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Source: *The American Naturalist*, Vol. 75, No. 758 (May - Jun., 1941), pp. 231-250

Published by: The University of Chicago Press for The American Society of Naturalists

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# REGIONAL DIFFERENTIATION IN PLANT SPECIES<sup>1</sup>

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## GENERAL RELATIONS BETWEEN PLANT AND CLIMATE

MANY species complexes of plants have an extremely wide vertical or horizontal distribution. Such complexes show a remarkable diversity of form and reactions that must be understood before a proper classification can be presented, and, more important, before the organization of the living world can be fully interpreted. Examples of such complexes are *Potentilla glandulosa*, *Achillea millefolium* and *Artemisia vulgaris*, all of which cover a large part of California from near sea level to around 11,000 feet altitude, and in addition have representatives circling the Northern Hemisphere.

The climates in which their California members live range from warm temperate to arctic-alpine. The weather graphs in Fig. 1 describe the climatic differences in such a transect across central California. The lowermost graph describes the climate in the mild, warm temperate, coastal region, where freezing temperatures occur only during a very limited period and continuous growth is possible for many herbaceous species. The center graph gives similar information for a locality midway up the western slope of the Sierra Nevada, at 4,600 feet altitude, where winters are cold enough to force most plants into dormancy for five or six months of the year. The uppermost graph presents data from a station near the crest of the Sierra Nevada at 9,600 feet altitude, and although it does not represent the extreme conditions found among the peaks, it does give an idea of the climate in the high mountains.

Plants of the same or closely related species from cli-

<sup>1</sup> Read at the Seattle symposium by Dr. Keck.

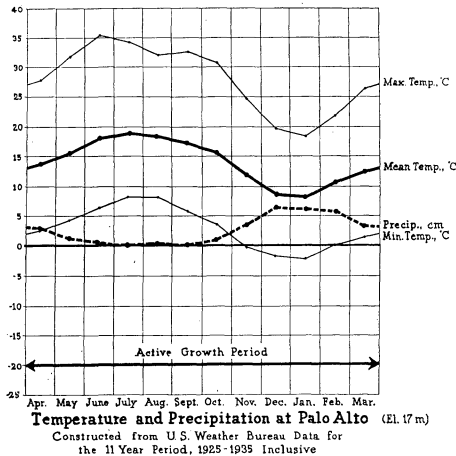
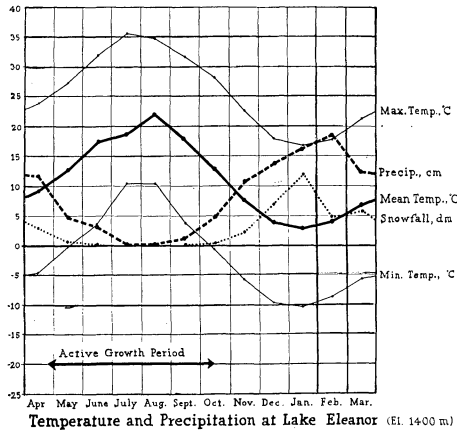
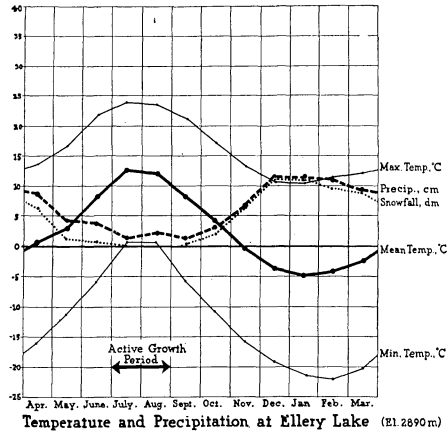


FIG. 1. Weather data from three stations on a transect across central California.

mates so unlike as the California coast and the high Sierra Nevada are very different in appearance and reactions. The alpine generally differ from their lowland relatives in size and other morphological characters, and also in their rate of growth, earliness, frost-resistance and other ways physiological. Series of intermediate forms connect the extremes.

Many questions arise concerning the nature of climatic forms: Are they due to the direct impact of the environment, and hence to be regarded as modifications, or are they hereditary in nature? Is it possible to change lowland forms into alpine by transferring them to the alpine environment as Bonnier (1895, 1920) reported, or do lowland and alpine forms remain distinct when grown side by side in a uniform environment as Kerner (1891) and Turesson (1925) found? If the differences are hereditary, what is their nature? Are they purely morphological, or are physiological characters also involved? If so, is each climatic belt populated with a race especially fitted to survive there? Finally, cytologists and geneticists raise other questions concerning possible chromosomal differences in such forms, the possibility of free exchange of genes in offspring of crossings between plants native to contrasting environments and the vigor of any such offspring.

