ECOLOGY

VOL. III OCTOBER, 1922 NO. 4

CONDITIONS INDIRECTLY AFFECTING VERTICAL DISTRIBUTION ON DESERT MOUNTAINS

FORREST SHREVE

Desert Laboratory, Tucson, Arizona

Differences in altitude carry with them differences in so many of the physical conditions affecting organisms that for many years we will have a rich field for ecological investigation in the study of these conditions, and of the relation in which they stand to the distribution and activities of plants and animals, including man. Dissimilarities in the character of the altitudinal changes, whenever any two separated regions are compared, add still further complexity to the series of problems which is presented by the biota of mountainous areas. The influence of altitude *per se*—that is, of differences in barometric pressure—has been studied by animal physiologists, but has yielded no conclusive results of importance at the hands of plant physiologists. It is the altitudinal differences of insolation, temperature, rainfall, humidity, evaporation, and a score of related conditions that make up what we were formerly pleased to call "the factor of altitude."

The desert areas of the southwestern United States offer an excellent field for the investigation of life and conditions as influenced by altitude, not only on account of the numerous mountains of all orders of magnitude, but also because the region has been so little disturbed by the activities of man. For several years the writer has been engaged in a study of the vertical distribution of plants in southern Arizona, with particular reference to the Santa Catalina Mountains, near Tucson, but with numerous visits to other mountains in Arizona and adjacent States. The principal aim of this work has been to bring together, on the one hand, data regarding the vertical distribution and upper and lower limits of vegetations and characteristic species, and, on the other hand, to determine the altitudinal gradients of some of the physical conditions of greatest importance to organisms. By the correlation of these two sets of data it is possible to determine the limiting groups of conditions with a precision which is at least akin to that secured in a series of cultures grown under controlled conditions.

On an ideal mountain, having the form of a cone, with uniform gradient from base to top, without irregularities of surface, and with identical soil

[**Ecology,** Vol. III, No. 3 (pp. 181–268) was issued September 18, 1922.]

throughout, it would be possible to determine very clearly the relation between the vertical ranges of the biota and the equally ideal gradients of conditions. However, under the natural departures from the ideal, it is necessary to make many interpretations of observed phenomena by way of separating the features due to the operation of the normal vertical gradients of conditions, and the features due to local departures from the normal.

The most common manner in which the topographic irregularities of a mountain may cause departure from the ideal vertical distribution of organisms is simply to raise or lower the limits. In all of the desert mountain ranges there is a marked difference in the vegetation of ridges or peaks and of the bottoms of valleys at the same elevation. There is also a striking difference between the vegetation of north and south slopes at all elevations. In both of these cases we have departures from the distribution that would be found on an ideal mountain cone or that actually found on a gently rising plain. It results in the former case in an interdigitation of contiguous zones of vegetation, and in the latter case in producing alternation or inversion of vegetations.

The object of this paper is to describe some other cases in which the variety of the earth's surface so greatly modifies the vertical gradients of physical conditions that dissimilar communities of plants and animals may be found at the same altitude in adjacent localities.

The general character of the vertical zonation of plant and animal life on the desert mountains of the southwest is similar in all of the ranges from the Colorado River eastward to the Pecos. Rising from plains with desert, desert-grassland transition, or grassland vegetation, the altitudinal zones may be roughly grouped as desert, encinal (open evergreen oak forest), and forest (chiefly coniferous). In mountains rising from plains of sufficient altitude to bear grassland the desert zone is not found, but encinal occupies the lowest mountain slopes.

The actual elevations at which encinal or forest will be encountered in ascending a desert mountain will depend primarily on whether observation is being made of a ridge or valley, or of a north or south slope. The normal lower limit may be defined as the average of the lowest occurrences on north and south slopes respectively; or in the comparison of different mountains it may be more convenient to contrast the lowest or highest occurrences on slopes of the same orientation, away from the local influence of streams or springs. The lowest occurrence in valleys is an extremely variable datum, as individual forest trees will sometimes descend along streams 3,000 ft. below their lowest north slope occurrence.

After the modifying influence of topographic irregularities has been thus eliminated, the lowest normal occurrence of encinal or forest will be found to depend secondarily on three features: (*a*) the elevation of the plain from which the mountain rises, (*b*) the total elevation that the mountain attains,

(*c*) the mineralogical character of the mountain and consequent nature of its soil.

