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A Study of the Physiographic Ecology of Mount Ktaadn, Maine

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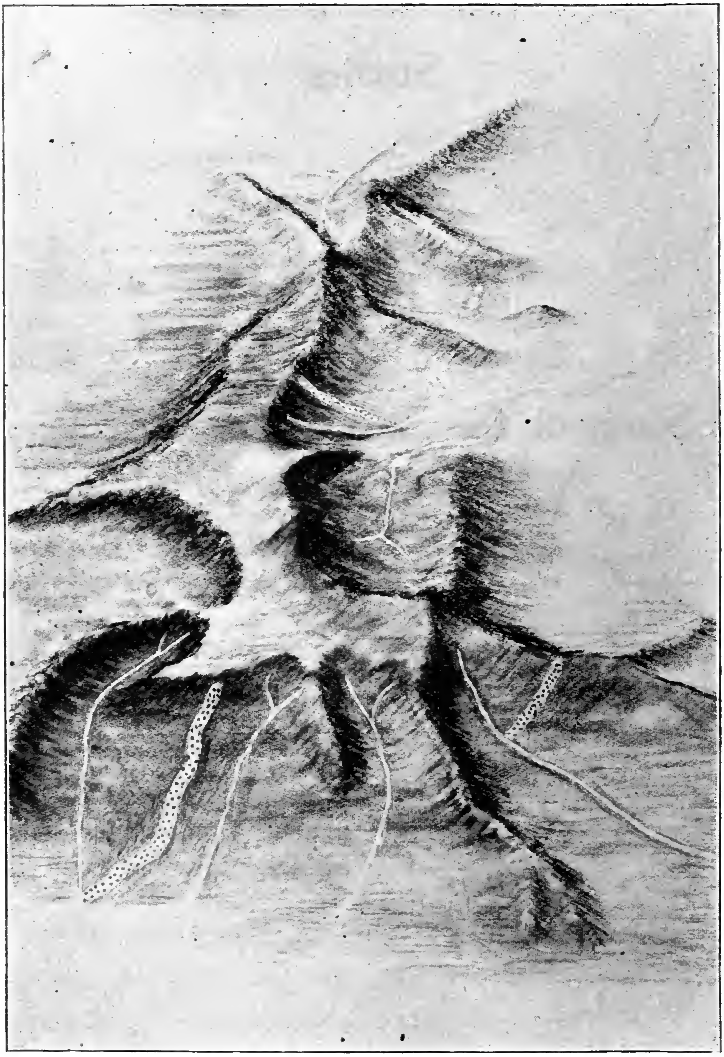

Figure 1. Relief map of Mt. Ktaadn, illustrating the topography of the upper 2,000 feet. The view point is from the south. The clear lines represent streams, the dotted lines land slides, and small clear spaces lakes. Further description in text.

A STUDY OF THE PHYSIOGRAPHIC ECOLOGY OF MOUNT KTAADN,* MAINE.

*In the spelling of this name Mr. Harvey has followed J. Hammond Trumbull, William Willis and C. E. Potter, authorities on the Abscalka language; also Thoreau, Dr. Chas. F. Jackson, and others.

From the White Mountains, on the eastern borders of New Hampshire, a mountain system traverses the State of Maine in a northeastern direction terminating in Mars Hill on the eastern boundaries of Aroostook county near the St. John's river. This system, presumably archean in age, has many notable interruptions and is represented now and then merely by widely distant hills and low peaks. From its southwest extremity in the White Mountains, of which Mount Washington (6,300 feet) is the highest peak, the elevation decreases toward the Kennebec river where the first appreciable break in the system occurs. Here the range gives way to an extensive stretch of low hills and broad swells reaching nearly to the eastern border of the State. From out this plain occasional high peaks arise, such as Mount Kineo on the eastern margin of Moosehead lake. In Piscataquis county the range assumes again a mountain character in Mt. Spencer and, increasing higher and higher toward the northeast, has its grand culmination in that majestic peak, Ktaadn. Again decreasing in elevation, the range continues its northeastern direction; Chase mountain in Piscataquis and Mar's Hill in Aroostook being the only two remaining peaks of prominence.

Ktaadn is a lonely mountain, rising with its foothills from an almost level plain which extends unbroken for miles to the south, west and north. Rising thus, in such a bold, abrupt manner, to an altitude of 5,216 feet above sea level and being the highest and most northerly peak[1] of any consequence in this northeast extension of the Appalachian chain, it is obviously exposed to all possible climatic vicissitudes and naturally becomes the most ideal place in the State for the study of alpine conditions, climatic influences, timber lines, ecological adaptions to alpine conditions, and the dynamics of mountain societies.

1. Mt. Ktaadn lies 161 miles to the northeast of Mt. Washington in Lat. 45°, 03', 40", thus being 1°, 37', 15", approximately 112 miles, farther north.

Though Ktaadn has been the goal of several botanical expeditions, extending over a period of some sixty-six years,[1] the flora has been treated wholly from the taxonomic and floristic aspect.

1. The first botanical records are those made by Prof. J. W. Bailey in the Am. Jour. Sci. **32**: 20-34. 1837. The mountain was described as early as 1804 by Chas. Turner, Jr., of Boston. "His account is preserved in the collections of the Mass. Hist. Society."

Exception might be made, however, of Dr. Harshberger's popular account[2] of the ecology of the mountain.

2. Harshberger, J. W. A botanical ascent of Mount Ktaadn, Me. Plant World **5**: 21-29. 1902.

The material for the present paper has been gathered from two visits to the mountain. The first made in 1898 during the last two weeks in September; the second in 1902 extending over the last two weeks in August.

The conclusions which the writer ventures are presented with the hope of exciting further ecological study in addition to purely floristic work upon the mountain. The conclusions drawn are given tentatively, but the writer fully believes that similar studies of the Mount Ktaadn flora, as well as of other alpine and alpestine regions would yield excellent results.

The author wishes to here express his obligation to Dr. Henry C. Cowles for many valuable criticisms and suggestions, Miss Nettie B. Dickson for the relief map of the mountain, and to Mr. John Thompson for figures 1, 7, and 10.

II. Topography and Physical Geography.

No attempt will be made to give a detailed description of the topography and physical geography of the mountain, for this has been thoroughly done by Hamlin,[1] Tarr,[2] and others to whose accounts the reader is referred. Only those facts will be presented which lend themselves to a better appreciation of the physiographic conditions bearing pertinently upon an ecological discussion. The writer has drawn very freely from the above articles. Subsequent reference, in this description, to the general features of the mountain will be rendered more intelligible by a study of the accompanying relief map (Plate I).

Mt. Ktaadn and its foot-hills constitute a continuous granite area eruptive through a vast region of stratified rock which forms even the lower slopes of the mountain itself. Though of the same range, Ktaadn is quite distinct as a mountain. To the south, east and west, stretches a vast plain whose elevation can scarcely be more than 550 feet above sea level. From this low

1. Hamlin, C. E. Observations upon the physical geography and geology of Mount Ktaadn. Bull. Mus. Comp. Zoo. Harvard. **7**: 206-223. 1881.

2. Tarr, R. S. Glaciation of Mount Ktaadn. Bull. Geol. Soc. Am. **11**: 433-448 1900.

extended expanse the mountain rises, not at first abruptly, but for miles by moderate gradations up to approximately one-half its altitude,—about 2,200 feet on the south side, and 2,900 feet on the east. To the East Branch of the Penobscot, 23 miles due east, there is from the South basin a gradient of more than 100 feet to the mile. From this gradual rise the upper half of the mountain rears itself abruptly, bounded by bare, precipitous cliffs and steep declivities sustaining vegetation.

