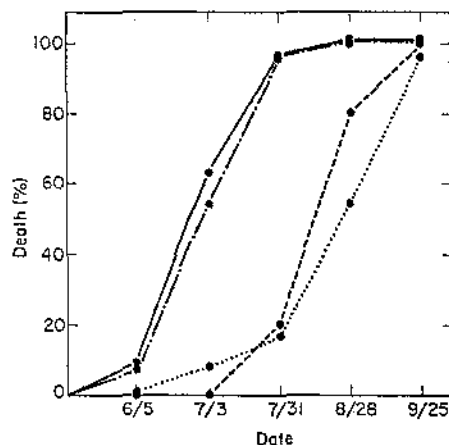

Fig. 7. Summer death rate of plants of two northern and two southern populations of *Oxyria digyna* under greenhouse conditions in Durham, North Carolina. ——————— 61° 23′ N; — . — . — . 68° 56′ N; — — — — 41° 20′ N; . . . . 48° 42′ N. From Mooney and Billings (1961).

and photosynthetic light saturation. Thus, the southern populations revealed a clear adaptation to growth under a 15-h photoperiod, while the northern populations reached active growth only in very long days and were brought into a state of dormancy by 15-h days. In respect to *temperature* they point to the clear adaptive significance of the lower temperature optimum for photosynthesis evident in the high latitude populations, which normally experience summer temperature maxima of less than 60° in their natural environment. The higher respiration rate shown by the northern populations they consider also to be adaptive in permitting rapid metabolic rates to be achieved under lower average day temperatures.

As a physiological investigation of genecological differentiation, the work of Mooney and Billings is exemplary in asking at the outset the essential question "How are the ecotypes related to their respective environments?", and in adopting field and laboratory methods and measurements designed specifically to answer it. Their study should set a pattern for others in this field.

IV. CONCLUSIONS

It is appropriate in conclusion to refer again to the synthetic nature of genecology as a discipline combining ideas and methods from genetics, taxonomy and plant physiology, and to emphasize once more the value of this kind of concerted approach to the problems of population differentiation and adaptation in plants.

An unfortunate trend during the post-war period has been apparent in recurrent attempts to assimilate genecology into taxonomy. Genecological investigations of infraspecific variation naturally tend to reveal facts of potential taxonomic significance, but taxonomic revision is not in itself an essential part of genecology. Should it be substituted for the original aims of analysing patterns of ecological adaptation and elucidating the means by which they are achieved, genecology becomes inseparable from the discipline commonly termed "experimental taxonomy" or "biosystematics". "Experimental taxonomy" seems first to have been used by Clausen *et al.* (1934), in substitution for "evolutionary taxonomy", previously used by Clements and others of the Carnegie group. The term was adopted by Gregor *et al.* (1936), and defined as the classification of evolutionary units on the basis of experimentally derived facts relating to distribution, ecology and cytogenetics as well as to morphology. Valentine (1961) gave a slightly more dynamic version, "the study of evolutionary processes in plants and of the bearings of this study on their taxonomy." "Biosystematics", as "Biosystematy", was introduced by Camp and Gilly (1943), with a broadly similar meaning: "(1) to delimit the natural biotic units and (2) to apply to these units a system

of nomenclature adequate to the task of conveying precise information regarding their defined limits, relationships, variability and dynamic structure''.

By definition, as well as etymologically, experimental taxonomy and biosystematics thus relate to a discipline that is part of taxonomy in the broad sense, which genecology is not. The distinction is no trivial one, since it is now possible to see that a conflict of purposes among students of infraspecific variation in plants has been a continuing source of dispute. Writing with the problems of evolutionary processes in mind, Epling and Catlin (1950) deplore the "conceptual error" which they state has led some workers to express ". . . the inter-relation between population and environment by typification and classification rather than by consideration of the adaptive relations of the interbreeding individuals." What these authors fail here to acknowledge is that to attempt this type of classification is a respectable enough activity when the purpose of a study *is* taxonomic. Conversely, the reservations voiced by Turrill (1938, 1946) about the contribution of genecology to taxonomy are those to be expected from a taxonomist who finds genecological aims and concepts incompatible, in part at least, with the process of perfecting a general system of classification and nomenclature.

Biosystematics (or experimental taxonomy) should accordingly be preserved as something distinct from genecology in so far as there is a difference of aims. Re-definitions of biosystematics which have the effect of making the word practically synonymous with genecology (such as that of Clausen *et al.*, 1945) are therefore undesirable.

This is not, of course, to argue that genecological and biosystematic aims cannot be pursued at one and the same time in any particular study of infraspecific variation, but simply to urge that if they are, they should be recognized as not being identical. Because the purposes of study *are* different, different kinds of evidence are required. Thus, ecological data and observations on genetic systems are a *sine qua non* of genecology, although by no means an essential part of taxonomy. Conversely, the nomenclatural and bibliographical studies which are an obligatory part of any taxonomic study are not necessarily significant for a genecological investigation of a species.

If the taxonomic aspects of genecology have often been over-emphasized, it is equally true that the genetical and physiological phases have been as frequently understressed. Baker's regret (1953) that so few studies of race differentiation up to that time had paid adequate attention to the role of breeding systems is less warranted now that publication of his own papers and Stebbins' fine "Variation and Evolution in Plants" (1950) have alerted authors to the importance of this and other genetical factors, but it is still true that genecological or near-geneco-

logical work is being published that reveals a lack of appreciation of some highly relevant facets of population genetics theory. This is reflected in deficiences in technique, particularly in respect to surveying and sampling methods. In this connection, critiques such as those of Wilkins (1959) and Harberd (1957, 1958), discussed at some length above, are of special note. Morley (1959), discusses the general limitation of survey methods as an approach to understanding genecological variation. Studies of population differentiation, he states, "should attempt not only to demonstrate the *existence* of selection pressure, but also to evaluate selection intensities, to specify mechanisms of adaptation, and to determine the effect of natural selection on population, distribution, structure and number." Genecological surveys "may disclose relationships between features of the habitat and characteristics of the plants, which hint at, or clearly propose, mechanisms of adaptation. Since selection coefficients cannot be measured by such relationships, characters of major importance cannot be distinguished from those of minor, though real, significance". Morley urges the value of the study of natural or artificial populations exposed to selective forces under experimental conditions for the measurement of selection intensities, and refers to work on cultivated plants and man-managed plant communities which has yielded evidence directly relevant to adaptation and population differentiation in wild species. That limitations of space have prevented any consideration of this work in the present review is not to be interpreted as implying that it is not significant for the main theme. Particularly in respect to biotic influences, work on agricultural plants has provided data unmatched as yet from wild populations, and there is every reason to suppose that agricultural experimentation will continue to supply a significant proportion of the evidence relating to selective processes in general.

The experimental study of selection in plant populations should obviously be complemented, where feasible, with investigations of mechanisms of adaptation, and we may expect to see much more effort in this field in the next decade or so. This is ensured, if by nothing else, by the increasing availability of controlled environment equipment, and by the steady improvement of the instrumentation necessary to study plant environment and plant responses. If the effort is to be rewarded by commensurate results in the improved understanding of adaptation and adaptive processes, there is no avoiding the necessity for a careful appraisal of the aims of physiological study of genecologically differentiated populations, and of the appropriateness of the techniques adopted.

This illustrates again the importance of an understanding of genecology as a synthetic discipline. It will be all too easy to deploy sophisti-

cated equipment on ill-conceived programmes generating quite the wrong kind of data, and this will certainly happen if physiological investigations come to be based upon too narrow an acquaintance with the many and complex factors involved in the evolution of plant populations.

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