Alpine Timberlines in the Americas and Their Interpretation

R. Daubenmire

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Edited by

J. E. Potzger
The Butler University Botanical Studies journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana’s vegetation in past decades. Authors were Butler faculty, current and former master’s degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler’s first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal’s publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor’s degrees and 75 master’s degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner, included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master’s students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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ALPINE TIMBERLINES IN THE AMERICAS AND THEIR INTERPRETATION

By R. Daubenmire

The State College of Washington

The literature of plant geography has long contained references to the facts that (1) in progressing from the poles toward the equator, alpine timberline increases in elevation above sea level, and that (2) the elevation of this timberline exhibits considerable variation at any one latitude on different mountain systems (Gannett, 1899; Smiley, 1921). More recently a third fact concerning the geography of this vegetation boundary has been documented; the latitude-altitude relationship is not rectilinear (Herzog, 1931; Daubenmire, 1943; Troll, 1948).

In the present paper the writer has undertaken to summarize all the published information on the elevation of American alpine timberlines that is available to him, the dry timberlines at the bases of the Cordilleras being completely ignored, in order to bring these three phenomena into sharper focus. Because of the extreme scarcity of prerequisite climatologic data, and the unavailability of most of these to the writer, no extended inquiry into the etiology of alpine timberline can be attempted. However, after describing the geographic facts, the principal theories as to the causes of upper timberline on mountains will be briefly reviewed in relation to certain data compiled with reference to alpine timberlines of North America.

ALTITUDINAL CHARACTERISTICS OF AMERICAN TIMBERLINES

In assembling data on the elevation of alpine timberlines at specific locations, one often finds considerable variation in values given by different authors for the same area. This may be attributed to (1) differences among writers as to whether they have given the elevation of the forest line (the upper edge of continuous forest), the tree line (the altitude of the highest stunted tree), or a point midway across this zone of transition between forest and alpine tundra, which is the interpretation favored by the writer. Additional discrepancies
undoubtedly have arisen out of the fact that the elevation of timberline is influenced to a certain extent by the direction of exposure, by the height and proximity of surrounding mountains, and by soil. Because of all these complications, latitude-altitude curves of timberline elevations as compiled from the literature require much smoothing, but even so, well-defined trends are revealed.

In Figure 1 are four curves based upon records assembled from scattered publications and from the writer's field notes. The short line A represents the altitudinal relations of timberline from Maine to New York. Only within this region are the Appalachians high enough to have a climatically determined upper timberline comparable with that of the Cordilleras.* Records for the high mountains along the Pacific coast from Prince William Sound, Alaska, to the southern Sierra Nevada Mountains of California, are indicated by + signs and represented by smoothed line B. Curve C represents the mean altitude of alpine timberline along the divide of the Cordillera from the arctic tundra to the equator. Curve D is redrawn from Troll (1948) who presented a diagram considered typical of the earth, combining data from Eurasia and Mexico to represent the northern hemisphere.

Figure 2 contains a continuation of line C in Figure 1 from the equator southward to Tierra del Fuego, based on the few separate accounts available to the writer. Line D is a continuation of Troll's diagram which is based on data from all parts of the southern hemisphere. Line E represents forest limits in the easterly range of the Andes, and F the same for the westerly ranges, both being redrawn from Herzog (1931). The gap in those curves based entirely on South American data is occasioned by the treeless segment (puna) of the Andes which finds no counterpart in North America.

* Timberlines of the southern tip of the Appalachians have the characteristics of climatic timberlines, but the altitude is far too low to fit into the otherwise harmonious altitudinal pattern of North American timberlines, and the climatic limitation appears to be of a very special character. These bald summits are probably no more than analogous with the usual type of montane timberline. In the writer's opinion, the closest homolog of these balds are the grass-covered southwest exposures of steep bluffs in forested regions just east of the mid-continent grassland. For highly suggestive meteorologic studies of the southern Appalachians, see Donley & Mitchell (1939).
In spite of discrepancies in the data from different sources, several facts seem well established. First, along the main axis of the Cordilleras, the altitude of upper timberline increases from the arctic and antarctic regions toward the equator to about the 30° parallel in the northern hemisphere, or the 25° parallel in the southern hemisphere, at which points the curves tend to flatten abruptly. From these points of flexure toward the equator, the altitude of timberline is rather constant except for a slight dip centered on the equator.

