EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES

I. EFFECT OF VARIED ENVIRONMENTS ON WESTERN NORTH AMERICAN PLANTS

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The experimental studies described in this volume have dealt with a large number of plants from many unlike species and families. These plants have come from a wide range of habitats. The detailed observations on their behavior in very different environments, covering a number of years, have impressed certain facts that seem to be of fundamental importance.

GENERAL PRINCIPLES

There are certain principles that apply generally to all the plant groups studied. These are listed here:

1. The individual plant is subject to the interplay between heredity and environment. When grown under different environments it may be quantitatively changed in various degrees. The changes induced by a new environment give no evidence of permanence, but have been shown to be reversible modifications. Some of these changes in vegetative characters are quite spectacular, yet they never obscure the individuality of the plant, which is retained irrespective of the conditions of altitude, light, and moisture in which the plant is grown.

2. Each individual has as part of its inheritance a certain capacity for modification when grown under different conditions. The modifications vary with different species, different races, and even different individuals from the same local population.

3. Modifications are quickly induced. Meristems developing under the changed environment seem immediately to give rise to organs with the modified characters. No evidence suggests yearly cumulative effects on perennial transplants.

4. Variation, of course, is of two sorts: that which is controlled by the environment (modifications), and that which is governed by

the heredity (genetic differences). Both contribute to the differences seen, not only between species and races, but also between individuals of one population. It is essential in following such investigations to keep clearly in mind the distinctions between these two sorts of variation.

5. Each species is composed of an assemblage of races, some of higher order and regional, others more local, graduating down to the individual population and its local variants. The races, regional or local, require many experimental data for their delimitation and elucidation.

6. Species with the widest distribution are observed to have the most races. Conversely, species of narrow distribution have fewer races and are less variable. For example, species exclusively of the lowlands or of high elevations have few distinct races, while those found in both situations have many. Wide latitudinal distribution, or occurrence at both coastal and interior situations, has the same effect, as shown both by Turesson (1930a) and by ourselves. Greater differentiation into regional races may therefore be expected in areas with more varied topography and climate, as, for example, in the Pacific Coast states.

7. The regional races of a species are heritably distinct ecotypes, not modifications. Detailed studies, involving records of hundreds of individual plants and their clone members grown simultaneously at different altitudes, show conclusively that there is no tendency for lowland and alpine plants to become morphologically identical when transplanted to the same garden, whether this be situated near sea level, at mid-altitudes, or at timber line. The dwarfing of lowland plants at high altitudes sometimes causes them superficially to simulate alpines, but their essential structural differences are retained. Moreover, physiological differences, as expressed in earliness of flowering and in capacity for survival in specific environments, are often accentuated in such experiments. These conclusions are based on experiments lasting from four to ten and even sixteen years.

8. The regional ecologic units of a complex are in some cases ecotypes, and in others ecocpecies. The two sorts of units—ecotypes and ecocpecies—are ecologically equivalent, but there is an important evolutionary difference between them.

9. The morphological and physiological differences between ecotypes of one ecocpecies may far exceed those between neighboring
ecotypes of two related ecosspecies (see Achillea, fig. 122, as an example).

10. Each ecotype or ecosspecies has a certain range of tolerance for varying environments. This follows from the capacity of their component individuals to adjust themselves to a range of conditions. The degree of tolerance for different environments is a characteristic of the ecotype.

11. The number of ecotypes or monotypic ecosspecies into which any ecosspecies of a geographic province is differentiated is relatively limited. This follows from the fact that each has its latitude of tolerance. In a transect across central California no more than six or seven regional ecologic units are required in any one ecosspecies.

MODIFICATIONS

This volume is replete with examples of modification. Each figure that shows members of a clone as they appear growing at Stanford, Mather, and Timberline illustrates it. We have spoken of the Stanford modification of a plant, for example, meaning the total impression of the Stanford environment on that individual, for modifications affect not only various structural characters but physiological processes as well.

One may interpret modifications from the viewpoint of Klebs (1909), and consider form to be a function of physiology, and the appearance of a plant to be the result of the interaction of environment upon physiological processes—subject, of course, to the limits set by heredity. Essentially the same idea has been expressed by various authors. These include Kerner (cf. p. 205), Raunkier (1895—1899, p. xvi), and Johanesen (1911). On the basis of the early results of the present investigations, Hall (1932) also discussed the interrelation between heredity and environment.

It is well known that changed temperature, moisture, and light relations will modify the velocity of physiologic processes. It is therefore quite natural that modifications in morphological characters and in manner of development take place in response to transplanting to different environments. Although such modifications may be linked with the tolerance of plants to changed environments, the evidence indicates that ecotypes as a rule are unable to succeed in conditions very unlike those of their native environs.