In order to clarify such questions as these, the Carnegie Institution of Washington undertook an investigation in which experiment stations were established in three very unlike climates in central California. The principal station is located on the San Francisco peninsula, near sea level, at Stanford University. The second is at Mather, near the western boundary of Yosemite National Park, at 4,600 feet elevation, and the third is situated near Timberline just east of the crest of the Sierra Nevada, at 10,000 feet elevation, in Mono County. The contrast between the climates at the three stations is striking, as shown by the weather graphs of Fig. 1, which were constructed from U. S. Weather Bureau data obtained near

the three experiment stations. At Stanford, the growth period for plants is ordinarily continuous the year around; at Mather, it is approximately six months long; while at Timberline, it is shortened to approximately three months. At the alpine station snows usually persist in the gardens until the first of July, and there are but three to six weeks of relatively frost-free weather.

Into the gardens of these three stations representatives of many climatic races from the Pacific Coast region were brought for an analysis of their reactions. Species from a wide range of plant families were used. Perennials only were employed, for this made it possible to propagate them asexually and grow parts of one individual simultaneously at the three climatically very unlike stations. This permitted a two-way comparison. Genetic variation was eliminated by comparing divisions of one individual grown in three contrasting environments, so the differences observed were due to environmental modification alone. On the other hand, by bringing races of the same or related species from contrasting environments into a uniform garden at one station, gross environmental differences were eliminated, and the hereditary differences between them could be compared. Systematic records in the form of yearly herbarium specimens, measurements and notes made it possible to study the plants in detail through a number of consecutive years. An analysis of these experiments, which were inaugurated by the late Dr. H. M. Hall, has recently appeared (Clausen, Keck and Hiesey, 1940).

From these experiments it is clear that the variations which one observes in wild plants are of two sorts: those due to hereditary differences and those due to environmental modifications. Both contribute to the complex differences observed, not only in comparisons between climatic or geographic races, but also between competing individuals of the same population.

Each species of wide distribution consists of an assemblage of biotypes and races, some local, others of higher

order and regional. Species are usually broken up into intermittent populations because of environmental conditions. Each population consists of minor local variants or biotypes, but its members as a whole share characteristic morphological traits that frequently serve to distinguish this population from others of the same species. The frequent development of the local population into a recognizable morphological-geographical unit is probably the result of partial geographic isolation alone. The local differentiation appears to be of no major importance for survival in a given habitat, for individuals from different populations in one climatic belt follow the same general pattern of reactions and survival when transplanted to the different climates of the transplant stations. However, plants from the same population have been found to show slight individual differences in their reactions to these contrasting environments.

A very different situation is uncovered when representatives of races native to climatically different belts are analyzed by the transplant method. Such races do not react alike at the transplant stations. They differ much in their periods of activity, time of flowering and capacity to survive at the stations. These reactions are correlated with the environment in which they are native, and plants of different families but from the same general climatic belt show basically similar reactions.

By classifying the plants as to their reactions in the different climatic gardens, it is possible to recognize several major or regional climatic races that recur with frequency in various genera and families. These correspond roughly to the major life zones, which are, of course, a biotic expression of climatic differences. It takes about five to seven major climatic races of a species to occupy the entire climatically diverse region across central California.

Like the life zones, regional climatic races replace one another in the territory occupied by the species. They are most homogeneous toward the center of their distribution, but frequently intergrade through hybridization

where they meet or even overlap. Sometimes observed differences in reaction between races can be correlated with morphological differences, thus providing markers for delimiting the climatic races quickly in herbaria after such a correlation has been established by experiment.

### POTENTILLA GLANDULOSA

An example of a species differentiated into climatic races is shown in Figs. 2 and 3. This is *Potentilla glandu-*