Secondly, upper timberlines on the three most important mountain axes in North America show the same north-south cant in temperate latitudes of approximately 110m per degree of latitude. There is a strong suggestion that the cant of timberline in temperate South America is essentially the same.

A third major conclusion is that where they may be compared along the same parallel, the elevation of alpine timberline in North America is lowest in the Appalachians, highest along the continental divide, and intermediate on the mountains near the Pacific coast.

Finally, timberlines in temperate South America are lower on ranges adjacent to the coast in comparison with others farther inland, which is likewise true in the extratropical Cordillera of North America and on low mountains in northeastern Canada (Hustich, 1954), but the reverse of the situation in tropical South America. As Herzog (1931) points out, the rule which fits all these cases is that alpine timberlines are lower on the wetter side of a major mountain system.

THE ETIOLOGIC PROBLEM

To the long-standing problem of the etiology of upper timberlines from the autecologic viewpoint, there may now be added three relatively new ones of geographic scope. We now need an explanation of the break in the altitude-latitude curves which falls at 30° and 25° in the north and south hemispheres, respectively. Also, the differences in elevation of timberlines on different mountain systems that cross the same meridian present a challenge, as does the reversal of this relationship within the Cordillera of South America.

The solution of these problems must be founded upon two bodies of facts, both of which are far from complete. One of these is
autecologic and concerns the evaluation of factor complexes that become inimical to trees above certain altitudes. The other is information on the altitudinal and latitudinal variations in climatic conditions.

Each of the tree taxa which forms a part of timberline in different parts of the world unquestionably has its own special limits of tolerance of the climatic vicissitudes of high mountains. The fact that timberline curves for the Americas exhibit such general uniformity of elevation over wide area, even though wholly distinct floras are involved, points to the existence of an important but as yet unknown ecologic principle. The relationship might well prove analogous to that of plants and the wilting coefficient of the soil, in which the environmental force withholding water abruptly increases beyond the absorbing capacities of all plants even though these capacities are variable. Another fact which may be interpreted as indicative of the existence of a principle of broad significance is that the many genera which form alpine timberline are represented by evergreen taxa at this ecotone.* Therefore, the evergreen habit appears more closely adapted to the peculiar climatic limitation than is the deciduous. If this view is correct, that potential differences in timberline elevation attributable to genetic differences among the trees involved are submerged beneath some fundamental environmental force that is most nearly compensated by evergreenness, the universality of the phenomenon would appear to immeasurably reduce the complexity of the ultimate explanation. This concept is in accord with the conclusion

*If the subalpine Betula tortuosa forests of the Scandinavian mountains appear to provide an exception to this generalization, the view may be taken that here in northwest Europe the circumpolar Picea-Abies-Betula forest has been decimated by glaciation so recently that nothing more fundamental is involved than the temporary (in the geologic sense) loss of local ecoregions of the two evergreen genera which nearly everywhere else in the northern hemisphere are conspicuous at alpine timberline. Referring back to the bald summits of the southern Appalachians, the historical factor cannot be used here, for the area immediately to the north and at comparable elevation, contains Picea rubens, Abies fraseri, and Betula lutea. The transition from temperate forest to grassland without intervening taiga, coupled with a conspicuous lack of widespread alpine floristic elements, may be taken as evidence that this grassland should not be placed in the same phytogeographic category as tundra. In certain parts of southern Europe, deciduous angiosperm forests also extend to upper timberline, as in the southern Appalachians, but taiga is the more usual type of forest here (Schröter, 1926).
of Hustich (1952) who considers the ecology of trees at the subarctic timberline to be "almost the same" even though different taxa form different segments of the line. It should be noted, however, that this opinion stands in sharp contrast to that of J. Braun-Blanquet (1951, p. 135) who considers alpine timberline not to be climatically equivalent throughout for the reason that the different taxa involved have different ecologic amplitudes.