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Physiological characteristics subject to modification include the time of inception of growth following winter dormancy, the rate and duration of growth, the ability to flower, the time of flowering, and the ripening of seed. Numerous examples have been cited of modifications in seasonal rhythm, including the observation that plants at Stanford begin spring growth two to three months ahead of propagules of the same individuals at Mather, which, in turn, are equally advanced over those at Timberline. Instances may be recalled of plants from the vicinity of the coast which are continually active at Stanford, but which have a definite period of dormancy at Mather. The opposite instance is just as interesting, with the alpine forms of Hordeum jubae dormant in their native habitat, but assuming the evergreen habit at Stanford. Another spectacular modification is growth habit: it is the change of the semi-shrubby coastal Zauschnerias to perennial herbs at the mid-Sierra station.

The distinction between modifications and hereditary differences was clearly stated by Baur (1914, p. 10), and Turesson (1922b) emphasized the fact that modifications may closely resemble heritable variations. That modifications and heritable variations have been confused by many botanists is evident in the literature. There has been a paucity of evidence showing to what extent plants may be modified in different kinds of environment, and how modifications compare with heritable variations. These comparisons have been emphasized in the preceding chapters, for such a study is fundamental to an understanding of plant interrelationships, and of plants in relation to their environment.

THE PRINCIPLE OF REGIONAL DIFFERENTIATION

In all species complexes that cover climatically different areas, the phenomenon of regional differentiation stands as a fundamental principle. Its operation has already been shown by Turesson in many European species of plants. Our results from west American groups not only substantiate Turesson’s general conclusions, but also add many facts. These have come to light largely because the transplants were studied at three altitudes instead of at one only, and because the environments in California are very different from those of northern and middle Europe.

The latitude of the California transect is that of the southern
Mediterranean. There is also considerable geomorphological difference between California and middle Europe. The California mountains follow a north-south direction transverse to the prevailing winds. They parallel the coast, rarely leaving room for an extensive coastal plain. The mountains of middle Europe follow an east-west direction and are distant from the sea. Therefore, as compared with the region from which Tüxen's plants came, the California region has more climatic belts which change rapidly and abruptly as one moves inland from the ocean.

The distribution of ecotypes and ecotypes. Regional differentiation may be expressed either as a series of ecotypes belonging to one species, or as a series of closely related ecotypes, or, more commonly, by both. Whatever the means of differentiation, the ecological result is the same, namely, that each climatic region is occupied by forms particularly suited to that environment. In Potentilla glandulosa, and probably in Sanguinaria bellum, one species has been able to occupy almost the entire transect across central California by a simple differentiation into ecotypes; in the Achillea millefolium complex the same transect has been covered by two ecotypes, and in the Artemisia vulgaris complex by three, some of which are differentiated into ecotypes.

Ecotypes and ecotypes of one complex frequently cover this area rather continuously, substituting one for another. The belts they occupy fluctuate in conformity with topographic irregularities and resultant climatic changes. This complicates their distribution and causes a moderate amount of overlapping. Where ecotypes or ecotypes of one complex meet, they may occupy locally different habitats, as in Potentilla glandulosa, where the foothill ecotype, ssp. reflexa, occupies the drier slopes, while the meadow and subalpine ecotypes, ssp. Hansenii and nevadensis, tend to occupy the moister meadows. Hybrids are found at such localities.

Differences in distribution of species. There are great differences in the capacity of species and complexes to occupy this area. This is shown in figure 154, which illustrates the distribution of the Potentilleae along the transplant transect in central California. Potentilla glandulosa occurs in the Coast Ranges from near sea level upward, but avoids the lowest altitudes of the interior valleys. It reappears in the Sierra Nevada at 225 m. and is a characteristic occupant of moist draws, open meadows, and slopes up to over 3350 m. On the eastern slopes of the Sierra Nevada it grows only at high altitudes and does not occupy the Great Basin except in the mountains.

Potentilla gracilis, on the other hand, is not found in the central Coast Ranges, but covers the Sierras from about 1000 m. to alpine altitudes on the west slope and occurs even in the Great Basin. A related ecotype, P. diverfolia, is restricted to alpine conditions, and another, P. pectinacea, occupies only the dry Great Basin. A characteristic difference between the members of the glandulosa

![Graph showing altitudinal distribution of certain Potentilla species](image)

and the gracilis complexes in California is that the latter do not approach the coast, but are able to populate desert flats east of the Sierra, while those of glandulosa flourish only on the west-facing slopes.

The Potentilla Drummondii complex is an example of a group restricted to subalpine and alpine altitudes. One of its species, P. brevifolia, is strictly alpine. In the genus Hordeum, a Sierran species, fusca, occurs from mid-altitude to alpine conditions, whereas other species, like H. californica and cusnea, are found only in the coastal region. Similar differences in the capacity of species to occupy various climatic belts of California were discussed in chapter VI for Zauschneria, and for other groups in other chapters.