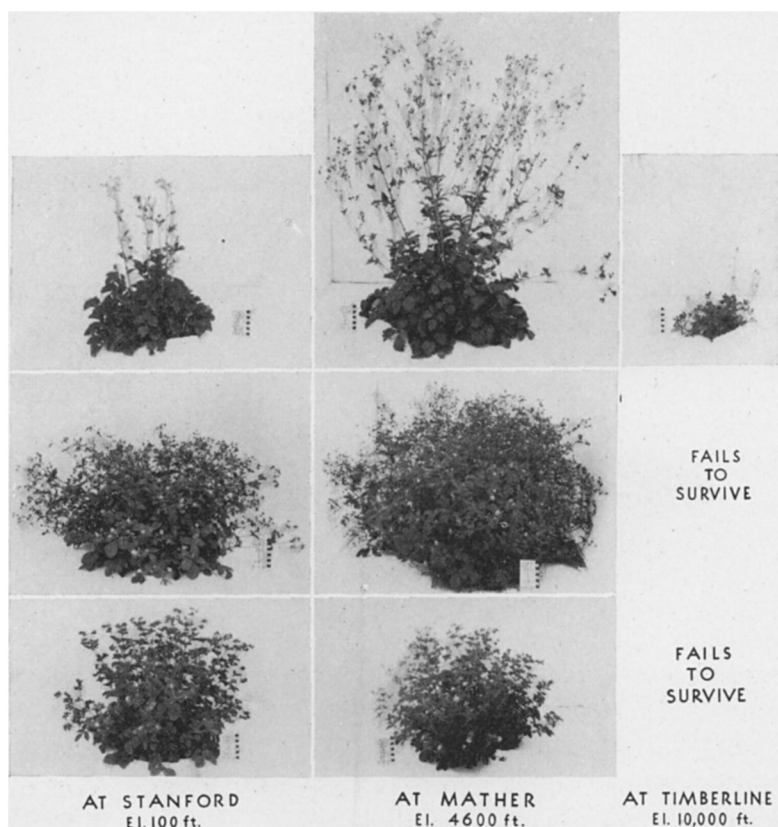


FIG. 2. Clones of three climatic races of *Potentilla glandulosa*. Lower row: plant of the Coast Range race, ssp. *typica*, from 600 ft. altitude; center row: the Sierran foothill race, ssp. *reflexa*, from 2,500 ft.; upper row: the mid-Sierran meadow race, ssp. *Hanseni*, from 4,600 ft. Horizontal rows show modifications of one individual at three transplant stations. Vertical rows show differences between races at any one station.

*losa* Lindl., of the rose family, whose California representatives are distributed from near the seacoast to about 11,000 feet elevation in the Sierra Nevada. The horizontal rows in the two figures represent divisions (clone-members) of individuals transplanted to the three stations. The differences seen between members of one clone are modifications imposed by the contrasting environments. The five individuals in the two figures were native at different elevations, as follows.

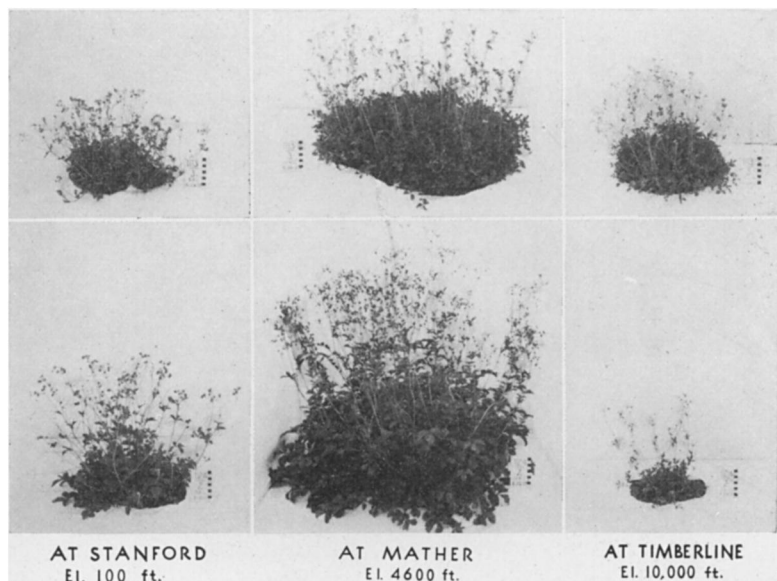


FIG. 3. *Potentilla glandulosa*: clones of the subalpine race, from 5,800 ft. altitude (lower row), and alpine race, from 10,000 ft. (upper row), both referable to ssp. *nevadensis*, showing modifications and racial differences at the three transplant stations.

The lower row of Fig. 2 is the clone of a plant representing the climatic race native in the Coast Ranges of California. This race grows well both near sea level at Stanford and at Mather at 4,600 feet, but it fails to survive at Timberline. Although it grows somewhat larger at Stanford than at Mather, it survives equally well in both environments. In its mild, native climate and in the



garden at Stanford it is in active but slow growth almost the entire year. It is sufficiently cold-resistant not to be injured by the frosts during the winters at Stanford. The more severe winters at Mather, however, force it into dormancy for some six months, thus delaying its entire seasonal development, but not interfering with its capacity to flower and produce ripe seed. Most of the plants of this species in the California Coast Ranges from 600 to 5,000 feet altitude are referable to this climatic race, for in spite of considerable individual variation, they have fundamental morphological and physiological characteristics in common by which they may be distinguished from all other races. Also, they react basically the same in the experiments regardless of the elevation of their native habitats. This climatic race is recognized taxonomically as subspecies *typica*.

In the warm, western foothills of the Sierra Nevada up to mid-altitudes, there is another regional race of the same species. The Stanford and Mather modifications of a typical plant of this race are shown in the central horizontal row of Fig. 2. Like the Coast Range race, it is unable to survive at Timberline. But unlike the representatives of that race, this plant grows taller and more vigorously at the mid-Sierran station than at Stanford. It flowers and produces seed successfully at both stations. Its leaves are susceptible to even light frosts, causing the plants to become dormant even at Stanford, with its mild winters, whereas the Coast Range race is active at this time. Consequently, at Stanford, its first spring flowers appear approximately two weeks after those of the Coast Range plants. At Mather, however, where both are forced into dormancy for approximately the same period, they flower almost together, as shown by the graph in Fig. 4.