**TIMBERLINE THEORIES***

*Excessive light.* Collaer (1934, 1940) has championed the theory that in the Alps the upward increase in light intensity impairs leaf functions and in this way is critical in setting the upward altitudinal limits of taxa and consequently of forests.

The writer knows of no source of climatic data in the Americas which would permit a critical test of the applicability of this theory to the problems under consideration, but there is a special situation that has an important bearing upon them. Maps published in "Climate and man" (U.S.D.A., 1941) show that the peninsula of oceanic climate which extends far inland into western North America along the Canada-U.S.A. border crosses both the Cascades and the Rockies. The number of hours of sunshine both in winter and summer (pp. 738, 739) is reduced, the average number of cloudy days (p. 743) is increased, and the number of days with dense fog (p. 737) is increased in this peninsula. If any component of solar radiation were rather directly related to the cause of timberlines, the curves in Figure 1 should be deflected in this latitude, but such does not appear to be the case. It must also be noted that Collaer resorts to dry winds or low winter temperatures to explain the fact that timberline elevations in the Alps vary within short space in such a fashion that the light hypothesis alone is inadequate.

*Carbon dioxide deficiency.* Decker (1947) has suggested that the vertical decrease in partial pressure of carbon dioxide in the atmosphere, which drops from approximately 22.8mm at sea level to 13.0mm at 4572m higher, may be a critical factor limiting the upward extension of plants. However, this can hardly account for timberline, for research has not indicated that trees have higher requirements for carbon dioxide than the shrubs and herbs which always

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*For historical background, see Takahashi (1944).*

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extend higher. Furthermore, carbon dioxide pressure varies directly with altitude, whereas timberline elevations vary greatly along both parallels and meridians. Although there can be little doubt that the usual carbon dioxide deficiency becomes progressively greater with increase in altitude, this gradient cannot be related to the latitudinal and longitudinal gradients, or local variations, exhibited by timberlines.

Snow depth. Two biologists have concluded that the excessive depth and persistence of snow is a major factor determining upper timberline in the Selkirk Mountains of southeastern British Columbia (Shaw, 1909a) and in the Cascade Mountains of Washington (Taylor, 1923). These observers based their hypothesis principally on the fact that at high altitude in these mountains, tree seedlings cannot get established in depressions which accumulate snow early in autumn and retain it well into the next summer. Ridges that accumulate little or no snow cover support trees that are symmetrical, but have dead lower branches that suggest smothering by snow.

On both these mountain systems there are ridges that remain essentially free of snow but extend far above timberline, so the question of why trees do not follow the ridges farther upslope remains unanswered. It seems sufficient to consider snow accumulation as a factor controlling only the amount and distribution of trees in the levels just below tree line. Griggs (1938) has also expressed doubt as to the adequacy of this hypothesis on other grounds. Certainly if the evidence supporting the snow-depth hypothesis is not conclusive in those limited regions where snow-depth is recognized as above-average for alpine regions, it is even less adequate as an explanation of any of the major geographic trends under consideration.

Wind. In most extratropical parts of the northern hemisphere, trees at upper timberline are so dwarfed and wind-trained that ecologists have long had before them the hypothesis that wind sets the upper limits of trees on mountains. This hypothesis seems well supported by interpretations of phenomena to be observed widely at upper timberline north of the Tropic of Cancer. (1) The trees are asymmetrically deformed, the direction of asymmetry being consistent among individuals so as to suggest the influence of strong winds from a constant direction. (2) Projecting twigs frequently show the effects of fatal winter-desiccation, and the net effect of
this is to maintain smoothly contoured canopies surfaced with compactly crowded laterals, a new whorl of which is sent out each time the terminal is winter-killed (Shaw, 1909b). (3) The last trees up-slope are situated in depressions or equivalent microhabitats which offer a measure of protection from wind (Sochava, 1944; Daubenmire, 1943; Griggs, 1938, 1946). (4) Timberline may extend as much as 518m higher on the leeward slope of mountains in comparison with windward slopes (Schröter, 1926). (5) Timberline conditions may be reproduced locally on exposed knobs, shoulders, or passes far below the average elevation of upper timberline, and tends to rise and fall paralleling the contour of a ridge situated at right angles to the wind (Schröter, 1926; Antevs, 1932).