These sharp declivities and precipitous walls terminate above in a narrow ridge or crest which bears the highest peaks and gives the mountain its general outline. From the lower slopes of this crest the various spurs arise. In shape the crest presents a striking resemblance to a gigantic fish hook with its bowl opening to the northeast. The shank, formed by the crest of the North mountain and the Northern ridge, curves strongly toward the northeast. The bowl and barb are represented by the Great Basin and Pomola respectively.

Along the southern base of the bowl, upon the peak-bearing crest, arise the two chief prominences of Ktaadn. They are less than 500 yards apart and differ in altitude some 15 or 20 feet. The two peaks are known respectively as the East and West peaks, the latter being the higher with an altitude of 5,215 feet, as determined by Prof. Fernald.[1] "Directly beneath the

1. Fernald, M. C. Bangor Daily Whig and Courier, November 9, 1894.

east peak (5,200 feet), shoots off to the southeast the longest of all the spurs, (the southeast spur) which, narrow above, widens greatly toward its foot." Beyond the peaks, a narrow much serrated crest, the outer limb of our hook, swings shortly northward forming toward its point, "first, the little tower-like peak known as the 'Chimney,' and then, across a narrow, square-cut notch, the peak, Pomola."

Pomola (4,819 feet) has a wide, convex northern face sloping off gradually with a precipitous foot to the floor of the south basin 1,900 feet below. In subsequent reference to Pomola this entire eastern limb of the mountain is to be understood. "Eastward from Pomola projects a narrow sharp ridged spur, the 'Horseback.' Towards its extremity, the 'Horseback' forks, and sends off to the northeast a lower, flat-backed spur." On the southern flank of this "Horseback" is the east slide.

Against the western limb of the bowl, and a few hundred feet below the crest, abuts the "tableland," an almost absolutely plane surface, inclined to the northwest at an angle of from five to seven degrees, and having a length of a mile and a half, and an area of more than five hundred acres. This "tableland" is bounded by a sharp brow from which extend several spurs. The South spur, a short, blunt projection widened at its tip, arises a few hundred yards west of West peak and runs slightly southeastward. The Southwest spur, a long, narrow ridge, has its origin at the southwest corner of the "tableland" and, bending sharply, runs a few degrees south of southwest. Midway between these two spurs and about a half mile below the brow is the head of the southwest slide.

From the West peak there is a sharp descent northward and westward, into which the "tableland" merges, down to the level of 4,250 feet; here, with the table land, it passes into the lowest part of the Central mountain, termed the "saddle." Northward from the saddle there gradually arises a rounded knob, the first North peak (4,700). By a moderate depression of the crest, this peak is separated from a second similar one, slightly lower and three-fourths of a mile farther to the northeast. Approximately one-half mile beyond along the crest is a third minor peak, some seventy-five feet lower than the first. The "saddle" thus naturally divides the peaks into two groups, known respectively as the North and South mountains.

From the First and Second North peaks two sharp, narrow spurs extend eastward enclosing the North basin. (Fig. 1). This basin, opening slightly south of east, resembles in shape the capital letter U. At the mouth, midway between the tips of the two spurs, is a knoll rising 50 feet, perhaps, above the floor of the basin proper (3,700 feet). About a mile long and half a mile wide it has an area of approximately 320 acres. In its floor are two small morainic ponds.

Between the more southern of these two spurs and the point of Pomola is enclosed the bowl of the hook, the great basin, (3,000 feet) which forms a vast amphitheatre. Viewed from above this basin bears a striking resemblance to an old volcanic crater. Approximately stated this great cirque is "from summit to summit east and west two and a half miles by a mile and a half from north to south" giving it an area of 2,240 acres.

From the southern end of the "saddle" a short spur juts out into the great basin which, with Pomola, encloses a second smaller amphitheatre, the South basin. In its floor (3,000 feet) lies Chimney pond (2,928 feet or 2,287 feet below West peak). The well nigh vertical walls of this basin terminate above in the crest which forms the heel of the hook and bears the "Chimney," Pomola, and the East and West peaks.

Beyond the peaks of the North mountain, the crest continues as the Northern spur extending some three miles to the northeast at a lower level (4,500 feet) and then drops abruptly. Russell mountain lies just beyond its tip.

The gradual slope directly west from the first North peak shortly passes into the Northwest spur which continues some three-fourths of a mile to the northwest at an approximate level of 4,400 feet. Between this spur and the walls of the Northern ridge, which here extend nearly north, is included the Northwest basin. The writer has recently described this basin and for details the reader is referred to this description.[1] Only the salient points will be repeated here. In general form the North west basin suggests the capital letter V with its base slightly rounded, and with a very broad gateway opening to the northwest into the valley of the Middle Wissattaquoik. Its eastern arm is formed by the precipitous west wall of the Northern ridge while the wooded north slope of the Northwest spur makes the other arm of our capital letter. By the confluence of these two arms as they join the North mountain, the rounded base of our letter is formed. The floor of this basin is virtually a shelf cut from the Northwest spur, apparently by glacial action. It has an altitude of 2,940 feet, 50 feet lower than South basin; and varies in width from 200 to 250 yards. From this shelf a precipitous descent of 250 feet leads to the valley proper below.

Nestled at the base of the Northwest spur and on the shelf described above, are four small ponds, evidently morainic in origin. Lake Cowles (2,938 feet) the largest and most western is about five acres in extent. Davis pond, next in size, less than

1. Harvey, LeRoy H., An ecological excursion to Mount Ktaadn. Rhodora 5: 42-46. 1903.

2 acres, occupies the eastern extremity of the shelf. Between these lie the two other ponds each less than half an acre in extent. The outlets of these ponds join sooner or later and empty as a common stream into the Middle Wissattaquoik some four miles down the valley. Rising up from, and occupying a large part of, the shelf are two *roches moutonnées* which with their flat tops and precipitous sides bespeak unmistakably a glacial origin.

The mountain then as an entirety is a long (9 miles), narrow, fish-hook-shaped, serrated crest, bristling with peaks and divided by the low Central mountain, the "saddle," into the North and South mountains from which jut out spurs in all directions, enclosing several well defined basins and preventing every conceivable exposure. A multitude of local conditions which largely determine the development of the varied plant physiognomy of these slopes is thus produced.

III. The Geology.

The entire mountain from the lowest point in which rock has been found in situ is, as noted above, composed of granite. Two varieties are very evident, especially so in the great basin; a gray, which composes the lower two-thirds of the basin walls, and a red, out of which the East and West peaks, Pomola, the Chimney, the North peaks, and the serrated crest are formed. This line of demarkation is not one of general distinctness, yet the main fact, as outlined above, still holds. From analyses[1] made by Dr. Wadsworth of Harvard, I take an example of each of the varieties:

1. Hamlin, C. E. Op. cit.

No. 3.—A gray granite, composed of feldspar, quartz, and biotite. The feldspar is of two kinds: a grayish-white variety with a pinkish tinge, is the most abundant, while subordinate to it occurs a milk-white striated feldspar. The powder of the rock is magnetic. Microscopic examination shows it to be composed of orthoclase, much decomposed, and plagioclase, slightly altered, quartz, biotite, and magnetite. This gray variety is generally very solid and occurs but rarely in process of disintegration.

No. 23.—A brownish red granite of similar composition with the preceding. Feldspars colored pink and greenish white.