The Sierran foothill race, known as subspecies *reflexa*, occurs from about 700 to 6,800 feet elevation, but at the higher levels it is found exclusively on the warmest slopes. Its natural populations vary considerably, but a series of morphological and reactional characteristics readily dis-

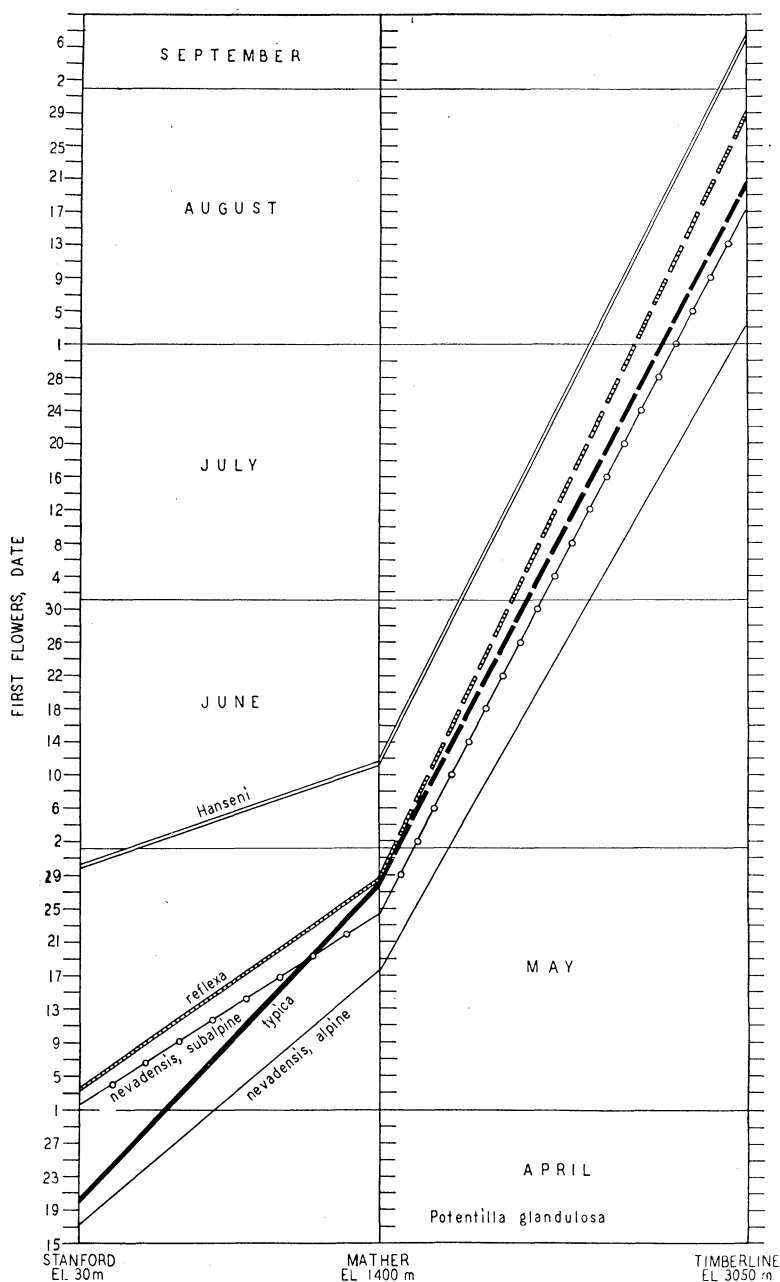


FIG. 4. Differences in dates of first flowers of climatic races of *Potentilla glandulosa* at three altitudes. Graphs represent 3-year averages of 134 clones, namely, 24 of *typicala*, 47 of *reflexa*, 6 of *Hanseni*, 26 of subalpine, and 31 of alpine *nevadensis*.

tinguish it from the Coast Range race. Many plants from the upper altitudinal limits of its range are somewhat reduced in size, but otherwise show no unique differences in reactions at the three stations, and die equally promptly at Timberline.

In middle altitude meadows in the Sierra Nevada another race is found. It differs from the foothill race not alone in its preference for moister, cooler habitats, but in a number of other characters and in its reactions. Three modifications of this mid-Sierran meadow race are shown in the upper row of Fig. 2. It is definitely most vigorous in the mid-altitude environment. Unlike both the foothill and the Coast Range races, members of the meadow race are able to survive not only at lower elevations but also at Timberline. Although greatly reduced in size and vigor, the clone-member at Timberline has been able to withstand the rigors of the alpine climate for ten years. It produces flowering stems there, but because of the shortness of the season, it is unable to produce ripe seed. At Stanford, the meadow race tends to die out of the cultures more frequently than the foothill form. It is the most modifiable of all the races of *Potentilla glandulosa*, yet close comparison reveals the fundamental identity in structure of clone-members at the three stations.