Within the tropics and beyond in the southern hemisphere these phenomena seem to be largely absent. The evergreen trees are commonly stunted and produce dense canopy-shells, but no other feature of the trees or their distribution suggests that wind is critical in these latitudes (Troll, 1948; for apparently local indications of wind importance, see: Haumann, 1918; Miller, 1918, p. 59; Lejungner, 1939).

In addition to the evidence afforded by the morphology and distribution of trees in the northern regions, climatic data (Table 1) show a pronounced vertical increase in winter wind velocities on mountain slopes. Bates' results (1924) are notable for the fact that just five hundred feet below timberline measurements of wind velocities were less than half the velocities at timberline. He was so impressed by this comparison that he stated: "There is no doubt in the mind of the writer that here (southern Colorado) the upper limit of timber growth is set by the mechanical effects of the wind and only indirectly by temperature conditions." A study in Italy that may be pertinent here showed the existence of a rather sharp increase in wind velocity at an altitude of 1800m, in a region where the land surface was 272m (Humphreys, 1916).

Despite the fact that wind data are very strongly influenced by the topographic setting of the measuring site, by the elevation of the anemometer above the ground, and by the nearness of trees, the meager data available appear to be adequate to draw certain conclusions. In Table 1 the stations are arranged according to their phytogeographic position with respect to upper timberline. The timberline elevations used in this case are intended as averages for the re-
For the purpose of this comparison, the use of average rather than actual timberlines seems desirable because (1) in most cases specific data for timberline elevations at the weather station are unavailable, or sources differ in their estimates, so that reference to smoothed curves makes for uniformity in comparison, and (2) some weather stations are located on windy knolls and others in protected valleys so that timberlines at their locations may be abnormally lowered or raised by wind or heat influence. Another deficiency of the method lies in the fact that some of the records, which have been compiled from diverse sources, represent only a few seasons' observations. The winter velocity records for alpine tundra are impressive, but a most significant series of data are provided for Sandberg, California, which shows even higher values than on high mountains such as Pike's Peak. Sandberg is situated on a relatively low knob surrounded by chaparral with scattered pines, therefore far below upper timberline, but with the anemometer 30 feet above the ground. The conclusion seems inevitable that wind alone cannot explain the elevation of upper timberline. It may cause a local thinning of the forest, and intensify adversity imposed by other factors so that tree form and distribution are conspicuously influenced, but at least the mean wind
velocity has no independent value in this problem of etiologic plant geography. Possibly with temperature decreasing upward at the same time wind increases, a critical ecologic sum may be quickly reached and exceeded that explains the relatively abrupt change from forest to tundra. However, a concept that cold soil may aggravate transpiration stress finds no support in observations by Polunin (1933) that tree roots at arctic timberline readily conduct water while imbedded in frozen soil. Also there are localities with timberlines conforming to the continental elevation-pattern as figured above, but where there is no asymmetry of the last trees which is essential for the hypothesis of wind control (Daubenmire, 1953). Finally, it may be pointed out that there is a tacit assumption by advocates of this hypothesis that the wind influences that so strongly modify the appearance and distribution of old trees is lethal to seedlings, but almost no direct evidence has been presented (Griggs, 1938, p. 559).

Desiccation during temperature inversions in winter. Studies of vertical stratification of the atmosphere in relation to alpine timberline in Europe have uncovered an interesting ecologic phenomenon which may prove to exist over wide enough area to have a bearing on the present problems. Michaelis (1932) has presented data show-
ing that the upper surface of a cool humid cloud layer coincides with upper timberline in central Europe. Immediately above this cloud layer bright insolation, high air temperature, low relative humidity, and scanty snow cover all conspire to increase transpiration stress at a season when the soil is cold and absorption may be sluggish. Such conditions are stated as being frequent in central Europe, but the degree to which they are attained elsewhere is unknown, and the meteorologic phenomenon has not yet been related to autecology in a convincing fashion.