The Lower Sonoran zone, in which the Great Valley of California
is located, is usually not occupied by the perennial herbs that entered into the transplant experiments. It is too dry and hot for this mainly northern floral element. Annual members of the Madroño, a subtribe of the Compositae extensively studied by us, occupy these valleys and the Sierra foothills, the Coast Ranges, and the maritime zone, but they have been unable to occupy the higher elevations. We know of no one species that has developed races for both the alpine and the Lower Sonoran zones.

**Parallel differentiation in non-adjacent areas.** Can a species develop parallel ecotypes in different parts of its range, where corresponding ecologic opportunities are offered? Several examples suggest an answer.

The alpine *Potentilla glandulosa nevadensis* is mainly restricted to California and Oregon, but in the alpine regions from Washington to Montana it is replaced by ssp. *pseudoruspestris* and in southern Utah and Arizona by ssp. *arizonica*. Only *pseudoruspestris* appears to be directly related to *nevadensis*. In the southern Rocky Mountains the role of the alpine ecotype has been taken over by another species of the same complex, *P. fiata*, although forms of *P. glandulosa* occur near by at lower elevations.

*Potentilla gracilis* has an alpine ecotype in the Sierras, but farther east it extends only to subalpine elevations; the alpine altitudes in the Rocky Mountains are occupied by its close relative, *P. pulcherrima*. *Artemisia ludoviciana* and *Achillea lanulosa*, however, have similar alpine forms in both the Sierras and the Rockies.

A composite analysis of a number of ecotypes in addition to those from California would be necessary before any suggestions could be offered as to causes for differences in distribution of west American alpines.

Turesson (1925, 1931b) pointed out that some species that cover the mountainous regions in both Scandinavia and central Europe have developed alpine ecotypes in only one of these areas, whereas other species have alpine ecotypes in both. *Melandrium rubrum* and *Soldago virgaurea* have alpines only in Scandinavia, *Silene noctiflora* and *Trifolium pratense* only in the Alps, although all four are common in both areas.

**Minor differentiations within ecotypes.** Each of the regional ecotypes contains a complex of biotypes. Not only is there consider-
1. The maritime and Coast Range ecotypes (or ecocpecies) are in more or less active growth throughout the year at the lowland station. If they have a rest period, this is usually in the late summer, and new growth begins with the advent of winter rains.

2. They flower early at Stanford, but are delayed at the mountain stations.

3. Frequently their herbage is relatively frost-resistant, a characteristic which enables them to grow during the cool rainy winters.

4. When transplanted to Mother, they usually become reduced in size. Coast Range ecotypes tend to survive indefinitely there, whereas maritime ecotypes and ecocpecies as a rule succumb within a few years.

5. They are unable to set ripe seed at Timberline, and rapidly decline there and die, although the harder species may survive a winter or two.

The perennials discussed in preceding chapters usually have coastal ecocpecies rather than maritime ecotypes. An exception is Siegesbeckia bellii. The coastal ecocpecies have been less extreme in their morphology and less restricted in their distribution than the truly maritime ecotypes observed in the annual Madiaea.

The latter are prostrate or short-stemmed and limited to bluffs and slopes directly facing the ocean.

**Foothill and Mid-Altitude Forms**

Most species have one or the other of these ecotypes, but some, such as Potentilla glandulosa, have both.

1. The foothill forms have a short period of dormancy at Stanford during the winter months, and a long rest period at Mother.

2. The mid-altitude ecotypes flower later at Stanford than the Coast Range ecotypes, but they are earlier at Mother.

3. Their herbage is not frost-resistant, so these ecotypes become dormant when frosts begin.

4. Usually they reach their maximum growth and are tallest at Mother; if they survive at the alpine station, they are much reduced.

5. At Stanford they may survive well, but some are attacked by disease. At Timberline they flower too late to produce ripe seed, or fail to reach the flowering stage (Eranthis), or even fail to survive.

**Subalpine and Alpine Forms**

These ecotypes differ from each other in size and extent, the alpines being the dwarfer and the earlier.

1. Both have a definite period of dormancy even at the lowland station—longer than that of mid-altitude forms. An exception is Rhexia fascia, which becomes evergreen at Stanford.

2. Subalpines are usually a little earlier than mid-altitude forms at all stations, while alpines are considerably earlier. In some groups, the alpine and subalpine ecotypes are unexpectedly delayed in flowering at Stanford, but not at Mother.

3. Alpines are often more frost-resistant than subalpines, and usually consid-

erably more so than mid-altitude forms. There is often great individual variation in this respect.

4. All subalpines and most alpines increase in height and vigor at the mid-altitude station. At Stanford their vigor and stature are lessened, as a rule.