The Sierran foothill and meadow races overlap in altitudinal distribution although the meadow race rarely descends below 4,000 feet. But a rather clear-cut ecological separation is maintained between the two, for the meadow race never grows on dry hillsides, and the foothill race very rarely invades the meadows. Hybrids between them are occasionally found near their parents on meadow borders. The meadow race is distinguished taxonomically as subspecies *Hanseni*.

Two race-complexes of *Potentilla glandulosa* are found in the Sierras above 6,000 feet. These form an intergrading series morphologically so that it is impractical to separate them taxonomically. Together they compose subspecies *nevadensis*. By their reactions, however, it

is possible to distinguish both subalpine and alpine races. This has been done, as in the other cases, by assembling a large number of individuals from a number of different habitats and elevations and observing their reactions. Representatives of these races and their modifications at the transplant stations are shown in Fig. 3. Both races survive at Timberline, but the alpine tends to be the more vigorous there. Both grow best and attain their largest size at Mather, where they are able to survive indefinitely. Neither does as well at Stanford, showing reduced stature, increased susceptibility to disease and reduced flowering, although both survive moderately well. The subalpine flowers better than the alpine at the lowland station. Both become dormant during the winter at all three stations; even at the lowland station they are dormant for two to three months.

The alpine race is one or two weeks earlier in flowering at all three stations, as shown by the graphs in Fig. 4. This difference in earliness is sufficient to permit it to produce ripe fruit consistently in the very short growing season at Timberline, whereas the subalpine plants can ripen seed only in the most favorable years. The alpine plants are so rapid in their development that, in spite of their winter-dormancy, even at Stanford they are able to flower before the Coast Range races. Moreover, the alpine plants are more frost-resistant than the subalpines, a difference which is most accentuated at Timberline. In the Sierra Nevada, plants reacting like subalpines are found at altitudes between 5,000 and 8,000 feet, and alpine-reacting types may occur between 7,500 and 11,000 feet.

Morphologically, subspecies *nevadensis*, with its subalpine and alpine races, stands out as a very distinct unit. Moreover, it is self-sterile, whereas the others are self-fertile. But the physiological differentiation within the subspecies, separating an early-flowering, dwarfish and alpine race from a later-flowering, taller, subalpine one, may be just as important as the differences distinguishing this subspecies from the others.

Close study of modifications, such as are illustrated in Figs. 2 and 4, discloses that the climatic races retain their morphological and physiological individuality in the three very different environments in spite of striking modifications in general appearance. Structural features such as habit of branching and density of inflorescences, shape, venation and general texture of leaves, character and density of pubescence, distribution of glands, presence or absence of anthocyanin in stems, size, color and shape of flowers, size and color of seeds, and similar characters serve to identify each climatic race, and even each individual. On the other hand, such characters as size of vegetative parts, number of stems and vigor of growth may be profoundly modified in different surroundings, although these also are characteristics of the various races. Moreover, the manner in which a given climatic race or individual is modified is as much a part of its character as a morphological feature. Each climatic race appears particularly adjusted to thrive in its native environment, although with competition removed, it may be even more vigorous in another environment. The entire cycle of development of each climatic race appears to be fitted to the environment in which the race is native.

Modifications resulting from exposure to changed environments are quickly reversible when plants are returned to their original environment. From these transplanting experiments there is no evidence that modifications have a durable effect on the plant, even after continuous exposure to a new environment for as long as eighteen years.

Many plant groups of different families from central California were investigated and likewise found to be composed of ecologic races. Those races from the same kind of environment often show morphologic similarities as well as parallel reactions in different environments. Such correlations point to the conclusion that we are dealing with a basic principle governing the ecological differentiation of plants. Moreover, they confirm the findings

of Turesson (1922, 1925), who found in more northern latitudes in Europe the same general type of climatic differentiation in other groups of plants.

These facts naturally lead to further inquiry as to the basis of climatic differentiation. It has been experimentally demonstrated that climatic races have a genetic basis. Their hereditary differences may be either purely genic or associated with differences in chromosome number, depending upon the evolutionary history of the forms in question. In the case of *Potentilla glandulosa*, all of the races have seven pairs of chromosomes, and no genetic barriers have been found between them. For example, the foothill and alpine races (the most unlike within the species morphologically and physiologically) hybridize without any difficulty and their hybrids are fully fertile. A large second generation has segregated nearly every conceivable recombination of both morphological and physiological traits, although there is considerable linkage, as would be expected with the low chromosome number. Nearly every morphological character was found to depend upon a small series of genes, each of minor but cumulative effect. Furthermore, traits that appear to have an adaptive value, like earliness of flowering, duration of dormancy, frost resistance, growth rate and self-fertility, segregate too, indicating a genetic basis for them as well as for the others.