**Heat deficiency.** A very old theory on the cause of arctic and alpine timberline is that it represents a point on the scale of diminishing heat beyond which this form of energy is inadequate to meet anabolic requirements. This theory is supported by two types of evidence.

The distributional peculiarities of trees growing at timberline on Mt. Shasta in the southern Cascades was interpreted by Merriam (1899) as indicating heat to be the most critical deficiency. At timberline on this mountain, trees are confined to ridgetops, from which they extend a short distance down only those slopes that face west. Merriam pointed out that such ridgetop habitats receive more insolation than the valleys between, and that west-facing slopes attain high temperatures because they are subject to insolation at the time of day when the air is warmest. Although this feature of timberline is well marked on Shasta, and the interpretation apparently warranted, the same feature of timberline is not generally characteristic of other mountains in the Americas. It is pertinent in connection with earlier discussion to note that all trees at timberline on Shasta are prostrate wind-cripples but are confined to the habitats most fully exposed to wind.

The second type of evidence for the heat hypothesis is indirect: the relation between isotherms and variations in the altitude or latitude of timberlines. The earliest quantitative work on this problem in the 19th century suggested that the climatic limits of cold timberlines coincide roughly with isotherms representing 10°C for the mean temperature of the warmest month. In 1903 de Quervain (see Schröter, 1926) showed that daily maximal temperatures in summer provide monthly means that are even more closely associated with the position of cold timberlines, and Brockmann-Jerosch in an ex-
tensive monograph (1918) verified this contention with data drawn from wide geographic area.

Owing to traditional methods of presenting weather data by the U. S. Weather Bureau, emphasis is placed upon averages of the daily maximal and minimal temperatures, with a result that the botanically important maximal values are so quickly buried as to be not readily available. If it may be assumed that the mean temperatures of the warmest months are a reasonable approximation, even if definitely inferior, of climatic differences that would be indicated by the maxima alone, the data from high mountain stations that are assembled in Table 2 are significant. Despite shortcomings of the data, as pointed out above, the fact is clearly established that the temperature of the warmest month is closely related to the position of the station with reference to timberline, whereas the actual elevation of the stations and of the timberlines show no relationship. Since the data show remarkable homogeneity despite their divergent latitudinal and longitudinal origins, and the shortness of the record in most cases, one must conclude that there is high probability of heat being critical or at least being closely related to a critical factor of wide importance for upper timberline.

Still another correlation between climatic records and timberlines is provided by a comparison of the curve B in Figures 1 and 2 with curves published elsewhere showing the latitudinal variations in elevation of isotherms representing mean annual temperature. Below an altitude of 8 km there is pronounced rise in altitude of all isothermal curves from north polar regions to about 24-14° N latitude according to Clayton (1923) or 30-20° N latitude according to Humphrey (1929), with a slight decline further southward to the equator. The curves for the southern hemisphere are essentially mirror images of these. Thus the temperature curves for latitude and altitude closely parallel the timberline curves for altitude and latitude.

The temperature and timberline curves described immediately above bear an interesting relationship to the air-mass source regions. Between 0-30° is the maritime-tropical air-mass source region which is characterized by relative homogeneity. This latitudinal belt corresponds closely with that part of the alpine timberline curve which is essentially horizontal. From 30-60° N latitude is a transition zone in which the maritime-tropical and the continental-polar influences
alternate in summer and winter respectively. Above 60° falls entirely within the continental-polar air-mass source region. It is obvious that the latitudes covered by the continental-polar air mass, even if only in winter, are characterized by a strong and uniform N-S cant in the alpine timberline curve. This correlation, if it may be assumed to have any direct significance, suggests that the intensity or duration of winter conditions controls timberlines, for the break in the timberline curve coincides with the southern extremity of the air-mass transition zone, and the continental-polar influence extends this far south only in the cold season.

