

B. *The Mojave Desert*: The Mojave Desert is a somewhat higher desert than the Colorado Desert and is broken up by a number of small mountain ranges. This desert extends into adjacent Nevada. It is rather poorly drained, and as a consequence there are numerous periodically inundated low areas that are now highly saline because of the influx of water during very wet years followed by evaporation of their contents in subsequent years.

8. *Great Basin and related areas*: North of the Mojave Desert and east of the Sierra Nevada are occasional valleys or upland areas that are basically the westernmost reaches of the Great Basin, which is a large, relatively high area that lies between the Sierra Nevada (and Cascades) and the Rocky Mountains and has its center in Nevada. To the north, in northeastern California, the Modoc Plateau is an area in which there are extensive areas covered by lava.

Climate of California

The climate of California is strongly influenced by the physiography of the state. Botanically, climate may be defined as the sum total of atmospheric conditions that influence the growth and reproduction of plants. In much of the United States, the latitude approximately fixes the regional climate. While this may be true in a general sense for California, the tremendous variation in topography exerts an influence which is equal to, if not more important than, the latitude. In California, the major factors determining the climate are the Pacific Ocean and the presence of mountainous masses of land.

Much of California has a maritime climate; this is in contrast with the continental climate of montane or inland areas. The following shows the extremes between these two climatic regimes:

MARITIME CLIMATE
Coastal location
Winters warm
Summers cool
Small daily temperature range
Small seasonal temperature range
High relative humidities

CONTINENTAL CLIMATE
Inland location
Winters cold
Summers hot
Large daily temperature range
Large seasonal temperature range
Low relative humidities

The climate of most cismontane California, that is, of that part of California lying west of the Sierra-Cascade crest, is a *Mediterranean* one. The summers are cool and dry; the winters are relatively warm and wet. There are even some genera, such as rock rose (*Helianthemum*, Cistaceae), sage (*Salvia*, Labiatae), and tree mallow (*Lavatera*, Malvaceae) that are common to similar climatic zones of California and Mediterranean lands, though different species occur in each of the two regions.

The climatic influences of the ocean are manifold. Low pressure areas that develop in the Pacific Ocean in the vicinity of the Gulf of Alaska are stationary during some parts of the year, but in the winter they frequently move southeasterly and bring cold weather, strong winds, and rain to much of California. In the summer, these Pacific lows are generally centered to the northward and as a result summer rainfall is rare in California, except for local thunderstorms in the mountains. During the summer, the moisture present in the cold oceanic air often condenses when this air meets the warm, dry air from the land. The result is the development of the coastal fog belt that is typical of much of the California coastline during summer months.

In most of the central and eastern United States, climatic zones tend to follow roughly latitudinal lines running from east to west across the continent. In California, however, the climatic zones generally run in a more or less north-to-south direction. This is due to the strong influence of the Coast Ranges and the Sierra-Cascade axis: since these mountains run in a north-south pattern, so does the climate over which they exert such a strong influence. For example, the winter storms that bring rain to California generally come into the state from the Pacific Ocean. The distribution of this rain within the state, however, is largely determined by topography. Much of the moisture in the Pacific air is dropped by the time it reaches the crest of the Coast Ranges, and a second portion of moisture is lost when the air reaches the crest of the Sierra-Cascade ranges. As a result, one finds that the immediate coast and the westerly slopes of both ranges have a higher precipitation than do areas slightly east of each. Since the Sierra-Cascade ranges are considerably higher than the Coast Ranges, rather little moisture-laden air reaches beyond this

mountain axis, and the result is that the Great Basin has a considerably lower winter rainfall than does that portion of California immediately to the west of these mountains.

In the same fashion that these mountains act as a barrier to the passage of moisture-laden winds, they also act as barriers to the passage of hot or cold air masses. During the summer, the Sierra-Cascade ranges protect much of California from the hot, dry air masses that develop over the central United States. This, combined with the proximity to the cool Pacific Ocean, explains why California has a generally cool summer climate. During the winter, these mountains serve to insulate California from the cold, dry air masses that develop over the inland portion of the continent. As a consequence, California has winters that are in general milder than one might expect at the latitude.