Calcite and a greenish talcose mineral occur as alteration products. In their section the feldspar is seen to be greatly altered. The biotite is partly decomposed. Dr. Wadsworth, however, regards these two varieties as parts of the same formation. This specimen was taken from the very crest and like all the rest of the top of the mountain is so decomposed as to yield readily to the hammer.

The lower two-thirds of the walls of the great basin, including approximately the upper limit of the gray variety, is "arranged (on the western side) in concentric sheets that dip west at an angle varying from 45° to 60°." On the southern wall the concentric layers dip north often at angles greater than 60°. The red granite caps these concentric sheets. Upon weathering it splits into blocks more or less regular in form which strongly resemble "courses of cyclopean, but crumbling masonry." So friable is this rock that it readily crumbles under the slightest weight, giving rise to a residual granitic soil, the only original soil of the mountain.

"The forms which the several parts of the mountain now present, and the condition of their surfaces, are largely due to the original structure and mode of weathering that characterize the rocks. As the highly inclined concentric sheets in the basin walls break away, and fall upon the talus below, other faces of equal inclination are exposed; while the red granite of the higher parts, deprived of support, in turn gives way, and thus the steepness of the walls is maintained." Similar explanation applies to precipitous faces upon other parts of the mountain.

That part of the crest between East peak and Chimney owes its form and preservation to the circumstance that the modified red granite which makes it up divides in weathering into plates which, when undisturbed stand vertically on edge * * * * a mere blade of rock from one to two feet wide, having upon one side the yawning gulf of the basin (South basin) and on the other cliffs too steep for climbing." These plates "vary in thickness from an inch, or less, to upwards of a foot." When they loosen, under frost action, and crash down the cliffs on either side, the plates remaining constitute the ever narrowing and lowering crest. Between East and West peaks the rock plates stand across the ridge at various angles. Loosened by frost the plates fall from the perpendicular, and the ridge bristles with these oblique projecting plates presenting "a savage and chaotic desolation that is probably without parallel in eastern North America."

The very diverse conditions of surface upon the other summits are due largely to simple differences in firmness of the constituent rock. "Thus, parts made up of the more friable red granite (not dividing into plates) are covered with small sized fragments, rounded by decay. These assume, over wide stretches, the size and almost the arrangement of cobble paving stones and in a few places the aspect of gravelled areas." Such conditions prevail particularly upon the slopes of the northern summits.

"Again, the middle of the northward slope, between the Tableland and the Saddle, is piled with blocks of the firmer red granite, riven from the mass beneath, of size so great as to render travel over them extremely difficult. The tableland is in parts smoothed by a covering of wholly disintegrated material, but in general is strewn with tabular blocks that increase upwards toward West Peak in size and number."

"The slopes south from the two chief peaks are covered with loose, angular, often tabular fragments, as far down as the (so called) tree-line, which is everywhere very low, leaving an unusual amount of naked rock above." "The whole rock surface of the mountain has been so shattered by frost action that only on faces of cliffs too steep to admit of an accumulation of detritus is rock to be found in situ."

The structure then of the red granite, which makes up the upper 700 feet of the mountain, has determined a variety of savage conditions from a blade-like crest to long slopes covered with huge angular or tabular blocks or fields of cobble stones. These conditions are all very significant in their bearing upon timber lines and the genetic development of plant societies upon the higher slopes.

IV. The Origin of the Mt. Ktaadn Flora.

In studying the flora of North America the identity of plants on isolated mountain summits and regions far to the north is a noticeable fact. The floras of Mt. Washington, Ktaadn, Labrador, and east Arctic America, localities widely separated by miles of lowland, impassable barriers for Arctic plants, are possessed of alpine species quite identical. These facts of discontinuous distribution of mountain forms and their strong Arctic affinities, many identical species recurring far to the north, demand an explanation since continuous distribution is the common condition. We are indebted to Prof. Asa Gray for an explanation of this interesting phenomenon, and the following paragraphs are largely adaptations of his views to the case of Mt. Ktaadn.

In the Pliocene epoch, in pre-glacial times, it is presumable that a quite homogeneous and uniformly distributed flora encircled the polar zone, there being then a postulated north polar land connection continuous around the globe. Destroyed by some great land movement, presumably toward the close of the Pliocene, only isolated islands, Greenland, Iceland, and others, now remain to mark its probable former course.

With the inauguration of the Pleistocene epoch great changes, cumulative from the Pliocene, came about. Huge masses of snow and ice, accumulated to the north and extended southward. The cause of this accumulation, made possible by the lowering of the temperature, is referred by Scott[1] to an epeirogenic movement in northern North America, and the polar zone. Dr. Chamberlin,[2] on the other hand, ascribes its cause to the gradual depletion of CO_2 from the atmosphere by organic and inorganic agencies, thus reducing the CO_2 blanket of the earth and facilitating radiation until the temperature became so lowered that ice accumulation ensued. Whatever the theory of the cause, the fact of glaciation remains the same. With the advent of ice accumulation and refrigeration, this uniformly distributed Arctic flora was driven southward in every longitude, retreating from the ever advancing ice sheet. Our temperate flora was likewise forced southward or exterminated by the glacial advance and by the fleeing Arctic species. From this general consideration of glaciation, we may now pass to its effect upon New England and in particular Ktaadn.

1. Scott, W. B. An introduction to Geology. New York. 1899, p 524.

2. Chamberlin, T. C. A group of hypotheses bearing on climatic changes Jour. Geo. 7: 653-883. 1897.

We have seen that as refrigeration progressed in the polar zone the Arctic flora travelled to the southward, closely followed by an Arctic ice cap which, according to the Canadian glaciologists, originated in North America from three distinct centers of maximum accumulation and flowed outwards in all directions. "One of these centers of maximum accumulation and distribution lay to the north of the St. Lawrence river, and on the highlands of Labrador, sending its ice-mantle southward over the Maritime Provinces, New England, and the Middle States, as far west as the Mississippi river." This ice sheet is known as the Laurentide glacier.

As this Laurentide ice-sheet advanced conditions of extreme cold were felt far beyond its edge. Thus the loftier mountains of New England, Washington and Ktaadn, feeling its chilling influence, became centers of ice accumulation. These mountain floras were consequently early forced down the mountain slopes into the plains below, uniting with the migrating Arctic forms from the far north. The nature of those pre-glacial alpine species is mere conjecture. However, they, as well as the accompanying lowland forms, doubtless exerted a modifying influence on the Arctic species. Yet the fact of their migration in unison precludes any marked modification of their mutual relations.

From these mountain centers, as general glaciation advanced, extensive ice-sheets flowed out in all directions, coalescing with each other and finally with the Laurentide glacier, and, united, advanced over New England even to the sea. This ice sheet was thousands of feet in thickness at its maximum, no mountain peaks, with possibly the exception of Mt. Washington, rising above the vast *mer de glace*. Before this all life retreated, many species of plants doubtless to the sea and extermination. This advance continued; the ice-sheet reaching at its greatest development to latitude 40°, about the middle of New Jersey. At this time our Arctic flora was doubtless enjoying a congenial climate along the Gulf.