As an example of the first of these cases, we may compare the southwest faces of the Santa Catalina and Pinaleno (Graham) Mountains. The basal elevation of the former is 3,000 ft. and the lowest pines and accompanying forest vegetation will be found at about 6,000 ft. The latter range has the same type of rock and soil and a basal elevation of 5,000 ft., and the lowest pines on south slopes are found at 7,800 ft. In other words, the increase of 2,000 ft. in basal elevation has pushed the forest upward about 1,800 in the Pinaleno Mountains. Since these two mountains are only 90 miles apart and almost identical in their orientation, character of rock and soil, and in their general vegetation, it would appear that the lower limit of forest is determined by the same conditions in each case.

It is obvious from meteorological considerations that we should have differences in the gradients of climatic conditions in two mountains of different basal elevation. One of the most important expressions of the conditions which control the lower limitation of encinal and forest is the ratio of evaporation to soil moisture. This ratio has been determined for several elevations in the Santa Catalina Mountains,[1] but it has not been possible to secure figures for the Pinaleno Mountains. Further investigation will doubtless disclose a close identity between the ratios for the lower edges of encinal and forest in the Santa Catalina and Pinaleno mountains, in spite of the difference in the actual elevation of "timber line" in the two.

A related case in which different types of vegetation may be found at the same altitude is to be observed in comparing small mountains with larger ones in close proximity and having the same basal elevation. The smaller mountains will be found to have desert species and to lack encinal species at elevations which are occupied by encinal in mountains of greater total height. On the Santa Catalina Mountains the lowest north slope occurrence of encinal plants is about 4,200 ft., and an open stand of junipers and evergreen oaks covers the south-facing slopes at 5,500 ft., while a closed stand of oaks, juniper, and pinon occupies north-facing slopes at that elevation. Twenty-six miles northwest of the summit of the Santa Catalina Mountains is a small isolated granitic range, Black Mountain, with a basal elevation approximately 500 ft. higher than that of the Santa Catalinas. This mountain attains an elevation of 5,583 ft. On the south face of the summit there are no arborescent representatives of encinal, while the north slopes are occupied mainly by a thicket of *Ceanothus greggii* and the shrubby oak *Quercus turbinella,* together with a few individuals of *Quercus emoryi* and *Q. arizonica* not more than 6 ft. in height (fig. 1 A). The latter are the commonest trees of the encinal and reach a height of 25 to 30 ft. at the same elevation and slope

[1]Shreve, Forrest, "The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors," Carnegie Inst. of Wash. Pubn. 217, 1915, p. 92.

exposure on larger adjacent mountains. In this comparison it is necessary to deduct 500 ft. from the elevation of Black Mountain on account of its higher basal elevation. We then have a north slope at the equivalent of 5,083 ft. exhibiting the same vegetation that is found at the lowermost edge of the encinal in the Santa Catalinas at 4,200 ft. In other words, the vertical gradient of environmental conditions on Black Mountain is such as to permit desert species to range about 900 ft. higher than they do in the Santa Catalina, El Rincon, Santa Rita, and other near-by ranges of greater elevation, and to push the encinal zone upward for a corresponding distance.

The altitudinal gradients of climatic conditions have not been determined for any of the smaller mountains of southern Arizona. There is strong likelihood that they would not correspond with the gradients for the larger mountains, but would more nearly resemble those that have been worked out from Weather Bureau data for a number of towns in Arizona which are situated at different altitudes in open relatively level country. There is little doubt

FIG. 1. Illustrating desert species reaching a higher elevation on rhyolite than on granite. *A*, low shrubby thicket on the north slope of Black Mountain at 5,500 feet. *B*, Encinal trees on the north slope of the summit of Mt. Fagan at 6,000 feet.

that appropriate instrumentation on the summit of Black Mountain would show it to have less rainfall and higher evaporation than the corresponding altitude in the Santa Catalinas.

In selecting examples to illustrate the influence of basal elevation and total elevation on the absolute altitude of vegetational limits, care has been taken to select mountains for comparison which have the same mineralogical and soil character. This precaution is necessary in view of the importance of the nature of the rock and soil in determining the vertical limits of vegetations when other conditions are alike. The lowest absolute elevations are reached by encinal and forest on gneiss and granite, and desert forms correspondingly attain lower maximum elevations on those rocks and their derived soils. The vegetational zones are higher on basalt, rhyolite, and other volcanics, and—at least with respect to certain conspicuous species—still higher on limestone.