In going up the western side of the Sierra Nevada, one encounters an increase in annual (mostly winter) precipitation up to a point at which it begins to drop off as one continues to ascend in elevation. The zonation of vegetation in the mountains reflects this variation in precipitation patterns. In the lowest portions of the foothills the vegetation types are characteristic of a relatively arid climate. In middle elevations the vegetation reflects the rather favorable precipitation patterns. Above the middle elevations, however, the vegetation acquires a more "arid" aspect. As one goes southward in the Sierra, these climatic zones move up in altitude, with the result that in the southernmost Sierra Nevada the zone of highest precipitation is considerably higher than it is in the northern Sierra.

Of chief importance to the distribution and nature of the plant cover of California is the amount and seasonal distribution of rain or other precipitation. The wettest portions of California are in the northwestern part of the state. Wet areas also occur on the western slopes of the Sierra Nevada and in the Santa Lucia Range of Monterey County. On the western slopes of the Coast Ranges, from coastal Monterey County northward to southern Oregon, the average annual rainfall exceeds 50 inches (127 cm) per year. This is also true for much of the western slope of the Sierra-Cascade ranges. On the other hand, the Sacramento Valley averages below 20 inches (51 cm) of rain per year and the San

Joaquin Valley has less than 10 inches (25 cm). The southeastern deserts receive an average of less than 5 inches (13 cm) per year, and in a few areas, such as Death Valley, some years may pass by without any measurable rainfall. The extremes in average annual rainfall range from an excess of 110 inches (280 cm) in parts of Del Norte and Siskiyou Counties to less than 2 inches (5 cm) per year at Furnace Creek Ranch in Death Valley.

Most of the rainfall that occurs in California falls during the winter months. The rainy season in southern California is generally during a period of five months between November and March; in northern California it is during a seven-month period between October and April. There are as many as 100 days of measurable rain on the average in parts of northern California; there are as few as 10 days in some desert regions. In the calendar year 1909, over 153 inches (389 cm) of rainfall were recorded at Monumental in Del Norte County; during one season (July 1 — June 30) over 160 inches (406 cm) of rain were recorded at one station in Monterey County. In southern California, there are frequent intense seasonal storms during which very heavy amounts of rain fall. For example, one storm in Los Angeles County in late January, 1943, dropped nearly 26 inches (66 cm) of rain in 24 hours. On another occasion, over 11 inches (28 cm) of rain were recorded in 80 minutes at Campo, San Diego County. Obviously, such heavy amounts of rain during very short periods are of little value to plants and may result in damaging floods in lowland areas.

Although the average rainfall for much of the state is so low that one might expect few plants to survive such conditions (because it falls mostly during the winter months), many arid areas provide shows of spectacular annuals which flower in early spring. Such displays are conspicuous in the southern end of the San Joaquin Valley and also in portions of the Mojave and Colorado deserts. The average rainfall figures for a particular area may not be very helpful in estimating what sort of a vegetation is present in the region, however, because of the yearly fluctuations in rainfall and because of the seasonal distribution of the rain. Prolonged periods of drought may have a negative effect on the survival of woody plants, with the result that shrubs or trees are absent from areas where one might expect them to be present.

Also, because of the prolonged summer drought in much of the state, plants that are unable to survive long periods without rainfall do not become established. In general, winter rains are more or less dependable, but there are some notable exceptions to this reliability. For example, in the winter of 1850-51 San Francisco received only slightly over 7 inches (18 cm) of rain, which is about one-fourth of its average rainfall. Clearly, that year was a "bad" one for the plants! Also, prolonged drought during the winter may also exert a negative influence on plants, even though early winter and late winter rains may produce an average total amount of rain for the year. It is these seasonal or yearly bottlenecks in rainfall that have a very important local effect on plants.

As mentioned above, the rain in California tends to be highly seasonal and the summers are generally very dry and rainless. In northern California, the occurrence of heavy fogs along the coast has a two-fold beneficial effect in alleviating some of the effects of summer drought. One of these effects is that the fogs reduce the amount of water loss from plants and from the soil so that what little water there is can be conserved. A second effect is seen in the familiar "fog drip" that occurs from the foliage and branches of tall trees along the coast. This is particularly noticeable in redwood forests, but also occurs in other coniferous forests, as well as in eucalyptus groves in some areas. The fog that condenses on the upper portions of the trees drips down to the soil and in some areas has been estimated to be equivalent to an extra ten inches of rainfall per year.