After an extended period of this general glaciation, warmth gradually returned, according to Prof. Chamberlin, by the re-establishment of the CO_2 blanket, thus restricting radiation. With this return the ice-sheet gradually retreated, closely followed by the Arctic life. This retreat in New England was presumably one of continuity, yet in Wisconsin there is strong evidence of five glacial and four interglacial stages, representing periods of advance and retreat respectively. As the glacier dwindled, some of the New England peaks, such as Washington and Ktaadn, soon projected above the surface. When sufficient area was thus exposed, the accumulation of snowfields was again permitted, and valley glaciers descended from the mountain tops. In other words, following the withdrawal of the great continental glacier, there came a period of glaciation. The northward migrating flora was now met by these local ice sheets and temporarily retarded. The continued shrinkage of these large centers finally gave rise to coalescing valley glaciers; again permitting the northward advance of plants toward these centers of local glaciation.

In this advance, most naturally, the Arctic forms were the pioneers, following closely the melting ice front and obtaining a foothold wherever morainic soil was exposed. This advance was, as pointed out above, in unison and was also one of latitudinal zonation; the temperate plants, following closely the progression of the Arctic forms. As the coalescing valley glaciers gave way to isolated ones, the migrating Arctic species came to the lowlands about these high peaks. As the snows melted above, and as these now isolated valley glaciers retreated in their cirques, a separation in the previously compact Arctic flora took place. Some individuals pursued the receding snows up the mountain slopes, occupying every inch of exposed ground, while the main line of migration continued northward with the ever shrinking glacier. As amelioration progressed and the valley glaciers melted these Arctic forms ascended still higher. The main body of migrants pushed onward in its northward journey; while mingled temperate and pre-glacial alpine forms, on the approach of normal climatic conditions, came to occupy the intervening space between the mountains. Thus we have Arctic products isolated upon Ktaadn.

When these Arctic species began their mountain ascent they were, because of migration in unison, practically unmodified and identical with their northward journeying brethren, which, as complete warmth returned, had once more come to occupy the Arctics. As they ascended, unlike the compact body migrating northward, they were subject to modifying influences in such factors as the co-mingling with pre-glacial alpine forms, seeking their original habitats, and new alpine climatic conditions, Again, it is not to be presumed that identical species ascended mountain peaks widely separated. We thus readily interpret any varietal, specific, or even generic peculiarities which may exist upon any mountain. However, the majority of Arctic and alpine forms have, through the fixity of the specific type, come down to us unchanged from glacial times. But we must not neglect the possibility of subsequent distribution from a center as the factor in maintaining this specific identity in Arctic and alpine species. *Lycopodium Selago* is identical the world over in Arctic and Alpine habitats. This identity may be due not to the fixity of the specific type, for in Alpine conditions it has been subjected to the modifying influences noted above, but to the fact of frequent introduction, by wind dispersal, of individuals of the specific type derived from the Arctic centers by distribution, and the consequent commingling.

The flora of Mt. Ktaadn is then glacial in origin, being isolated, as a glacial relict, by the northward retreat of the continental ice sheet. We may now examine in particular its genesis upon the mountain. We have seen that, as the isolated valley glaciers, such as those occupying the North, South, and Northwest basins, retreated before the increasing warmth, Arctic plants approached the mountain base, and, as this local recession continued, the flora arrived at the base of Ktaadn.[1]

1. With the establishment of the isolated valley glaciers, it is quite probable that the higher peaks of the mountain arose as menataks above the local glacier; and with the ever increasing exposure must have formed a foot hold for these Arctic forms. It seems more probable, however, that the principal encroachment was from base to summit.

The first forms to reach the mountain were, in all probability, lichens of the crustaceous type, such as *Buellia geographica,* which found ready foothold on the increasing exposure of granitic rock. Following closely the ascent of the pioneer lichen society was that of the reindeer-iceland-moss combination, encirling the mountain as a basal zone and ascending as the pioneer society advanced. Encroaching upon this zone from below came that of the Alpine tundra, extending out into the lowlands, followed in turn by the *Krummholz* and passing gradually into the *Picea-Abies* forest which doubtless covered the entire southern part of the State at this time. Beyond, to the south, lay a wide belt of the white pine, and in turn beyond it came the deciduous forest. Encroachment of one zone upon another above has been continuous, societies gradually ascending, resulting in the present distribution of plant societies upon the mountain. It is obvious that this encroachment was one of horizontal zonation but for any one place it is a story of vertical succession. This progression will be considered in the section upon plant societies.

The place where this isolated Arctic flora first encroached upon the mountain is an interesting point of conjecture. From the retarding effect of the basin glaciers, the very favorable opportunity on the gentler incline of the stoss side of the mountain, and the greater sun exposure, it would seem probable that the first advance was from the southwest and west. This idea would seem to be confirmed in the present distribution of the spruce and fir. Their higher ascent on this side, their apparently greater age on the south and west slopes, and the advance of the *Krummholz* from this section, all indicate more favorable conditions, past and present, on this part of the mountain. As to the east side of the mountain, and in particular the basins, it seems very evident, from the present conditions, that the Great basin was the first to be claimed by the plant migrants, and that the North basin (Fig. 1) resisted this encroachment for a much longer time. In fact, presenting as it does a desolation simulated only on the highest slopes, it would seem that the disappearance of the valley glacier from this basin was comparatively recent.

V. Factors.

If a bird's eye view be taken from the summit of the mountain a varied panoramic picture greets the eye. A vast forest, coniferous in places, deciduous in others, dotted here and there by sphagnum bogs and a multitude of lakes whose shores are fringed with meadows, extends for miles, an unbroken landscape feature. If the mountain is now considered in particular, one sees in contrast, bare exposed rocks, mats of appressed growth, scrubby forest forms, and alpestrine meadows. That there are at least two distinct sets of causes operating in this region is very obvious. One determines the general plant physiognomy; the other controls the local aspect. One determines the coniferous forest; the other controls the formation of the alpestrine meadow and the Alpine-Tundra.

The question now most naturally presents itself: why in one place do we have the forest and in another its entire absence? Why is the coniferous forest dominant here, and the deciduous there? The present condition of these various plant societies is evidently the resultant of the inter-action of a complex of natural agencies operating upon them. Hence an interpretation of these conditions will largely depend upon an understanding of these determining factors. For convenience of discussion they may be treated under four heads, climatic, edaphic, biotic, and historical.

A. CLIMATIC FACTORS.

The factors to be treated under this head are composite and inclusive in nature. Of these temperature and moisture are, perhaps, the most important. A general survey of our entire country shows us a central prairie region bordered east and west by forest formations. The Atlantic and Middle States present a forest because the resultant of these factors produces a condition congenial to forest development. For similar reasons the Pacific coast is dominated by a vast coniferous belt. The absence of these favorable forest developmental conditions in the middle west, results in a climatic prairie formation.

Within this great Eastern forest we find a varied physiognomy. The Central states are dominated by a deciduous forest, while the extreme Northern states are coniferous in aspect. These differences are likewise climatically determined, being due to a different adjustment of the determining forces which vary in different latitudes. Such homogeneous plant groupings are known as climatic formations.

The Ktaadn region lies within the Northern Pine Belt of Sargent,[1] the boreal of Merriam,[2] the black spruce-fir balsam combination being the climatic mesophytic type. The entire absence of temperature and rainfall readings in this region makes a discussion of the climatology impossible, but a general consid-

1. Sargent, C. S. Tenth Census Rpt. 9: 494. 1880.

2. Merriam, C. H. The geographic distribution of life in North America. Rpt. Smith. Inst. 1891: 365-415.

eration has shown us that the interaction of these complex agencies has probably determined the coniferous nature of this forest.