To illustrate this feature a comparison may be made between Black Mountain, which has already been mentioned, and Mt. Fagan, an isolated outlying summit of the Santa Rita range, situated 63 miles S-S-E of Black Mountain, and having the same basal elevation and a summit altitude of 6,175 ft. Black Mountain is granitic, while Mt. Fagan is formed of rhyolite throughout its upper elevations. The vegetation of the north slopes of Mt. Fagan near the summit is similar to that on the north slopes of the summit of Black Mountain. The evergreen oaks are fewer on Mt. Fagan (fig. 1 B), but attain greater size, and the shrubs form occasional clumps rather than a continuous thicket (fig. 1 A). The two mountains, having the same basal elevation and differing only 592 ft. in elevation, exhibit approximately the same phase of the altitudinal gradient of vegetation on their summits. Such desert types as the cactus, *Opuntia chlorotica,* and ocotillo, *Fouquiera splendens,* reach the summit of Mt. Fagan, but do not attain the lower summit of Black Mountain. In short, the difference in the mineralogical character of

FIG. 2. Open forest of Arizona pine *Pinus arizonica* in Bear Canon, Santa Catalina Mountains, looking west along a north-facing slope at 6,000 feet

the two mountains appears to influence the vertical distribution of plants by about 600 ft. Under identical amounts of precipitation the granitic and rhyolitic soils would differ in penetrability, water-holding power, and in their capacities for losing water by evaporation; and these differences will undoubt-

edly be found to explain the higher elevations reached by desert plants on volcanic soils as contrasted with granitic ones.

The combined influence of the mineralogical nature of mountains and their total elevation is well exemplified in comparing the north slopes of Mt. Fagan just below the summit, at 6,000 ft., with a north slope on the granitic soil of the larger Santa Catalina Mountains, 34 miles distant (compare figs. 1 B and 2). North slopes bearing vegetation similar to that of the north slope of the summit of Mt. Fagan may be found on the Santa Catalina Mountains 1,800 ft. below the stand of pines shown in fig. 2. From this must be deducted 500 ft. to allow for the difference in basal elevation of the two mountains. This offers some evidence that the separate modifying influences that have been described are additive, since the effect due to the character of the soil is equivalent to about 600 ft. of elevation, and that due to the total elevation of the mountains is about 900, while their combined effect in the case cited is 1,300 ft.

The influence on the vertical limitation of desert species which is exerted by limestone and its derived soil may be clearly observed in the Empire Mountains, a small range 31 miles southeast of Tucson, with a basal elevation of approximately 4,000 ft. and a summit elevation of 5,360 ft. Creosote bush, *Covillea,* reaches its highest elevations on granitic outwash in the Tucson region at about 3,050 ft., occasionally appearing up to 3,500 ft. in small colonies. On the limestone slopes of the Empire Mountains it reaches 4,500 ft. in characteristic dense stands, and occurs infrequently up to nearly 5,000 ft. Ocotillo, *Fouquiera splendens,* ceases to be a characteristic plant of the desert slopes of the Santa Catalina Mountains at 4,600 ft., and the highest isolated individuals are found at 5,600 to 5,800 ft. On the limestone soil of the Empire Mountains it flourishes in great abundance up to 5,000 ft., and on limestone in the loftier Swisshelm Mountains, 48 miles to the eastward and with the same basal elevation, it ascends to 6,700 ft. On volcanic soils its highest observed elevation is 6,175 ft., on the summit of Mt. Fagan.

Appropriate localities have not yet been examined for determining the lowest elevations of encinal and forest on limestone soils, and more extensive and diversified outcroppings must be examined in order to complete our knowledge of the upper limits of numerous desert species that have not yet been detected on that type of soil.

The physical texture of volcanic soils, with the exception of that derived from basalt, is such as to offer a ready explanation of the high elevations reached by desert plants on them, since the coarse texture prevents the retention of moisture and carries the soil moisture conditions of the desert up to elevations at which the rainfall may be 50 percent greater than it is on the desert floor. In the case of limestone soils, however, the texture appears to be favorable to the retention of moisture, and the causes underlying the high altitudinal limits of desert species on these soils requires investigation.