Snow is also important as a source of moisture for plants and serves as an important insulating agent for many plants in alpine areas that have severe cold and strong winter winds. Snowfall in the winter can be expected in the Sierra Nevada at any elevation above 2,000 feet (610 m). Above 4,000 feet (1,220 m) the snow may remain on the ground for long periods of time, and at higher elevations snow remains on the ground during the entire winter. The coastal region is mostly free of winter snow, although peaks in the Coast Ranges and the southern California ranges may have snow on the ground for days or weeks at a time. The snow season in the Sierra is between October and June, the actual length of time depending on the season and on the elevation.

Snowfall may be extremely heavy during some years. For example, at Tamarack, Alpine County, a total of 884 inches (2,245 cm) of snow was recorded during the 1906-07 winter. This is equal to almost 74 feet (22.6 m) of snow!

Although the temperature regime over much of California is moderate, extreme temperatures have been recorded for various localities. The lowest temperature recorded in the state was -45°F (-43°C) at Boca, Nevada County, which is east of Truckee. This amazingly low temperature was recorded on January 20, 1937. Since Boca is only at about 5,500 feet (1,676 m) elevation, it is quite probable that even lower temperatures have occurred in the state but have been unrecorded. The highest temperature in the state (and almost the highest temperature for any station on earth) was 134°F (57°C) in Death Valley. Both temperature extremes occurred in areas that are well vegetated, so some plant species are able to tolerate them.

The frost-free season, which agriculturalists call the growing season, varies in length from place to place. The longest growing season is 365 days along parts of the extreme southern coast of California. In the Central Valley the season is about 260 days long. In northeastern California, it is 100 to 120 days long, and at elevations of 6,000 feet (1,829 m) or above it rapidly drops off to below 100 days. There are some areas in the state, therefore, which rarely if ever experience a frost; other areas in the high montane region may have night-time temperatures that frequently drop to freezing or below even in midsummer.

The average climate of a region is important in determining what sort of vegetation and plant communities occur there. However, extreme deviations from the average climate may also have a striking effect on the plants of an area and may exert a determining role if these extremes occur frequently. For example, in parts of northern California there was a very hard freeze with unprecedented low temperatures in December, 1972. This exterminated or damaged large plantings of orchard crops and ornamentals, and also damaged a number of native trees and shrubs. Similar freezes in the southern part of the Great Basin have been known to kill or damage vast acreages of the native Creosote Bush (*Larrea divaricata*, Zygophyllaceae) at the north-

ern edge of its range. In addition, prolonged droughts may also be effective in reducing or eliminating populations of certain perennial plants.

In general, winds in California are relatively unimportant in their influence on plant life, but in many coastal areas the persistent and occasionally very strong winds may have an effect in influencing the growth patterns of woody plants. For example, at Point Reyes, Marin County, just north of San Francisco, winds in excess of 75 miles (120 km) per hour are recorded regularly during each month from January through May. Although there are few trees on the coastward portions of Point Reyes, the trimming effect can be seen in the pine and bay forests that occupy the exposed ridges just inland from the coast. In southern California, the occasional dry, gusty "Santa Ana" winds may blow toward the coastal regions from the north or northeast. Likewise, in the Sacramento Valley, there are periods during which the dry "Northerners" blow. If these strong winds occur during the growing season, they may contribute to a rapid drying of the soil which in turn results in a rather poor growth of native annuals. If these winds occur during the summer months, they considerably increase the danger of grass, brush, or forest fires and also aid in spreading fires once they become started.

At one time in the geological history of California the state had a mild, wet climate with abundant rainfall distributed throughout the year. Since Pliocene times, however, the summer season has become longer, warmer, and drier. Total rainfall has decreased and has become limited to the winter months. This increasing aridity over a long period of time resulted in striking vegetational changes in the state and was associated with the rather rapid evolution of a large number of plant species that are adapted to the modern climate of the state. At the same time that these species were evolving, a number of plant species and entire plant communities became extinct in the state.