In contradistinction to these comprehensive and far-reaching climatic factors, are those which are decidedly local in their effects. Mount Ktaadn presents within itself a varied physiognomy. The Alpine-Tundra, the heath, the cliff bogs, the *Krummholz,* and the alpestrine meadow are but phases resulting from the local influence of the several co-operating factors. Yet these many and distinctive plant societies are all within the same climatic formation. Rising as Ktaadn does, from an extensive lowland, it introduces abnormal climatic conditions for this region. Its height brings about new relations as to exposure, light, moisture, wind, and temperature which are superimposed upon the normal climate of the region. We may expect then the physiognomy of these mountain societies to be in direct response to the resultant of the imposed conditions.

In the section of this paper devoted to the origin of the Ktaadn flora, we recognized and commented upon the strong resemblance our mountain flora bears to that of regions far to the north, but at that time offered no suggestion as to why this isolated Arctic flora had been able to so successfully sustain itself there. We have upon Ktaadn a flora which is probably much like the climax type of Labrador and Arctic North America but which is here, as noted above, largely determined by local climatic conditions; that is we have repeated in a local way upon high mountain peaks the far-reaching climatic conditions of regions farther to the north. Or, in other words, a mountain repeats altitudinally conditions latitudinally true of more Arctic regions. In concluding this general discussion, it may be well again to emphasize the existence of a local climate as well as a general one; the former condition is strikingly exemplified upon high mountains.

These local climatic factors are several: heat, light, and wind may be mentioned as the most significant. Operating through space they act directly upon the aerial parts of plants through the atmospheric medium which surrounds them. Other parts are affected indirectly, as will be brought out in the following discussion. We may treat these factors under two heads, radiant energy and wind.

(a)—*Radiant Energy.* The ultimate source of all our energy is the sun. It manifests itself upon the earth as ether vibrations which give rise in our bodies to the sensations of light and heat depending only upon their rate of vibration. With the plant, however, it is simply a difference in energy, not sensation. So closely are these two factors related that it is almost impossible to differentiate their effects. However, light would seem to be the more important, controlling as it does one of the vital processes, photosynthesis. Ascending the mountain the atmosphere becomes rarer, hence the intensity of the light proportionally greater as higher altitudes are reached. Plants able to withstand this greater intensity must possess protective structures. They have become "light loving" species, as expressed by authors. It would seem more pertinent, however, to designate them as light enduring forms. The absence of broad leaved species, the high development of cutinization, and palisade structures may be, in part, responses to this high light intensity.

Closely related to the function of photosynthesis, is that of transpiration or water loss. Both these functions are largely dependent upon the stomata for their efficiency, at least in the alpine forms under consideration. The stomata are primarily paths of gaseous exchange, but are also the canals of water loss. The latter necessarily occurs where wet membranes are exposed to an atmosphere of less diffusive tension. The amount of transpiration is dependent in part upon the aperture of the stomata, which is in turn dependent upon the light intensity, the temperature of the air and its relative humidity. This transpiration loss is vital in the economy of plant life and especially is this true of alpine regions where the absorption, due to the low temperature of the soil, is at a minimum and the transpiration, on account of the high wind velocity, greatly augmented; it should be said, however, that some experiments seem to show lessened transpiration in alpine regions.

In response to these precarious conditions we find protective adaptations which tend to mitigate the harmful effects which might otherwise arise. Whether they have been developed primarily in relation to light or to transpiration is of course problematical, yet the fact that the same ecological adaptations exist where the light condition is normal (the sphagnum bog) but the ratio of transpiration to absorption is high, would tend to favor the latter view. Further discussion of high transpiration and its resulting protective adaptations may be more advantageously considered under wind, and will be reserved for that section.

With the increased light intensity also goes an abnormal temperature relation, varying greatly from that of the surrounding region. It is a point of common knowledge that with an increase of elevation there is a corresponding decrease in temperature, depending upon the increasing ease of radiation as the atmospheric density decreases. No systematic temperature observations have ever been made upon the mountain. The United States Weather Bureau has, however, had from 1870 to 1892, a station upon Mt. Washington at an altitude of 6,279 feet. Tables of the maximum and minimum temperatures for a series of years compiled from the annual report of the chief signal officer, are very instructive and may be considered quite representative of the conditions upon Ktaadn.

*TABLE I—MAXIMUM TEMPERATURE.

Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.
1873........	0.	—5.	0.	.6	10.	15.	17.2	13.9	13.9	14.4	1.1	3.3
1874..........	5.	2.8	3.3	4.4	15.	16.1	.....	....	16.1	6.1	4.4	1.1
1875..........	1.7	2.8	2.2	2.2	15.	15.6	12.8	15.6	16.7	5.	1.7	4.4
1876..........	5.	1.1	5.6	6.1	11.7	18.9	17.8	22.2	14.4	8.9	5.6	—5.6
1877..........	—2.2	1.7	2.2	5.	12.8	16.1	16.1	17.2	15.6	13.9	3.3	3.9
1878..........	.6	.6	1.1	7.2	14.4	21.7	20.	15.6	16.7	12.2	2.8	1.1
1879..........	—3.3	—10.6	1.7	5.6	16.7	21.1	15.	16.4	15.6	12.2	6.7	4.4
1880..........	4.4	1.7	2.8	4.4	16.1	15.	16.7	18.9	18.3	10.	8.3	—.6
1881..........	—3.9	2.2	1.7	5.6	16.1	20.6	22.2	19.4	17.5	12.2	8.5	4.8
1882..........	1.1	1.6	2.6	2.3	7.5	17.2	15.6	18.6	13.6	14.4	6.8	0.
1883..........	3.3	6.1	1.7	10.	16.3	18.6	15.8	14.6	15.6	12.5	7.8	2.9
1884..........	2.2	3.9	5.3	7.3	12.8	19.4	19.3	18.3	17.2	13.6	2.8	6.1
1885..........	2.8	0.	—2.2	13.3	16.7	17.2	20.6	16.7	12.8	12.2	10.6	5.6
1886..........	2.8	5.	5.	11.1	9.4	14.4	19.4	20.6	16.7	9.4	7.2	0.
Total mean.	1.4	.9	2.3	6.1	12.6	17.6	17.7	17.5	15.	11.2	5.5	2.2

*TABLE II—MINIMUM TEMPERATURE.

Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.
1873..........	—25.	—20.5	—18.3	—10.	—7.8	—2.8	.55	—.55	—7.8	—13.3	—30.	—27.8
1874..........	—45.4	—33.3	—35.	—27.8	—20.5	—6.7	—.55	—2.2	—5.	—12.8	—27.2	—26.7
1875..........	—50.8	—37.2	—32.7	—26.1	—73.3	—7.2	0.	—2.2	—9.4	—15.5	—37.2	—40.
1876..........	—34.4	—43.6	—31.7	—17.8	—13.9	0.	0.	—6.7	—6.1	—15.	—23.3	—43.6
1877..........	—37.8	—26.7	—29.4	—15.	—11.7	—3.9	4.4	1.1	—6.7	—11.1	—18.3	—25.
1878..........	—37.2	—27.2	—27.6	—9.4	—10.5	—9.4	1.6	1.6	—10.	—12.2	—23.3	—26.1
1879..........	—33.9	—30.5	—23.1	—21.7	—10.5	—9.4	0.	—.55	—11.7	—17.8	—28.9	—32.2
1880..........	—28.4	—32.8	—25.	—24.4	—18.3	—1.1	—.55	—2.8	—5.4	—15.5	—26.7	—33.3
1881..........	—34.4	—37.8	—22.2	—27.2	—13.3	—8.8	0.	1.7	—2.2	—19.4	—26.4	—29.
1882..........	—39.4	—29.	—28.5	—25.1	—15.5	—5.7	—1.7	—3.3	—8.3	—12.2	—21.7	—31.7
1883..........	—33.9	—33.5	—36.7	—23.3	—12.6	—6.3	—2.2	—6.4	—9.6	—14.4	—27.	—41.8
1884..........	—33.9	—34.4	—32.2	—16.8	—10.8	—2.9	—1.1	—5.8	—10.2	—15.2	—22.6	—43.9
1885..........	—58.	—38.9	—54.4	—23.3	—18.3	—9.4	1.7	—5.	—10.5	—12.2	—14.4	—26.7
1886..........	—28.3	—39.4	—28.3	—16.7	—7.8	—4.4	—2.2	—2.2	—11.7	—18.3	—18.9	—31.7
Total mean.	—36.9	—33.2	—30.4	—19.7	—13.2	—5.5	—.05	—2.4	—8.1	—14.7	—24.9	—32.9

* The readings are in centigrade.