We find, therefore, in *Potentilla glandulosa* a remarkable differentiation into major ecologic races fitted to occupy very contrasting environments. This differentiation depends upon a multiplicity of genes in a few chromosomes, but these genes are interchangeable without upsetting the physiological balance of the offspring. The apparent absence of genetic barriers within this group indicates that all these climatic races belong within one species.

#### ACHILLEA

A different pattern of regional differentiation is found in the western yarrow of the *Achillea millefolium* com-

plex. Its members have an even wider distribution than *Potentilla glandulosa*, and cover many climatic zones with different races. However, a difference in chromosome number separates the West American representatives into two large groups. Plants from mid-elevations on the west slope of the Sierra Nevada eastward across the crest of the range, the Great Basin and the Rocky Mountains have 18 pairs of chromosomes. Those west to the coast have 27 pairs. Since these differences in chromosome number impose a definite barrier to interbreeding, at least two species are involved. The coastal species is *Achillea borealis* Bong., the interior one is *A. lanulosa* Nutt., and in each there has been ecologic differentiation into races fitted to different climates.

The change in chromosome number in *Achillea* has offered no complication to the formation of climatic races across California very parallel to those found in the *Potentilla*. Some of these are illustrated in Figs. 5 and 6. The reactions of two races of *A. borealis* at the transplant stations are shown in Fig. 5. The upper row shows clone-

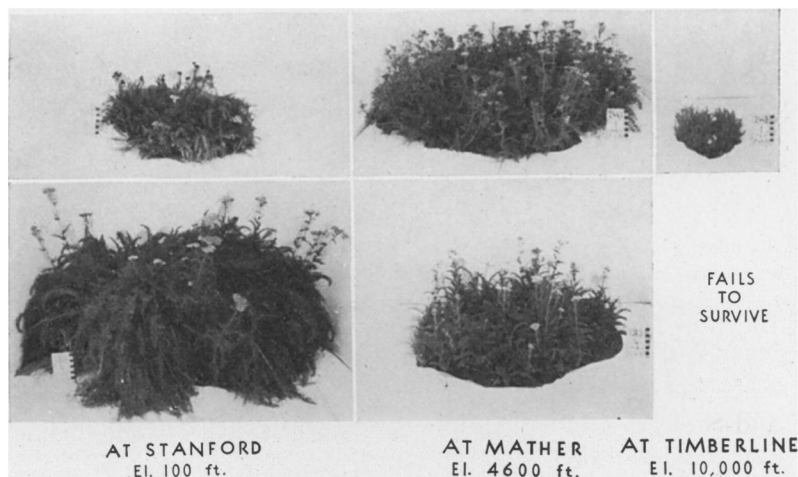


FIG. 5. Clones of two latitudinal races of *Achillea borealis* at three altitudes. Both are hexaploid,  $n=27$ . Above: plant from Seward, Alaska; below: plant from Berkeley, California; both from near sea level but separated by  $22^\circ$  of latitude.

members of a plant from coastal Alaska as they appear at the three transplant stations, while the lower row shows corresponding clone-members of a plant from the central California coast, 22 degrees of latitude farther south. The Alaskan race is able to live at all three stations and is early flowering, but its stems are very susceptible to

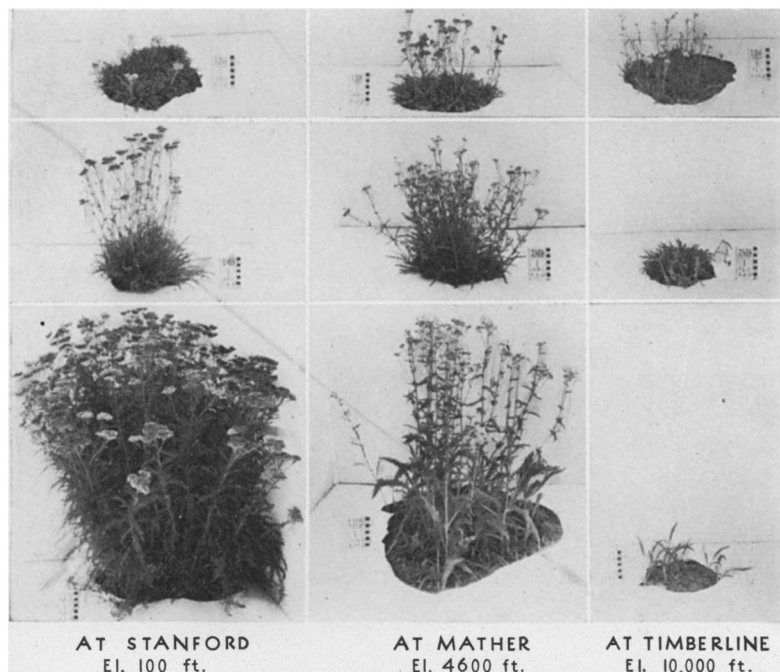


FIG. 6. Clones of three altitudinal races of *Achillea lanulosa* at three altitudes. All are tetraploid,  $n=18$ . Top: an alpine, from 10,700 ft. altitude; center: a subalpine, from 7,100 ft.; bottom: a mid-Sierran plant, from 4,675 ft.; all from the Sierra Nevada along the station transect.

frost and are killed at Timberline before they are able to ripen seeds. By far its best growth is attained at the mid-Sierran station. The southern race, on the other hand, cannot survive at Timberline, and it even suffers a loss of vigor at the mid-Sierran station. It grows most successfully at Stanford, near its native habitat. At both stations it is in flower a month and a half later than the Alaskan plant.