About half of the plant communities present in California are strongly characteristic of the state and are closely adapted to its present Mediterranean climate. Some of these plant communities are restricted to California, or extend only slightly into adjacent areas. Other plant communities are adapted to wetter conditions

or are better developed and more extensive outside the boundaries of the state.

Adaptations to Aridity

How do California plants cope with the Mediterranean climate and its prolonged periods of summer drought, as well as with the unreliable winter rains? There are several ways in which plants have responded to this climatic regime.

Annuals are plants that complete their life cycle within a year; that is, the seeds germinate and the plants grow, flower, and set seed in less than 12 months. Many California annuals have evolved interesting mechanisms that are direct adaptations to growing in areas with a highly seasonal rainfall. Studies by a number of workers, in particular a group of biologists who worked at the California Institute of Technology in Pasadena some years ago, have investigated these adaptations. For example, the seeds of several annual species do not germinate unless they have been drenched with more than a half inch (1.3 cm) of rainfall (or its simulated equivalent in the laboratory). This water must come from above and actually wash over the seeds; placing the seeds in a bed of wet soil will not induce them to germinate. The basis of this behavior is the leaching of chemical inhibitors from the dormant seeds of these annuals, or the leaching of germination-inhibiting salts from the soil. A desert plant which germinates after the first slight rain in the autumn has a very low chance of continuing to survive and grow to maturation, and some desert annuals do not germinate immediately after the first heavy rains but exhibit a delayed germination phenomenon. The adaptive value of this trait is that such a delay, until after one or more heavy rainfalls, increases the chance that the seedlings will be growing during a period of good soil moisture. All the germination patterns that have been studied in desert annuals are explicable in terms of the average pattern of winter rains in desert areas. Obviously, any species that is unable to respond to this average pattern will have a poor chance of survival over a period of many generations.

Some of the southern California deserts receive summer rains in addition to the winter rains. It is of interest to note that in a

lowland cismontane non-desert station such as Berkeley, for example, the average monthly rainfall for the month of August is only 0.05 inch (0.1 cm); in Indio, in the desert, the August rainfall averages 0.38 inches (1 cm). Summer rains generally are less reliable than winter rains, and the amount of rain that falls during the summer in these desert areas usually is much lower than that which falls during the winter. As a result, some areas of the Colorado Desert (particularly that portion located in Arizona) support two somewhat different sets of annual plant species. Winter annuals germinate and grow during the winter and flower in the spring; these species provide the spectacular displays in such areas as the Anza-Borrego Desert in southern California. Less well known is the smaller number of summer annuals which germinate after summer rains and flower during summer months.

The winter annuals that have been studied germinate only when the temperatures are relatively low, thus being prevented from germinating during the summer rains. In addition, such plants will not flower until the days reach a critical length in the spring, after the cool wet winter season. These winter annuals are "informed" that spring has arrived by day-length rather than by temperature or moisture conditions, perhaps because over the long run day-length is a more reliable indicator of season than are other environmental conditions. In contrast, summer annuals germinate only at a warm temperature and thus appear during the summer but not the winter. These plants have no photoperiod requirement for flowering; they will flower when the plants have reached a suitable size for the production of flowers. Because these plants carry out their growth during the relatively benign temperature regimes that exist in the summer, they do not require a further mechanism to delay their flowering until a specific season has been reached.

Another class of plants that live in arid regions are called *phreatophytes*. Phreatophytes are perennial plants that have extensive and deep root systems that enable them to tap underground sources of water. Greasewood (*Sarcobatus vermiculatus*, Chenopodiaceae) is an example of a phreatophyte that occurs in desert regions. The young seedlings of most phreatophytes produce extensive root systems very rapidly during the winter

growing season, and if these roots reach the permanent underground water supply, further growth of the plant is not directly dependent on local rainfall. However, most seedlings produced by phreatophytes are not successful in reaching ground water supplies and as a consequence seedling mortality is generally very high.