(b)—*Wind.* The influence of wind upon vegetation is great and manifests itself in a variety of effects. Indirectly, plant life is influenced by the wind in furthering dissemination and facilitating anemophilous pollination. While more directly the external form, internal structure, and vital processes may be greatly modified and disturbed by the mechanical impact on the one hand and the desiccating effects concomitant with high wind velocity and extreme exposure on the other. The extent of these influences is largely dependent upon two conditions; the plant's exposure and the strength and prevalence of the wind. These two conditions exist in a superlative degree upon mountains and are proportionally great as the altitude increases. As the action of wind induces a complex of consequences in plants, it will be well to discuss the various effects independently.

The study of seed dispersal has two aspects: the pure ecological standpoint dealing with varied adaptive structures facilitating seed dissemination, and the floristic phases treating of questions of origin and present distribution. The large per cent (about 30%) of the flora possessed of adaptations furthering wind dispersal is at least deserving of passing notice.

Wind is a factor not to be underestimated in its relation to pollination. Though many insects abound even to the summit they are presumably of little significance in entomophilous pollination, belonging as they do to groups whose members aid only slightly if at all in pollen transportation. Further, the majority of forms are strongly anemophilous. The great efficiency of the wind in the formation, as well as the dispersal, of seed is to be properly accorded in the consideration of any alpine flora.

The most evident wind effect upon plants is the modification of morphological form. Though formerly controverted, it now seems well established that this influence is partly mechanical and largely due to the force of impact of the wind blast. It directly follows that the extent of this modification varies with exposure and the velocity and constancy of the wind. We may expect to find then upon Ktaadn drastic evidence of wind influence upon external form. As one ascends the slopes he passes successively from forest trees which clothe the plain below through those whose branches just overtop his head, those that are shoulder-high, those that are knee-high, and at last he remarks at finding himself walking upon the crowns of trees which lie prostrate beneath his feet upon the higher slopes. This diminution in size, with the increased altitude, is accompanied by a no less marked effect on form. The scrubby, scraggly, gnarled, knotted, and twisted character of the trees is most striking. To this condition of morphological modification the Germans have applied the term *Krummholz.* The *Krummholz* covers the north basin, the higher slopes, and a greater part of the "tableland" and "saddle," extending far up toward the North and South peaks. (Figs. 2, 3). Its gnarled, scraggy, and interlacing branches make it an almost impenetrable mass.

So closely wind trimmed is this growth of spruce and fir that its surface presents an almost level green. If one approaches the "saddle" from the east slope a much different impression is conveyed than if his first view is obtained from the west. If viewed from the east a striking condition presents itself. Residual granitic soil, bare rocks and boulders, the alpine mat, prostrate firs and spruces, and the *Krummholz* in receding succession from the brow of the slope confront one. (Fig. 4). Passing back into the *Krummholz* these much dwarfed trees gradually attain a greater height, ascending gently to the leeward until at the west bow of the saddle they reach about one-fifth their normal height.

This gradual and successive extension in height is due to the increased protection afforded by each succeeding tree, the inclined plane rising to the leeward. But if, on the other hand, the approach is from the west, (Fig. 4) not this heath-like condition, but a diminutive forest confronts one, and he is not aware that conditions other than those exist upon the saddle.

If attention is now focussed upon a single tree far to the windward, the direct effects of the wind become still more obvious. The very general inclination of the crowns to the leeward shows strongly their tendency to conform to the direction of the prevailing wind. In extreme cases the entire crown is to the leeward of the trunk which may itself be inclined at no gentle angle, in many cases lying even prostrate. The straggling nature of the trees and the great number of dead branches in the crowns are also characteristic features.

A closer examination reveals another striking fact. The trunks themselves in cross section have an ellipsoidal tendency with the longer axis lying parallel to the direction of the prevailing wind. The high development of bark and the small diameter and great age are but other evidences of this same factor. We thus see that a high and constant wind not only defines the whole landscape but determines the individual plant form as well. The modification of internal structure resulting from the mechanical impact of the wind is evidenced in the great increase of mechanical tissue; and it is to this increase that the trunk owes its ellipsoidal form, mechanical tissue developing only abnormally where the stimulus of the strain is focused, obviously on the leeward side perpendicular to the wind impact.

The influence of wind upon transpiration though not the most evident is by far the most significant. Other things equal, the rate of transpiration is dependent upon the difference in diffusion tension of water vapor within and without the plant body. The desiccating influence of a wind blast is well known and needs but to be recalled in this connection. This desiccating effect, along with the constant replacement of the atmospheric environment, reduces the external diffusion to a minimum, thus augmenting transpiration greatly beyond its normal amount. Furthermore, during winter, the resting periods of plants, the wind reaches its highest velocity (see Table III) thus keeping the peaks and higher slopes bare a large part of the time and reducing the available moisture in the soil to a minimum. Coincident with this maximum wind velocity are the minima of precipitation and temperature. (See Tables II and V). It likewise dries the plant itself, even thawing the frozen sap, thereby increasing the transpiration at a time when this excessive drain can least well be met, concomitant as it is with a period when absorption, because of the dryness of the soil and its low temperature, is highly impaired if not entirely prevented. We have thus a condition of excessive transpiration and diminished absorption. In other words, the ratio of transpiration to absorption is at a maximum. The existence of this high transpiration ratio throughout the year and its accentuated value during the resting period produces a condition very precarious to plant life.

*TABLE III—WIND VELOCITY IN MILES PER HOUR.

Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.
1881..........	130	110	132	120	78	94	60	90	90	165	108	170
1882..........	126	120	118	120	100	95	92	80	113	100	98	116
1883...... ...	152	126	150	88	96	128	80	94	108	94	100	132
1884...	130	130	122	92	100	74	96	88	96	92	128	96
1885..........	120	108	128	90	98	100	96	92	90	94	95	96
1886..........	122	138	115	110	88	94	84	88	100	89	99	100
Total mean.	130	122	127	103	93	86	85	89	99	105	105	118

* Data from Mt. Washington.

It is not surprising in view of this great desiccation and high transpiration ratio, to find that alpine plants have suffered adaptive modifications which tend to mitigate these harmful effects. The excessive development of cutin in epidermal layers, producing the sclerophyll type of leaf, high development of the tomentose character in several species, absence of dorsal stomata, reduction in the number of ventral stomata, the reduction in number and size of transpiring surfaces, and the cespitose habit of growth are all evidences of protective adaptations and adaptations without which this mountain flora would be unable to withstand the adverse conditions of its environment.