5. Both the subalpine and alpine ecotypes survive at Timberline, but only the latter matures seed there every year. Races of some species that are native around the alpine station mature only in exceptionally long seasons and are considered to be subalpines that are pioneering in an alpine environment. At Stanford both ecotypes may survive, but many alpines are short-lived and not very floriferous, and may even remain vegetative for years. Some are attacked by diseases, and many emerge from their winter dormancy in a visibly weakened state, but regain strength during the summer.

**Great Basin Forms**

Data from Great Basin forms are not as complete as from the others. In general, they react much like mid-altitude plants. They are, however, more frost-resistant, and usually survive better at Timberline, even though they are unable to mature seed there. Most of them thrive at Mother, but Potentilla recta is an exception in being notably weak at this station. At Stanford Great Basin forms grow and survive fairly well.

**Plants from High Latitudes**

Plants of certain species from high latitudes in northern Europe were found to grow well at Stanford, including Achillea millefolium, Artemisia vulgaris, Viole comin, and V. Riviniana. Others show a marked decrease in size and vigor, as, for instance, Potentilla recta, Euphorbia purpurea, Carex medvediana, and Dryas boopis eucan. Also Achillea berolita from Alaska.

**The Basis for Regional Differentiation**

Regional differentiation of the species complex to fit various climatic zones appears to be general. The transplant experiments have shown that the regional races are not environmental modifications, but are heritably different. Whenever the ecotypes have been tested by breeding, as in Eranthis, Potentilla, and in many unpublished cases of Madiaea, they have proved to be constant in that they reproduce their kind. What is the basis for the differences between ecotypes? Are genic or chromosomal differences involved, or both? Of the perennial plant groups investigated, most have both genic and chromosomal differentiation, but in some cases species with a constant number of chromosomes occupy very different environments. Changes in the number of chromosomes are, of course, basically
genic, for the complex balance among all genes in all the chromosomes is altered. This viewpoint has been crystallized through the results from the investigations on Datura (Blakelee, 1931).

Differentiation without differences in chromosome number. Potentilla glandulosa is an outstanding example of genic differentiation alone. The genetic differences between its alpine and foothill ecotypes have been discussed (see pp. 116-124). It was determined that both morphological and physiological characters showed genic segregation, and that such characters evidently depend upon a series of genes with minor effect. The existence of genetic linkage between taxonomic characters and those of importance for survival of the ecotypes was also pointed out. Similar complex segregations were observed in hybrids between ecotypes of Zauschneria. These and unpublished experiments on hybrids between ecotypes of Madia indicate that differentiation is produced by numerous genes of the multiple type, each with a cumulative effect. Mutations and hybridization may have worked hand in hand to produce regional differentiation. Furthermore, absorption of genes from related ecotypes may contribute to the variation.

Differentiation with differences in chromosome number. When the chromosome number changes, free intercrossing between the groups is prevented, and a species difference has been set up. Within a conspecific, differences in chromosome number ordinarily mark the limits of ecotypes. Such differentiation may sooner or later become accompanied by genic differentiation.

A summary of the results of both kinds of differentiation from the more important groups in central California that we have investigated is shown in figure 155. This diagram is intended to represent the approximate distribution of each species complex along the transplant station transect, the extent of its ecotypes or ecosecies, and the chromosome numbers. Three cases of simple genic differentiation without change in chromosome number are represented.

The first complex that is represented by only one chromosome number is Stipastrum bellum. It probably constitutes a single species that has differentiated ecotypes for maritime, Coast Range, mid-altitude, alpine, and Great Basin environments. It is still an open question whether a distinct subalpine ecotype can be recog-
nized in this species, hence the wavy line in that zone. Some of the
ectotypes of *Siegheimia* are shown in figure 141.

The second example is *Penstemon procera*. This species does
not occur in the Coast Ranges, but mid-Sierran, subalpine, alpine,
and Great Basin ecotypes are found. Some of these are shown in
figure 107.

*Potentilla glandulosa* furnishes the third example, and has pro-
duced ecotypes for all the major climates in the region except the
Great Valley and the Great Basin, although its maritime ecotype
is no more than incipient. The overlapping of foothill and subalpine
ecotypes is indicated, but the more limited meadow ecotype, which
occurs in this zone of overlapping, is omitted. Illustrations of its
ecotypes are found in chapter II.

The other cases indicated in the graph represent species complexes
in which the chromosome number changes somewhere along the
transcet. Differentiation in these involves both ecospecies and eco-
types. The examples studied happen to be all of the polyploid type,
none being "aneuploid" or dysplloid (a term coined by Tischler,
1937a).