Xerophytes include succulents, which are plants such as various cacti or members of other families having fleshy stems and leaves that enable them to store water for long periods of time. Succulent xerophytes frequently have shallow root systems and thus are able to utilize the soil moisture that results from a light rainfall or from heavy dew. Such plants take advantage of what little precipitation falls in desert regions and store this water for months or years, during which time it is slowly and economically used in the metabolism of the plant. Many succulents, such as most cacti, are leafless and are so shaped that they present a minimum surface area from which water loss can occur.

Non-succulent xerophytes, such as some species of the sagebrush genus *Artemisia* (Compositae), Creosote Bush, and Ocotillo, have developed various means other than water storage in succulent tissue to endure long periods of drought. The means by which xerophytes deal with the scarce water supply vary. Some of these plants are able to obtain water from the soil even when it is present in very low amounts, because they have a high diffusion pressure deficit within their root cells, thus enabling the roots to take up what little water is present in the soil long after rains have fallen. Many of these xerophytes have developed combinations of other characteristics which enable them to economize on water. These include the presence of a heavy waxy cuticle on the leaves and stems which reduces water loss from these tissues; presence of dense mats of hairs, which have the same function; vertical orientation of leaves which places the leaves at such an angle that they receive the full sunlight obliquely rather than directly, and thus do not become heated; grayish color of leaves and stems due to pigmentation, waxes, or hairs which also reduces heating-up of plant tissues; leaves curling (or dropping) during drought periods to reduce the surface area from which water loss may occur; sunken stomates (pores) on the

leaves to reduce water loss; and wide spacing of plants, perhaps in response to the low water supply. Further, a variety of thorns, spines, or essential oils may serve to discourage browsing animals from eating the leaves and stems of xerophytic plants.

Ecotypes and Life Zones

Many wide-ranging species of plants are variable throughout their range. This variability may be expressed in morphological characteristics such as height of plant or size of leaves; in "behavioral" characters such as time of flowering or season of leaf fall; or in subtle physiological characters such as tolerance to specific soil conditions, such as serpentine soil. Some environmental characters, soil type, for example, show a discontinuous distribution, and plants respond accordingly. However, one important environmental feature which shows a graded variation is that complex of phenomena which we collectively call climate. Climatic factors such as average rainfall, average temperature, etc., tend to show rather gradual changes from one area to the next. The difference in the average annual climate between a locality at 3,000 feet (914 m) in the Sierra Nevada or San Gabriel Mountains and one at 4,000 feet (1,219 m) in the same mountains is very slight. The difference between 3,000 and 5,000 feet (914 and 1,524 m) is stronger. Obviously the difference between the average climate at sea level in coastal California and the top of Mount Dana in the Sierra Nevada or Mount San Jacinto in southern California is very great. Few plant species occupy such a diversity of habitats, but there are a few plant species in California which are widely distributed and occur in a variety of climatic regimes. In view of the interesting adaptations demonstrated by soil ecotypes of such species as *Gilia capitata*, what adaptations to climatic differences can we expect in a climatically diverse plant species which occurs in a wide variety of habitats in California?

The Carnegie Group

In the 1930's, a trio of botanists in California began a long series of investigations aimed at answering the question posed above. Their results were published primarily in a monographic

series entitled *Experimental Studies on the Nature of Species*. The trio consisted of Jens Clausen, a Danish cytologist (a biologist who investigates chromosome number, structure, and behavior), William Hiesey, a plant physiologist, and David Keck, a plant taxonomist. These three men worked at the Carnegie Institution of Washington's Division of Plant Biology housed on the Stanford campus. The Carnegie group established three gardens which provided the growing grounds for some of their experimental plants. These gardens are located at Stanford, Mather, and Timberline.

The Stanford garden is situated in the South Coast Ranges at an elevation of about 90 feet (27 m). The natural vegetation of this area is (or was) oak savanna, which belongs to the Valley and Foothill Woodland plant community. The average growing season here is about 280 days. There is no winter snow and freezing temperatures are uncommon. The average rainfall is about 12.5 inches (32 cm) per year, most of which falls in the winter. The summer is dry and relatively warm.

The second garden, at Mather, is on the western slope of the Sierra Nevada. The elevation of this garden is somewhat over 4,000 feet (1,219 m). It is located in a well-developed coniferous forest which belongs to the Montane Forest plant community. The growing season here is 145 days long and there are moderate winter snows. The annual precipitation averages 38.5 inches (98 cm) and, although July, August, and September are generally dry, occasional rains may fall during these months.