B. EDAPHIC FACTORS.

Soil factors operate upon plants, not through the atmosphere but through the substratum in which they live. The soil being an anchorage as well as a source of food materials, its importance becomes at once very apparent. Schimper has considered the influence of soil and its properties so significant in the determination of the local distribution of plant societies that he has designated those societies so determined edaphic formations and the soil and its properties edaphic factors.

The soil and its influence has long been a subject of interest and investigation. As early as 1836 Unger[1] studied its chemical

1. Unger F. Uber den Einfluss des Bodens auf die Vertheilung des Geachse.—Vienne 1836. Review. Ann. Sci. Nat. 8: II, 75-93. 1837.

nature, deciding that it was the all important factor in soil influence upon plant distribution. On the other hand Thurmann[1]

1. Thurman Jules. Essai phytostatique—quant a l'influence des roches sousjacents. Paris, 1849. Review. Ann. Sci. Nat. 12: III, 335-343. 1849.

in 1849 became the sponsor of the physical theory of soils as influencing the distribution of plant societies. From its variety of nature, and physical properties, the soil invites a variety of conditions in regard to food, heat, and moisture content. Of these factors it is perhaps the last whose influence is predominant in determining the physiognomy of plant societies. Upon this basis, the water content of the soil, Thurmann (1849) proposed a classification which was more fully developed later (1896) by Warming,[2] who divided plant societies into three

2. Warming, E., Okologische Pflazen geographie. Knoblanch translation, p.116 Berlin, 1896.

classes, hydrophytes, mesophytes, and xerophytes, those plants inhabiting respectively soils rich, medium, and poor in moisture.

The source of soil water is primarily the rainfall of the region. Though we have no readings from Ktaadn, data from Mt. Washington can not fail to be pertinent. High as these mountains are they intercept moisture-laden clouds and precipitation is almost daily (see Table IV) and frequently excessive. A high precipitation is the result. (Cf. Tables V and VI).

TABLE IV—RAINY DAYS.

Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	Total per cent.
1884....	16	22	20	12	19	13	22	16	17	22	18	22	57.1
1835....	22	9	13	17	14	15	20	20	13	12	20	22	53.8
1886....	20	11	21	11	13	18	15	14	16	17	19	20	53.
Total mean	19	14	18	13	15	15	19	17	15	17	19	21	54.6

TABLE V—PRECIPITATION IN INCHES.

Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	Total.
1873....	3.39	5.2	5 81	2.72	4.55	3.2	13.54	5.81	13.66	9.23	5.5	5.95	78.56
1874....	4.4	2.47	6.71	5.74	6.53	13.44	7.97	9.51	5.52	2.96	2.34	3.07	70.66
1875....	1.82	1.	2.13	2.	2.5	6.83	7.4	7.95	11.34	6.3	2.67	3.84	55.78
1876....	2.8	3.5	6.21	3.12	7.83	9.32	14.51	2.2	14.89	3.21	3.49	6.48	77.56
1877....	2.06	.33	11.64	3.4	3.72	8.78	11.27	11.11	2.79	7.75	17.55	6.01	86.41
1878....	8.54	5.88	10.66	23.41	9.28	7.67	11.	11.35	7.37	5.78	4.78	8.77	114.49
1879....	7.13	7.01	7.51	6.79	4.4	11.84	10.23	9.55	6.53	5.03	9.53	5.56	91.11
1880....	4.24	2.56	4.87	3.47	5.51	5.86	7.24	5.82	15.23	7.96	9.37	7.80	79.93
1881....	3.94	6.62	8.51	5.08	12.5	7.03	9.93	11.96	6.13	18.38	15.10	15.15	120.33
1382....	7.20	5 94	14.52	11.20	8.91	11.4	10.03	2.81	13.32	6.19	3.25	2.64	97.41
1883....	4.16	5.65	4.18	6.29	9.10	11.30	11.14	6.66	6.9	5.55	3.72	2.66	76.71
1884....	2.45	7.55	4.16	3.29	9.54	8.08	2.39	8.63	7.58	12.91	7.99	4.7	100.78
1885....	5.49	1.87	.95	2.66	2.29	11.34	11.34	14.26	5.56	11.11	6.67	4.83	78.37
1886....	4.5	9.03	3.11	3.36	3.25	6.07	6.3	8.34	8.52	5.09	6.48	3.10	64.03
Total mean	4.46	4.40	6.50	5.88	6.43	8.72	11.08	8.10	8.95	7.68	6.96	5.61	85.15

TABLE VI—TOTAL MEAN PRECIPITATION AT ORONO. ALT. 150ft.

Year.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	Total.
1868–1900..	4.37	4.15	4.24	2.82	3.64	3.62	3.33	3.57	3.35	4.07	4.44	3.73	45.33

A study of these tables brings out several important facts. It will be noticed that the greatest rainfall is coincident with the growing period, June-September, a fact very significant in the development of the flora. Upon this and its daily distribution is the presence of the mesophytic undergrowth, which extends far up toward the limits of the *Krummholz,* only explainable. While the precipitation is frequent and high, its retention is by no means complete. The thin residual soil, allowing the water to soon reach the underlying granite, permits a rapid drainage. The thick Alpine-Tundra topographical irregularities, and many adaptations for water retention in the lichens and mosses however raise this retention ratio. Yet, all in all, it is the frequency of precipitation rather than amount that determines the mesophytic effect.

C. BIOTIC FACTORS.

A general survey of the plant world convinces us of an internal and mortal combat. We see from purely physical reasons that no two plants can occupy identical soil at the same time. From this necessarily arises a struggle for supremacy of position leading to a more favorable life relation. This struggle for existence is threefold. It may take place between individuals of the same species, between individuals of different species, and thirdly between plant societies. The line along which two societies meet is pronouncedly that of greatest aggression and struggle. It is along this tension line that the ecologist finds his most interesting study. For it is here, above all other places, that he may analyze the influencing factors and study the encroachment of one society upon another. Where the conditions for life are most favorable, the struggle of society with society, species with species, and individual with individual is the most severe and the tension line becomes the battlefield of mortal combat.

The influence of animals upon the plant life here is at a minimum. The absence of man and the slight effect of the winter grazing of droves of caribou, which come from the north to feed upon the lichens and heaths laid bare upon the higher slopes, leaves the flora of the mountain in a delightfully primeval state.

D. THE HISTORICAL FACTOR.

This factor deals with and involves a question of time. Hence it gives us a conception of movement and of change, for we recognize that our world is not one of statics but of dynamics. Nothing is fixed; all is movement. There is a continual and progressive change in the physiography of any region, a destructive and constructive cycle, tearing down there, building here. This progressive introduction of new physiographical conditions has brought about a corresponding succession of plant societies, a thing which must inevitably follow. This succession may of course be either progressive or retrogressive. Hence we have a continual readjustment of plant societies. Considered geologically all this movement has its temporary end, the pene plain for the land, the climax mesophytic forest for the plant society. I say temporary end, for epeirogenic or orogenic movements would rejuvenate the physiography and bring about a readjustment of the plant societies and inaugurate the redevelopment of the climax forest. It is evident then that the stage in the plant cycle at any one period is directly dependent upon the then existing physiographic stage.

The purely geological phase of this factor must not be neglected. If we speak of the physiographic factor in terms of years, so must we speak of the geological in centuries, embracing vast periods of time. It is in the latter phase of this historical factor that we have found the origin of the Ktaadn flora.