*Zauschneria* is a ecospecies with a diploid ecospecies, *Z. cana,*
in the coastal region, and a tetraploid species, *Z. californica,* from the
coast to subalpine altitudes. The diploid species is monotypic, but
the tetraploid is differentiated into a maritime ecotype, *spp. angusti-
folia,* a Coast Range ecotype, *spp. typica,* and a mid-altitude ecotype,
*spp. latifolia.* The last-named form extends upward to 2700 m., but
it is rare above 1800 m. and all its members in the experiments react
the same way as mid-altitude plants. These units are shown in
figures 84 and 85.

The ecospecies *Viola purpurea* was not mentioned in the previous
book, but it is the subject of papers in preparation by M. S. Baker
and J. Clausen. It contains two ecospecies, a tetraploid in the Coast
Ranges and Sierran foothills and a diploid in the Sierras and the Great
Basin. The latter has developed morphologically distinguishable
mid-altitude, subalpine, alpine, and Great Basin forms; therefore, in
this ecospecies the greatest variation and ecologic adaptability are
shown by the diploid species, not by the tetraploid as in *Zauschneria.*

In the *Aster ascendens* complex there are at least two members
in a polyploid series. In this case it is the Sierran species that is
tetraploid, whereas the supposedly primitive diploid species is found
in the climatically extreme Great Basin. The tetraploid includes
mid-altitude, subalpine, and alpine ecospecies (see fig. 140).

In *Artemisia* there is again a new pattern. The diploid *Subaskarii*
is strictly maritime. The tetraploid member of the complex, *A.
laudoviciana,* is a species of the Great Basin and the Great Plains,
but it has developed a high-montane ecospecies. This ecospecies is
subalpine in transplanted reaction, not alpine. The hexaploid *Douglasii-
dana* occupies the zones between the diploid and the tetraploid species
from the coast to mid-altitudes in the Sierras, including even the
Great Valley. It appears to consist of only one ecospecies, although
it occupies climatically different zones. Figures 128 and 129 show
examples of the *Artemisia* complex.

The Achilleas of the *willifolium* complex are differentiated into
a tetraploid and a hexaploid ecospecies with no diploids known.
The hexaploid *A. borealis* occurs from the coast to the Sierran foothills,
being absent in the Great Valley. It has a distinctly maritime and a
Coast Range ecospecies. The tetraploid *A. lanulosa* has developed the
usual three Sierran ecospecies in addition to the one in the Great
Basin (see figs. 117, 122).

*Herbella* *californica* (fig. 83), which is tetraploid, and *H. cuneata,*
which is diploid, are maritime species. The diploid has been able
to produce a Coast Range ecospecies, while the tetraploid has not.
Neither of these occurs in the Sierras, but the diploid *H. juncea* (fig.
78) is found at higher elevations there, and covers an appreciable al-
titudinal range, although it appears to be composed of only subal-
pine and alpine ecospecies. The basic chromosome number in this
genus is 14, as compared with 7 in *Potentilla.*

The Potentillas of ecospecies *Drammondii* and *gracilis* present a
picture of chromosomal irregularity with high polyploidy, which is
presumably associated with facultative apomixis. They vary in
chromosome number within the ecospecies and even within the popu-
lation. Most remarkable is the fact that the ecospecies are fairly well
differentiated in spite of the oscillating chromosome number.

In ecospecies *Potentilla Drummondii* the dea- to 14-ploid *P.
Breveri* has evolved only an alpine ecospecies (see fig. 72). *Potentilla
Drummondii* has, however, developed both subalpine and alpine ecospecies
(fig. 71). There is probably no significant difference between the
chromosome numbers in the subalpine and the alpine ecospecies.

In the ecospecies *Potentilla gracilis* the only member that is ey-
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Tologically regular is Potentilla pectinifera (see fig. 53, lower), a hexaploid species of the arid Great Basin. Members of this ecospecies with high and oscillating numbers are found in the more mesophytic climates of the Sierra Nevada and other ranges.

Potentilla diversifolia (see fig. 55), another member of the gracilis complex, has evolved only an alpine ectype, whose chromosome number varies from 12- to 14-ploid. Potentilla gracilis (fig. 49) has the greatest variation in chromosome number of any member of its complex; it has also the widest altitudinal and geographical distribution. Four major ecotypes are found, ranging from the nona- to 16-ploid mid-altitude ectype, through the octo- to 12-ploid subalpine and alpine ecotypes on the west side of the Sierras, to the Great Basin ectype, in which 12-ploid forms have been found. In this species there is some tendency for plants with the highest chromosome numbers to be found at lower elevations. All the four ecotypes of P. gracilis belong to one morphological subspecies.

The examples summarised in figure 155 present an illuminating picture of the variation found in nature. No two plant groups in this list, which covers the main subjects of these experiments, have identical patterns of distribution. Scarcey two are closely similar. Yet, the major ecotypic differences are found over and over again in slightly different patterns.