Three altitudinal races of *A. lanulosa* of the Sierra Nevada are illustrated in Fig. 6. The reactions of clone-members of a mid-Sierran individual (lower row), a sub-alpine (center row) and an alpine (upper row) are shown at Stanford, Mather and Timberline stations. The mid-Sierran race (from 4,675 feet) survives only two or three years at Timberline and seldom is able to develop more than a few basal leaves there. At Stanford, however, it develops even more vigorously than in its native habitat at Mather, but it is far more vigorous at Mather than the coastal form. The subalpine race, from 7,100 feet elevation, survives well at all three stations, but is unable to ripen fruit at Timberline because the stems are frost-killed before maturity, as shown in the figure. The alpine race, on the other hand, thrives at all three altitudes, but grows more vigorously at both mountain stations than at Stanford; it is early and frost-resistant enough to be able to mature in its native environment in favorable years. The most frost-resistant race (not illustrated) comes from the Great Basin, east of the Sierra Nevada. It is a fairly tall form, which remains green and active at the alpine station long after the other plants are frost-killed, but is so slow in its development there that it is unable to mature fruit.

Accordingly, in *Achillea*, as in *Potentilla glandulosa*, the regional races appear to be well adapted to their natural environments, although they do not always make their maximum growth in the climate in which they are native.

#### OTHER SPECIES

A summary of a survey of regional differentiation in several groups of widely distributed California plants is presented in Fig. 7. The diagrammatic profile at the top indicates the elevations in a transect across central California. The approximate distribution of regional races of various plant groups is shown below the profile and also their differences in chromosome number. It will be seen that some of the plant groups are distributed across