Jensen (1949) has attempted an autecologic interpretation of timberlines. He points out that trees have the life form with the largest unproductive, but matter-consuming mass (i.e., stem and root). Thus timberline is set at that point along the scale of diminishing heat where the total annual production of dry matter is balanced by carbon compounds needed for respiration plus the formation of new leaves, so that none is left over for wood accumulation. This hypothesis is not difficult to accept after one has closely examined trees more than a century old but with stems less than a meter in length and 2 cm in maximum diameter.

Although the evidence in support of the heat deficiency hypothesis is relatively strong, it must be pointed out that indirect information of this type is only suggestive of likely points of attack for experimental work in fundamental autecology. The temperature hypothesis must undoubtedly comprise a significant part of the final explanation for timberline positions, yet it cannot furnish the sole basis of explanation. Locally the details of tree distribution (as described earlier) show far more correlation with wind exposure than with altitude which varies rather directly with temperature. The fact that in the Rockies the largest trees of timberline species are found just below timberline, whereas in the Appalachians trees are gradually reduced in stature over nearly a thousand feet of altitude (Antevs, 1932), suggests that if different factors are not concerned in these two regions, at least different emphasis need be placed on the constituents of the same factor-complex.

Light deficiency. Since ultra-violet, light and heat energy are all derived from solar radiation, it is difficult to isolate these factors to study their separate influences, although this is desirable from the
physiologic standpoint. It is, therefore, not unnatural for the hypothesis to have been advanced that light deficiency, resulting from the upward increase in cloudiness in certain mountain regions, may be critical in setting the altitude of upper timberlines. Kolaevsky (1939) assumes that precipitation varies somewhat directly with cloudiness, then he uses the more abundant precipitation data to test his hypothesis that light deficiency plus heat deficiency are critical. His studies in Eurasia tended to confirm the hypothesis, and Zotov (1938) reached the same conclusion from studies in New Zealand.

In North America, precipitation during the main season of vegetative activity, at least, is unrelated to timberline altitudes, according to the compilations in Table 2. Since, on the other hand, the heat supply, as indicated by temperature measurements, bear a close relationship, the heat form of energy appears the more important. But it is to be noted that the superiority of the heat hypothesis rests in part upon the assumption that light variation is adequately estimated from precipitation data.

SOME CONCLUDING REMARKS

Whatever the causal factor-complex that determines the position of climatically determined alpine timberlines, it is one which affects tall and low plants differently, for at the alpine timberline trees are generally reduced in stature, but the limitation does not prevent shrubs and herbs from extending much farther upward. In other words, the critical intensities of the atmospheric complex do not extend all the way down to the ground surface. It is to be noted that alpine herbs and shrubs have life-forms that enable them to take advantage of the warm layer of air near the ground, and that tree taxa which are capable of producing shrubby ecophenes often form a broad belt of scrub that extend well above those individuals exhibiting the tree form.

On a broad scale temperature and biologic data are so consistently related that some aspect of the temperature factor must be accorded high importance in any adequate explanation of alpine timberlines. On a small scale the temperature-determined timberline may be lowered in extratropical regions by strong winds or later-persisting snow cover, to elevations somewhat lower than a position which temperature would more directly set. But despite the striking effects
of wind and snow in such places, their influence upon timberline elevations is too small to disrupt the pattern of gradual change in elevation across a wide range of latitude. Thus the regions where timberlines give the appearance of being wind-induced or snow-induced alternate without causing recognizable modifications in the configuration of curves representing all mountain systems of North and South America.

It is possible that the increasing emphasis on high altitude meteorology in connection with aviation will result in the accumulation of data which will throw more light on the timberline phenomenon. Yet past experience has shown that those aspects of weather which attract attention from the professional meteorologist are not necessarily those which are biologically critical. In the last analysis the ecologist will have to resort to direct experimentation in the field and collecting his own environmental data to make a significant physiologic evaluation of the complex of factors that vary with altitude.

SUMMARY

Along the main axis of the North American Cordillera, the elevation of alpine timberline rises steadily at a rate of about 110m per degree of latitude between about 60 and 30°, then declines very gradually to the equator. In those latitudes where comparison is possible, alpine timberline is lower in the mountains near the Pacific Ocean and still lower in the Appalachians, but the rate of change along each axis appears identical.