Turesson (1925) found four regional hereditary adjustments in plants of central and northern Europe. These were the maritime, lowland, subalpine, and alpine ecotypes. The chromosome numbers of most of these have not yet been systematically determined, although, according to a recent paper (Turesson, 1938), twenty-five of the species appear cytologically constant over large areas. In addition to these a few polyplid complexes similar to the Californian were found. Such complexes were Galax odorata latifolia with a tetraploid race (n=18) in Bavaria and a diploid (n=9) farther north in Sweden and Latvia, and Sedum telephium, which is diploid (n=12) in the vicinity of Vienna, Budapest, and Moscow, and tetraploid (n=24) in Sweden and Siberia. From these data it is therefore impossible to determine accurately to what extent polyplidly has been a factor in ecological differentiation in northern and middle Europe.

HAS CHROMOSOME NUMBER AN ECOLOGICAL SIGNIFICANCE? It is obvious from this survey along the transplant transect that closely related plants differing in chromosome number usually occupy different environmental niches. The groups do not agree as to where the cytologically primitive forms with the lowest chromosome numbers are located. In some instances they are along the sea, in others in the high mountains, and in still others in the desert. From this the conclusion is reached that the hereditary differences observed so generally in plants along the transect are not correlated with differences in the number of their chromosomes, but strictly with the environment.

This view becomes still more evident as we study the literature bearing on this subject. Until very recently an opinion has been rather widespread that in polyplid complexes, forms with the higher chromosome numbers occupy the more adverse environments. Recent literature, however, is replete with examples that substantiate the observations made in the present investigations that there is no support for this view.

The correlation between differences in chromosome number of closely related species and their ecology was first brought to attention by Hagerup (1927, 1938, 1939) in his investigations on Euphrasia, on the Ericaceae of arctic and middle European distribution, and on other plants from the southern part of the Sahara. From this study he concluded that polyplidness is associated with extreme or unfavorable environments. However, after discovering that in the Vaccinium uliginosum complex the diploid form microphylla is strictly alpine, while the tetraploid angustissima is arctic and northern temperate, Hagerup (1939) altered the formulation of his theorem to read: "Polyplid forms may be ecologically changed so as to grow in other climates and formations where the diploid form will not thrive." There is nothing in our findings to conflict with this statement.

Slomovitz (1933), Tischler (1936, 1937a, 1937b), and Rubczer (1930, 1937) have emphasized that maritime plants tend to have high chromosome numbers. That this is no general rule is shown by the present investigations, where the coastal species are diploid in three complexes and tetraploid in only one. The investigations on chromosome number and distribution by the Tischler school are based on statistics in which a chromosome number is assigned to each species as a whole, not on counts of races from distinct habitats.

The risk one assumes in determining the chromosome number of a species by counting only those of one race is clearly shown in the investigations by Masson (1934, 1937) on Bartschella herpetica. This proved to be a complex that has a diploid species in the nonglacial lowlands of middle Europe and a tetraploid species in the Alps. Grössinger (1937) found similar cytological differences in Arenaria serpyllifolia, but here the distribution was reversed: the alpine subspecies was diploid, while the lowland and subalpine forms were tetraploid. Fagerlind (1937, p. 354) discovered that Galium verum and G. mollugo similarly are

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ploidy complexes. Here the diploids are southern, and center in the Balms, while the tetraploids are found in middle Europe, Scandinavia, and England. But in the *Campanula rotundifolia* complex (Böcher, 1936), the more southern forms from Denmark are tetraploid, while the arctic forms from Greenland are diploid and tetraploid, as in *Vaccinium uliginosum*. An example of chromosome difference between the American and the European components of a circumpolar complex is *Potentilla fruticosa*, which is diploid (n=7) in Alberta, Canada, and tetraploid (n=14) in islands of the Baltic, near the type locality (Turecows, 1935).

Another example of correlation between chromosome number and distribution is the *Iris versicolor* complex of the eastern United States (Andersen, 1930). *Iris versicolor* is the most northern and has the lowest number of chromosomes (n=19), *I. virginica* (n=33) is the most southern, and the allopolyploid *I. versicolor* (n=51) is found between its supposed parents. Another pattern of distribution was observed in *Tradescantia* (Anderson and Sx, 1936), with the diploid and the tetraploid forms coexisting. No morphological differentiation had taken place between diploids and tetraploids in this genus.

The extensive literature on the subject of polyploidy has recently been discussed by Müntzing (1936). Further examples have been mentioned there. In evaluating his conclusions it must be remembered that Müntzing's definition of allopolyploids (p. 31f) would include many allopolyploids whose parents belong to different species.