The third garden is at a locality called Timberline, which is just east of the crest of the Sierra Nevada at an elevation of over 9,000 feet (2,743 m). This is an alpine area located in a montane meadow near the vegetational timberline. The growing season here is only 67 days long and there are heavy and prolonged snows in the winter months. Precipitation is 29 inches (74 cm) of rain and snow per year, and there is no distinct dry season during the summer.

The Carnegie group was interested in learning how certain widely distributed plant species are adapted to the climatic regime that occurs over much of California. They selected as their experimental plants some relatively widely distributed species which

included the Yarrow (*Achillea*, Compositae, Plate 4A). Since the taxonomy of the *Achillea* is a bit complex, it is sufficient to say that this plant belongs to the *Achillea millefolium* group. For our purposes, we can consider that it consists of a single species in the area studied.

Seeds of *Achillea* were collected from natural populations distributed across California from the sea coast to the alpine regions. Seedlings from these wild plants were grown at Stanford and each of 60 seedlings was subdivided into three rooted cuttings. One cutting from each seedling was planted in the Stanford garden, one at Mather, and one at Timberline. The three individuals obtained in this manner from a single parent together constitute a *clone*, which is a term that refers to all individuals vegetatively propagated from a single "mother" plant. Each of the 60 seedlings was cloned, and the result was that each of the 60 individuals at Stanford had an identical mate at Mather and at Timberline. Use of the clone method enabled Clausen, Keck, and Hiesey to study the behavior of 60 "individuals" grown in three different places at once.

After a suitable time interval, the Carnegie group started the first of a series of measurements of the plants in the three gardens to determine their responses to the different climatic conditions that prevail in these three localities.

Although several characteristics were measured and several populations were studied, the following synoptical table gives measurements for three characteristics of four sample populations of *Achillea*, since this condensed version of the extensive experiments suffices for illustrative purposes. All figures given in the table are means. The term "Bodega population" refers to plants that originated near Bodega Bay, Sonoma County, an area on the immediate coast of northern California not far from San Francisco. The Clayton population came from the vicinity of Clayton, Contra Costa County, near Mount Diablo, which is at the edge of the Central Valley east of San Francisco. The Mather population originated at Mather in the vicinity of the Mather garden in the Sierra foothills. Big Horn Lake is over the crest of the Sierra Nevada at approximately 11,000 feet (3,353 m). Its climatic regime is similar to that of Timberline.

CHARACTER MEASURED	STANFORD	MATHER	TIMBERLINE
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Bodega population

Stem length (\bar{x})*	48.9 cm	30.8 cm	died
Number of stems (\bar{x})	19.3	18.2	---
Time of first flowers (\bar{x})	May 21	July 11	---

Clayton population

Stem length (\bar{x})	70.0 cm	37.3 cm	died
Number of stems (\bar{x})	16.0	7.5	---
Time of first flowers (\bar{x})	April 13	June 17	---

Mather population

Stem length (\bar{x})	79.6 cm	82.4 cm	34.3 cm
Number of stems (\bar{x})	7.2	28.3	0.7
Time of first flowers (\bar{x})	May 15	June 30	Sept. 20

Big Horn Lake population

Stem length (\bar{x})	15.4 cm	19.5 cm	23.6 cm
Number of stems (\bar{x})	2.9	3.3	3.7
Time of first flowers (\bar{x})	April 29	June 6	August 14

*(\bar{x}) = mean measurement.