The graminoid vegetation of the mountain summits of the southern Appalachians is only analogous with the usual alpine timberline, appearing to owe its existence to aridity resulting from peculiar airmass phenomena.

In South America there is a similar cant in timberline elevations, but the point of flexure in the curve is closer to the equator (ca. 25°) and the relative height of timberline near and remote from the Pacific is reversed in temperate and tropical latitudes.

Because a great many genetically distinct trees contribute different segments of a timberline pattern that has remarkable geographic conformity, the hypothesis is suggested that a major autecologic principle is involved that may be analogous to the wilting co-
efficient of the soil, in which some environmental complex abruptly exceeds the tolerance of all trees regardless of variation among them.

The factor-complex is one that operates directly upon the tree life form, for shrubs and herbs extend well above timberline. From this it may be inferred that the critical conditions do not extend quite down to the soil surface.

The most promising autecologic theory to explain timberline is that it represents a point on the scale of diminishing heat supply where solar energy is adequate only to meet the annual requirements for respiration plus the requirement for foliage renewal, with a result that none is left to permit the development and maintenance of a large mass of non-productive cells as comprise the stem and root system of a normal tree. Evidence in favor of the heat-deficiency hypothesis is provided by (1) certain regions where the highest trees are on the best insolated habitats, (2) the conformity of timberlines to isotherms representing the mean of the daily maximal air temperatures of the warmest month, (3) the conformity of the north-south configuration of the timberline curves to the altitude of isotherms, and (4) the known fact that temperatures are higher in the layer of air near the ground, to which trees often become confined at their upper limits and in which shrubs and herbs extend far above timberline.

Winter winds and later-persisting snow may locally alter the appearance and elevation of timberline in extratropical parts of the northern hemisphere, but these influences never have enough significance to disrupt the general conformity between timberlines and isotherms. Hypotheses suggesting the importance of ultra-violet, of light, of carbon dioxide deficiency, and of desiccation during temperature inversions in winter all appear to offer little in explaining the position of alpine timberlines.
### TABLE I

Wind velocity in relation to mean timberline elevation in the U.S.A.

<table>
<thead>
<tr>
<th>Station</th>
<th>Elevation in Meters Above Sea Level</th>
<th>Mean Wind Velocity in Miles per Hour of Most Windy Month</th>
<th>Mean Wind Velocity as Miles per Hour of Most Windy Month</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pike’s Peak, Colorado</td>
<td>+800</td>
<td>25.0</td>
<td>25.0</td>
</tr>
<tr>
<td>Mt. Washington, New Hampshire</td>
<td>+400</td>
<td>42.5</td>
<td>42.5</td>
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<tr>
<td>Boulder County, Colorado</td>
<td>+350</td>
<td>16.5</td>
<td>16.5</td>
</tr>
<tr>
<td>Pike’s Peak, Colorado</td>
<td>+100</td>
<td>20.8</td>
<td>20.8</td>
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<td>Pike’s Peak, Colorado</td>
<td>-50</td>
<td>7.6</td>
<td>7.6</td>
</tr>
<tr>
<td>Boulder County, Colorado</td>
<td>-350</td>
<td>13.4</td>
<td>13.4</td>
</tr>
<tr>
<td>Sandberg, California</td>
<td>-1870</td>
<td>21.1</td>
<td>21.1</td>
</tr>
</tbody>
</table>

1 Instrument 3m above ground.
2 Instrument 6m above ground.
3 Instrument 9m above ground.

### TABLE II

Climatic data in relation to mean timberline elevation at different latitudes in the U.S. A. and Canada.

<table>
<thead>
<tr>
<th>Station</th>
<th>Elevation in Meters Above Sea Level</th>
<th>Mean Temp of Warmest Month in °C</th>
<th>Mean Monthly Precipitation in Inches</th>
</tr>
</thead>
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<tr>
<td>Pike’s Peak, Colorado</td>
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<td>5.1</td>
<td></td>
</tr>
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<td>8.9</td>
<td>6.26 6.10 6.15 7.48</td>
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<td>Old Glory Mtn., Brit. Col.</td>
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