Generalizations based on few examples should be considered critically. Suggested correlations between chromosome numbers and size, environment, earliness, and other characteristics of plants have proved to be specific, not general. Examples of contradictions to commonly accepted trends include the octoploid *Artemisia Rothrockii* of the high mountains, which is earlier than its close diploid relative, *A. Bolanderi* of the desert flats. Likewise, *Potentilla diversifolia* is distinctly earlier and more dwarfish than the closely related alpine *P. gracilis*, although its chromosome number is higher. On the other hand, the diploid *Artemisia Sukkertolki* is earlier than its tetraploid and hexaploid close relatives, but it is of maximum size.

If we relate these results to the actions of the genes in the chromosomes rather than to an effect of the chromosome number itself, then it is quite understandable that polyploidy does not have the same effect in all plants. With many genes in action, some delaying and others accelerating the processes, and some decreasing, others increasing the size of plants, it is to be expected that autopolyploidy will produce different effects, depending upon the kind of genes in preponderance in the original stock.

Balances of this nature probably determine the fate of the poly-

ploids. Doubling of all genes in an autopolyploid would be expected to shift the physiology of the plant, because the balances are so delicate. If this happens, the plant may be able to occupy a new environment. Differential selection then may effect secondary changes in morphological appearance, so that the polyploid may become a distinguishable taxonomic species. This differentiating factor is not operative if the diploid and the polyploid remain in the same environment, and a situation results like that in *Tradescantia*.

An allopolyploid similarly depends upon the balances in the genome of its parental species. Because of the many genes involved, we should expect an allopolyploid ordinarily to be intermediate, both in appearance and in physiological makeup. We usually find it lodged between its probable parents in nature. It may even crowd out one of its parents or another member of the same species.

The discovery of a high percentage of polyploids in perennials from the Sierran tract has aided in solving some of the difficult taxonomic problems. It also impresses us with the probable importance of polyploidy in plant evolution in certain environments. When Winge (1917) published his theory on the origin and importance of chromosome numbers, it was impossible to foresee how fruitful the study of polyploidy would become within the next twenty years. We do not yet know whether polyploidy is equally frequent in all environments. Investigations on plants from other parts of the world in different environments with different geologic histories are needed before this question can be answered.

**EQUILIBRIUM BETWEEN PLANT AND ENVIRONMENT**

Natural selection doubtless determines the character of the plants that occupy a given environment. Since physiological processes, which change in rate with differences in temperature, moisture supply, and other external variables, are profoundly influenced by environment, successful plants must be fairly accurately adjusted to their surroundings. When they are removed from this environment and brought to a climatically different region, their physiological processes will act at a pace determined by the physical conditions of the new environment, and by heredity. If the plant's heredity is such as to enable it to accommodate itself to the new environments and to compete, the plant may prove to be a success in the new climate.
It may be more or less successful than it was in its original home, depending upon the accuracy of its adjustment to the new surroundings. The chances are, however, it will be less successful, because its very existence in its original habitat bears testimony to its superior suitability for that kind of situation as compared with plants that are not found there.

In the earlier chapters, many examples of disturbances in equilibrium between transplanted individuals and their new environments were described. Among the most conspicuous examples were lowland plants that were unable to complete their annual cycle in the alpine environment, and alpines that grew with much reduced vigor and flowering in the lowland environment. Furthermore, certain plant groups are more specialized in their requirements than others. Some alpines, for example, are distinctly unsuccessful when brought to the mid-altitude station at Mather, while others become even more vigorous than in their native alpine environment. In the latter instance we infer that it is not the physiological unsuitability in itself that keeps them from occupying the mid-altitude environment, but some other factor, such as competition from genetically taller races.

The reaction patterns observed after transplanting various groups of plants indicate that the interrelation between plants and their environment is very complex. No two plants are exactly alike in this respect, although they arrange themselves into certain major groups according to their reactions.

RELATION BETWEEN INTERNAL AND EXTERNAL EQUILIBRIA. Not only must a plant be in equilibrium with its environment in order to succeed, but its entire gene activity must be in balance. Even a single pair of genes of the sublethal type may throw the physiologic processes entirely off balance, but individuals with such genes face elimination by selection. Hundreds, possibly thousands of genes interact in each individual, all influencing the plant slightly in one direction or another. Of necessity, all processes regulated by them must be synchronized in the proper order and adjusted to the environmental conditions if the plant is to succeed.

Experiments have shown that the ecotypes is composed of a group of individuals that can exchange genes with each other without disturbing this internal balance. Considering the great morpho-

logical and physiological dissimilarities between alpine and foothill ecotypes of a species like Potentilla glandulosa, one wonders that a system so intricate can be so well synchronized.

Each ecotype represents a different equilibrium. When two species exchange their genes the balance is upset, as for example in the hybrid of Eosaccharina camas × septentrionalis (fig. 102) and scores of Madiinae and Viola hybrids.