Before commenting on the results given in the above table, some explanation must be given. In nature, the plants of *Achillea* native to coastal areas grow actively all year round. They occur in an area which has cool, foggy summers and cool, rainy winters. Frosts are uncommon. Because of frequent exposure to sea winds, many of the coastal plants are dwarfed in stature. In contrast, plants of *Achillea* native to the valley areas grow rapidly during the wet season of winter, and become dormant with the onset of drought in the late spring. The plants that occur naturally at Mather generally become dormant in the winter because of the cold weather, although plants from slightly lower elevations are winter-active just as are the valley plants. Plants that occupy alpine areas (such as Big Horn Lake) are dormant during the long, cold winters and during much of the winter-time are covered by heavy layers of snow. Such plants grow and flower only during the short summer months after the snow has left the ground. In nature, therefore, *Achillea* shows a diversity of responses which

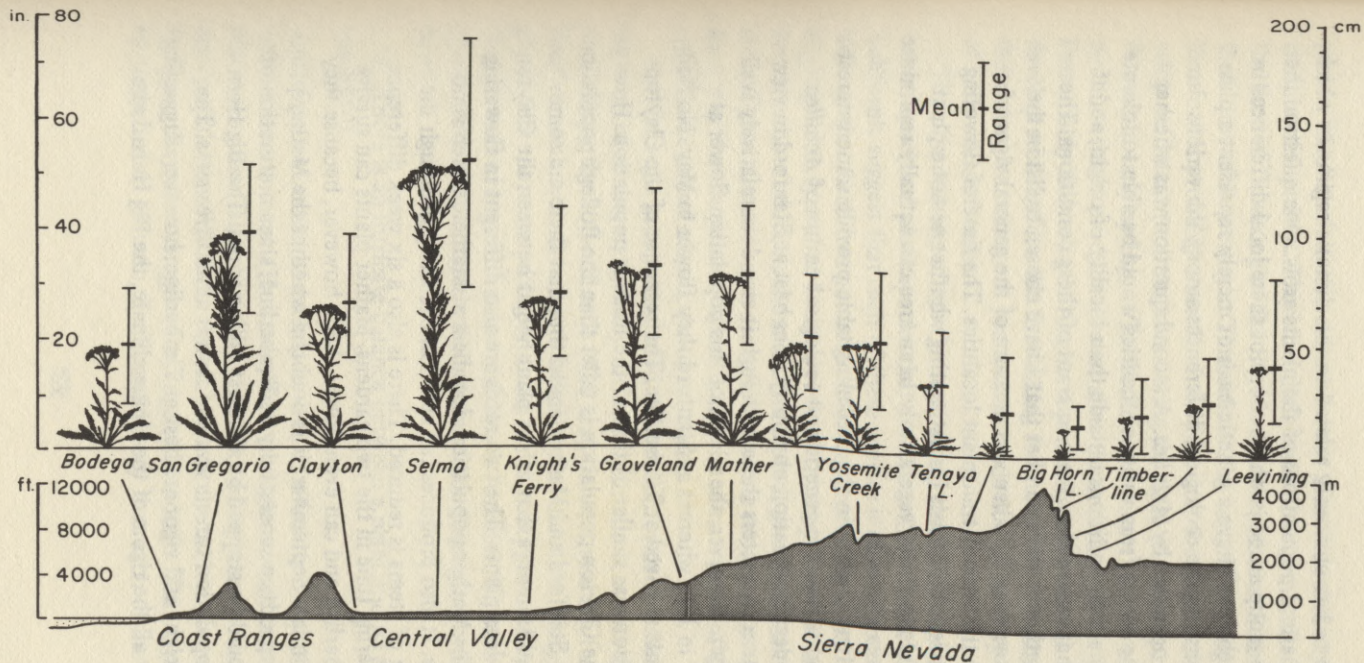


Fig. 7. Diagrammatic transect across central California showing origin of several *Achillea* populations studied by the Carnegie group. Plant specimens represent the mean height of each population grown at Stanford.

are more or less obviously related to the climatic regime in which various natural populations of the plants grow. One question the Carnegie group asked is whether or not these local differences in plant "behavior" have a genetic basis or merely represent a plastic response to the ecological differences among the various habitats occupied by *Achillea*. A second question was whether or not the plants from various localities would be able to tolerate environmental conditions outside their locality of origin, and if so, to what extent they were tolerant of these conditions. The stem length and stem number that I have chosen to list in the table above may be taken as a measure of the general vigor of plants in the various transplant localities. The time of flowering may provide some basis for estimating whether or not a plant that is able to thrive vegetatively in an area can actually reproduce in the area via seeds.