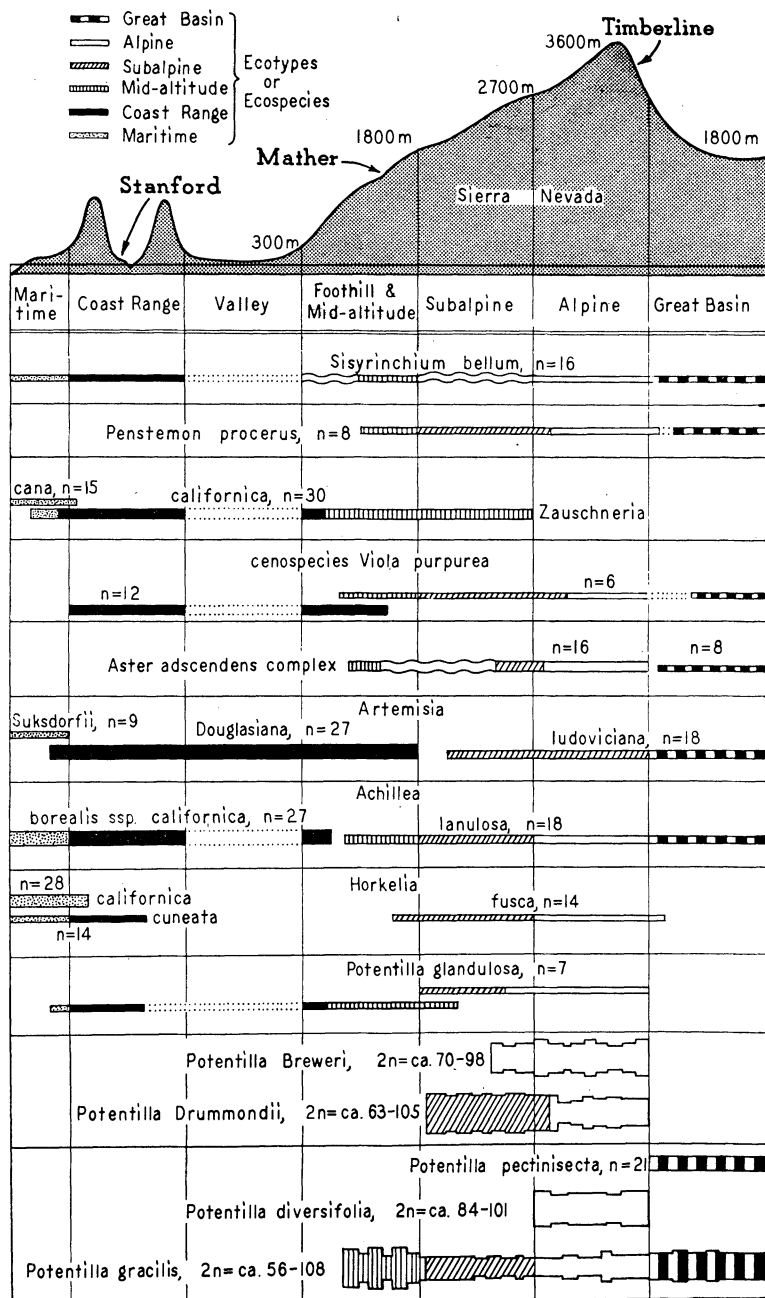


FIG. 7. Distribution of major climatic-races within species complexes in a transect across central California. The width of the symbols roughly indicate the degree of polyploidy. Further explanation in text.

the entire transect, while others occur on only a part of it. Almost all are absent from the San Joaquin Valley, an expanse populated primarily by annuals.

Of the eleven complexes shown, three have effected their differentiation without change in chromosome number, namely, *Sisyrinchium bellum*, *Potentilla glandulosa* and *Penstemon procerus*. The remainder have simple or complex differences in chromosome number within them. The *Potentilla* species of the two complexes shown at the bottom of Fig. 7 are the antithesis of *Potentilla glandulosa* cytologically. In contrast to the extreme regularity of the latter, these species present differences in chromosome number even among the individuals of one population (as suggested by the varying widths of the symbols in the graph), and all plants have many unpaired chromosomes. These groups probably reproduce asexually through apomixis. Yet despite this great variability in chromosome number and lack of pairing at meiosis, they have developed climatic races very parallel to those found in *P. glandulosa*.

In the remaining six cases in the graph the chromosome number changes somewhere along the transect. The component races of almost all these complexes are so closely related that at one time or another they have been combined in one species. However, the differences in chromosome numbers produce genetic barriers that prevent free interbreeding, and these differences are usually correlated with differences in morphology. This makes it possible to recognize the chromosomal groups as taxonomic species. Closely related species differing in chromosome number usually do not overlap very much in distribution, but replace one another in different climates.

There is no observable correlation between degree of polyploidy and environment, for in some complexes the forms with low chromosome numbers are at high altitudes, in others, at low altitudes, in some, near the sea, in others, inland. Irrespective of what the chromosome number is, however, or where it changes, each complex

has developed a series of climatic races of parallel reaction, fitted to the climates in which they are native. An exception to this rule is found in *Artemisia Douglasiana*, for no well-defined climatic race has been discovered in this species, which, nevertheless, covers a rather wide range of environments. There is some evidence that this species may be an amphidiploid of comparatively recent origin, produced by the addition of the chromosomes of the maritime *A. Suksdorfii* with those of *A. ludoviciana* from the interior mountains and desert plateaus. The combination of chromosomes from such ecologically different species should produce a form capable of inhabiting a wide variety of environments.

### CONCLUSIONS

This survey and the one conducted by Turesson in Europe indicate that the genetic-physiologic differentiation of a plant group is correlated with the climatic zones it occupies. This follows from the fact that the same kinds of environments are occupied by races that have similar patterns of reaction, even though they belong to unrelated genera or families. This is found to hold irrespective of whether or not the regional forms differ in chromosome number.

The usual pattern of differentiation is purely genetic, with relatively few major steps involved; but superimposed upon this one often finds a cytological differentiation, with one or two changes in chromosome number across the California transect. However, the effects of increases in chromosome number must have been far overshadowed by the selective influence of the environment in determining the appearance and reactions of plants. From these considerations it appears that it is the genes in the chromosomes, and not the number of chromosomes, which determine the climatic adaptation.

From the point of view of fitness to the environment it is evident that the ecologically important unit is not the species, but the regional climatic race, or, to adopt Tures-

son's term, the *ecotype*. Several of these may combine to form a species, or a single ecotype may develop an isolating genetic barrier to form a monotypic species, such as *Zauschneria cana*, *Artemisia Suksdorfii* and *Horkelia californica*, in Fig. 7. Such monotypic species occupy a narrow climatic belt and show little variation and adaptability. However, it makes little difference whether a given area is populated by a series of ecotypes belonging to one species, or by a series of monotypic species belonging to one species complex, or by a combination of both. The evolutionary past and future differ, however, in the three instances.

Evolutionary processes have left plants arranged in groups of various order and separation, such as populations, ecotypes, species and species complexes. These groups indicate stages in evolutionary differentiation, and they have evolved only where there is a diversity of environments.

There are many mechanisms by which living things can increase their hereditary variation, but regional differentiation requires the discriminating selection offered by unlike environments. We have no evidence that the direct influence of environment produces fundamental hereditary changes in species, but major alterations in environments provide new habitats and refuges for the products of nature's continual experimentation among all the plant species that populate a given area.

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