In view of these exacting requirements, it is understandable that evolution is a slow process. It is to be expected that a certain inertia against changes may be experienced in a system of this nature, for it is not a simple matter to develop a new equilibrium to meet the demands of an environment. The very nature of the double demands of internal balance and fitness to the environment is evidently the most important cause of the apparent discontinuity in nature.

APPLICATIONS TO CROP BREEDING. Cultivated plants have to meet essentially the same requirements as plants in the wild. They have their ecotypes or agrotypes just as the wild species have. In general, the more they resemble wild plants in being able to take care of themselves, the more successful they will be. Crop plants have some advantage over those in the wild through the removal of competing plants, and through benefits from cultivation practices. However, these factors merely modify, and do not alter, the operation of the principles outlined above.

The transplant experiments suggest that yield depends to a large extent upon the adjustment between a plant's heredity and its environment. The problem of the breeder is to produce strains to fit a given environment. The unpredictable reactions observed in the transplant experiments indicate the need for test stations located in environments generally similar to those in which the crop is to be grown.

THE NATURAL UNITS

The ecotypes and ecoceses are the natural ecologic-evolutionary units. They are built from many genes into complex morphologic-physiologic-cytogetic systems. Both ecotypes and ecoceses may differ by many morphologic characters, in addition to many of a purely physiological nature. Each character is usually determined not by one but by many genes, each with minor cumulative effects, giving a blended type of segregation. There is no fundamental dif-
ference between ecotypes and ecotypes with respect to their gene
differences. These so-called modificatory genes may be the most
important in evolution—a conclusion reached by Baur (1924, 1932),
Tanner (1925), and East (1935).

Ecotypes are grouped into ecospecies, and ecospecies, in turn, into
cenospecies. The cenospecies is made up of the ecotypes of one or
more ecotypes. Its ecologic subunits occupy separate niches within
the area of the complex. Gene exchange is still possible between
these subunits, but not between different cenospecies. This makes
the cenospecies a unit of superior evolutionary importance. In most
cenospecies evolution is probably still going on. Related cenospecies
are only able to add their genes by the rare formation of new species
through allopolyploidy.

A species with many ecotypes is for evolutionary purposes a more
flexible unit than a series of monotypic ecotypes. The least flexible
pattern of differentiation is a series of monotypic cenospecies.

Species building requires many tools. Simple gene changes are
among the first of these. They are expressed in gradual morpholo-
gical differentiation. Natural units are found that represent transi-
tional stages of genetical and morphological separation. Some eco-
types are still imperfectly differentiated, while others are on the way
to becoming independent ecotypes. From the presence of all stages
of differentiation in nature, we infer that purely genetic separation
is a very slow evolutionary process.

In other instances chromosome differences, such as polyploidy, may
arise suddenly and permit the species population to migrate into a
new environment. In this case morphological differentiation is or-
dinarily a secondary process aided by isolation and selection in a new
environment. In sexual species diploids and polyploids of one com-
pact rarely inhabit the same territory. An allopolyploid is almost
predetermined to occupy a different habitat from its parents, because
they fit ecologically unlike regions.

Dysploidy (“aneuploidy” of usage) is still another pattern of
differentiation. This course of evolution has been followed by the
Cyperaceae and the greater number of the California Madianae. A
principal difference between polyploidy and dysploidy is that the
latter will tolerate single chromosome differences, while in the former
the entire diploid genome acts as a superchromosome.

Reorganization within the chromosomes through inversions or re-
ciprocal translocations is still another pattern. The result has often
the effect of a premature interspecific differentiation. The gene con-
tent remains the same in the new form and its parent, and the eco-
logical requirements are unchanged, but the chromosome rearrange-
ments, if sufficiently numerous, may render the forms entirely inter-
sterile. Secondary changes, altering their ecologic requirements, may
aid some of the forms to migrate to new environments, with subse-
quent morphological differentiation. Outstanding examples of this
kind of differentiation are the Drosophilas (Dobanowsky, 1937) and
the genus Holocarpha of the Madianae.

Evolutionary processes have left plants arranged in groups of vari-
ous order and separation, such as ecotypes, ecospecies, and cen-
ospecies. These groups indicate stages in the evolutionary differen-
tiation. Ecotypes and ecospecies are features of regional differentia-
tion within the cenospecies, and they have evolved only where there
is a diversity of environment.

There are many ways in which living things can increase their
variation, but regional differentiation requires the discriminating se-
lection offered by unlike environments. We have no evidence that
the direct influences of the environment produce fundamental hered-
ity changes in species, but major alterations in environments pro-
vide new habitats and refuges for the products of nature’s continual
experimentation among all the plant species that populate a given
area.