The figures given in the preceding table provide some interesting insights into the genetic and ecological nature of *Achillea*. The Bodega population obviously does best at Stanford in view of its stem characters there, although it also does relatively well at Mather. However, the plants of this population flower at Mather in July whereas at Stanford they flower in May. No Bodega plants survived at Timberline. The response of the Clayton population was similar to that of the Bodega population. However, the Clayton population is taller than the Bodega population at both Stanford and Mather, indicating that there are some genetic differences that affect plant height between the Clayton and Bodega plants. The two races are also different in flowering time. The Mather population does best at Mather, which is no surprise. It also produces tall stems at Stanford, although the number of stems is reduced. There is also a six week difference in flowering time in the two gardens. Mather plants can survive at Timberline and can even flower there; however, because they flower in late September, it is doubtful whether the Mather plants could reproduce successfully at Timberline, since maturation of seed would be stopped by the first killing frosts. The Big Horn Lake population can survive and flower at all three sites. The plant height and vigor are best at Timberline, however, suggesting that for all the rigors of the alpine climate, the Big Horn Lake

plants "like" their native climate better than the relatively gentle climate of Stanford. There is a difference of four months between the time of flowering of the Big Horn Lake plants at Stanford and their time of flowering at Timberline. The early flowering at Stanford is probably a result of the fact that the plants can develop sufficient food reserves during the mild winter to produce flowers in early spring; at Timberline, the plants require about two months to produce flowers after the snow leaves the ground. Presumably flowering in August is generally early enough to develop seeds before the first killing frost of autumn, although there must be numerous years when seeds do not develop because of early severe freezes.

The observations of the Carnegie group on *Achillea* and some other, unrelated plant species that are also widely distributed in California suggest that each of these species is able to occupy a wide range of habitats not because of the great plasticity of a single genetic type, but because each of these species is subdivided into a number of local, climatically adapted, genetically different races. These climatic races are called *climatic ecotypes*, in the same way that serpentine-tolerant and -intolerant races of *Gilia capitata* are called *edaphic* (soil) *ecotypes*.

The Carnegie group concluded that in California *Achillea* is made up of eleven statistically different climatic ecotypes that occur along the 200-odd mile (322 km) transect running from the Pacific coastline to the eastern boundary of the state. They suggested that there are probably hundreds of ecotypes of *Achillea* over its entire range in Europe and North America. To paraphrase some of the major conclusions of the Carnegie workers based on their transplant work:

1. There is an intricate balance between a plant and its environment.
2. Species consist of ecotypes, each of which is in equilibrium with its environment. (However, their transplant work indicated that there was a fair amount of variability of response within each population. While the figures given in the table above are averages, they are averages of a range of responses. This variability suggested to Clausen, Keck, and Hiesey that each of the

populations of *Achillea* has the potential for responding to gradual changes to its environment, that is, these populations have not become so closely and invariably adapted to their immediate habitat that they would become extinct as a result of slight environmental change.)

3. A species is widespread only if diversified into local ecological races or ecotypes. (This generalization may not be true of weedy plant species or some forest trees.)

One practical consequence of an understanding of the genetic complexity of wide-ranging plant species is that now, when foresters choose seeds of forest trees to provide seedlings for reforestation of logged or burned areas, an attempt is made to select seeds originating from populations growing near the area to be re-seeded, or at least from a population occurring under similar ecological circumstances.

Life Zones of California

Much of the preceding discussion has been concerned with factors that affect the distribution of plant species in California. Any factor that influences the distribution of a plant species will also have an influence on the distribution of plant communities, since a plant community is an aggregation of several plant species.

An early attempt to describe the biotic composition of North America was made by the American biologist C. Hart Merriam in the 1890's. Merriam recognized that as one ascends a mountain the vegetation is stratified into horizontal zones or bands that are characteristic of certain elevations. In a very general way, these changes in the vegetation that are observed as one ascends a mountain are similar to the latitudinal vegetational changes that occur from sea level in the southern parts of North America to sea level in the northern part of the continent. For example, the tundra vegetation of mountain tops in the central Rockies bears a general similarity to the vegetation of the arctic coast of Alaska — or at least this similarity seemed to be a real one to Merriam. As a consequence of these general observations, Merriam formulated the *Life Zone* concept. The essence of this idea