Having discussed the various factors instrumental in the determination of the plant aspect of the mountain, we may now take up in detail the study of the many plant societies which give it its characteristic tone. But as we pass to this treatment let us have clearly in mind that it is to the interaction of these complex climatic, edaphic, biotic and historical factors that the mountain presents its varied plant physiognomy.

VI. The Plant Societies.

The study of the historical factor and the origin of the Ktaadn flora showed that the life of the plant covering of Ktaadn has been one of progressive dynamics. Further, the plant societies, as they are seen there to-day, represent the various and successive steps of this horizontal development. For any one place, however, the story has been one of vertical succession. So by the one the other may be interpreted. It is the object of this section of the paper to trace the genetic development of these plant societies in so far as it is possible.

A. Rock Societies.

In the discussion of the physiography of the mountain it was noted that Ktaadn is one solid mass of granite. With such a vast rock exposure, it offers an admirable opportunity for the genetic study of this type of society. It is on the higher peaks, the crest, and the upper talus slopes, where vegetation has yet been unable to encroach, that we may best study the pioneer plant society.

(a). *The Crustaceous Lichen Society.* Along the crest, where frost action splits the red granite into vast blocks which, losing their perpendicularity, still remain as oblique projecting plates in chaotic desolation, we find the bare rocks with only a crustaceous lichen covering. The most abundant and pioneer form is *Buellia geographica,* of universal distribution. With its yellowish-green cast it gives a tone most lurid to the vast talus slopes and weathered crest. The growth of *Buellia,* as well as other forms, is centripetal and as the lichen expands in circumference it dies behind at the center, becoming black. There are several other less prominent associated forms.

Beginning in small patches these crustaceous lichens expand into mats and mats into islands as it were. Finally uniting they may cover entire boulders. Needing no soil the crustaceous lichen is essentially a lithophyte. To fit it to this extremely xerophytic and precarious life, it must first be able to form an attachment to the rock upon which it lives and secondly it must have ability to obtain food from its rock substratum the air. By means of holdfasts its position is secured. From rain and drainage various compounds may be absorbed. Again the symbiosis of fungus and alga in the lichen perhaps fits it as a pioneer form. Finally the ability to dry up and suffer no injury, reviving with the next rain, admirably fits the lichen to its xerolithophytic life. Several foliaceous forms may accompany this crustaceous covering. *Umbilicarias* are not uncommon even at the very summit, yet they never become conspicuously prominent. Upon this lichen mat, and even upon the bare rocks, occur several species of lithophytic mosses. *Andreæa petrophila, Rhacomitrium sudeticum* and *R. aciculare* may be mentioned.

The wash, decay, and disintegration from the lichen-moss-mat lodging in angles where rocks adjoin, in cracks, crevices, or niches, gradually form a slight soil and prepare the way for plants whose demands are higher. To this organic decay must be added the more efficient weathering which so disintegrates the granite that it often crumbles beneath the feet. Under the action of these two forces a residual soil is soon formed and new plants make their appearance.

(b). *The Reindeer-Iceland Moss Society.* In these rock angles and cracks, only a very shallow soil having accumulated, the fructicose lichens now appear. As pure growths they never form mats of large extent for, having no means of secure attachment, they are easily dislodged by heavy winds and rains and washed away. So the excessive development of this society as such is retarded. *Cladonia rangiferina, C. rangiferina alpestris,* and *Cetraria isandica* may be mentioned as the characteristic components. With them are associated several less prominent forms. *Cladonia cristatella* may be noted. Several mosses may also attain prominence in this society. *Bazzania trilobata* is not an uncommon form, frequently forming extensive patches.

This mat once established becomes a center of accumulation, retaining the detritus of wash and erosion as well as that of local plant decay which is not a little, for these lichens and mosses grow above, dying down behind in a manner not unlike that of *Sphagnum.* Very soon a sufficient soil exists and still higher ecological forms have their introduction.

(c). *The Alpine Tundra.* With the accumulation of soil the food material becomes greater and of a higher nature. The grasses and sedges first appear and, spreading with their interlacing roots, soon make the precarious lichen-moss mat a fixity. *Hierochloë alpina, Agrostis rubra, Deschampsia flexuosa, Carex vulgaris hyperborea, C. canescens alpicola,* and *Juncus trifidus* are perhaps the most characteristic of these forms, pioneers of the Alpine Tundra. Many less prominent forms are associated. By the coalescence of mats a turf is formed. Some of the lichens still persist but have been largly forced out. Many mosses are also common at this stage, probably as pioneers rather than relicts of a former stage. *Polytrichum juniperinum* and *Mielichhoferia nitida elongata* form dense isolated patches, while *Polytrichum commune* and *P. Ohioensis* are more ubiquitous forms.

With the grasses and sedges, possibly earlier, appear *Lycopodium Selago, L. annotinum pungens, Arenaria grœnlandica,* and *Potentilla tridentata.* Edaphic conditions seem to largely determine the nature of the pioneer forms. *Prenanthes trifoliolata, P. Bootii, Solidago macrophylla,* and *Scirpus cæspitosus* are associated forms less common but not rare.

The heaths follow next. *Empetrum nigrum, Vaccinium Vitis-Idæa, V. pennsylvanicum angustifolium, V. uliginosum, Diapensia lapponica* are among the pioneers. *Ledum latifolium, Kalmia angustifolia, Kalmia glauca, Arctostaphylos alpina,* and *Rhododendron lapponicum* are of less frequency but are associated forms. Of more local occurrence are *Bryanthus taxifolius, Loiseleuria procumbens,* and *Cassiope hypnoides* being largely restricted to the lower slopes.

The Alpine Tundra mat (Figs. 2, 3) is widely distributed, covering more than one-half the upper part of the mountain. (Fig. 2). On the crest, summits, and table-land it reaches perhaps its highest and most characteristic development, yet it extends down upon the "saddle," spurs and higher slopes, and is in a very characteristic state upon the floor of the North basin, for reasons which have been sufficiently set forth above in our discussion of the origin of the flora. Its composition is not uniform, varying much in its species with edaphic conditions. In one place *Vaccinium Vitis-Idæa* is dominant, *Diapensia lapponica* characterizes the alpine mat in another, *Arctostaphylos* in another, *Ledum latifolium* in still another, while still again the mat may be almost wholly peopled by *Juncus trifidus* and the heaths conspicuously absent.

Along the brow of the "tableland," "saddle," and various spurs a very different condition exists and consequently the plant succession is modified. Here disintegration is rapid and drainage excessive. For several feet, in places yards, back from the brow a gravelly granitic soil of four or five inches in depth is destitute of vegetation. The crustaceous lichen stage is absent, as are also the fruticose forms which are excluded on account of their inability to take root and hold their position. The conditions then for plant life are very severe and only particularly adapted forms are enabled to withstand these strenuous conditions. *Arenaria grœnlandica* with its multitudinous rootlets and branching habit, *Solidago virgaurea alpina* and *Potentilla tridentata*, similarly provided, are pioneers upon this very xerophytic habitat. *Diapensia lapponica,* with its cushion habit, is also a pioneer and reaches here its greatest development, being characteristic of this stage. *Salix uva-ursi, Rhododendron lapponicum, Arctostaphylos alpina* follow closely upon *Diapensia* forming almost a definite zone. These forms, on passing back from the brow, soon give rise to a definite mat in which occurs *Vaccinium uliginosum* which latter becomes here the character plant of the Alpine Tundra. It is accompanied by *Empetrum nigrum, Ledum latifolium, Kalmia glauca,* and *K. angustifolia.* Several grasses and carices, *Juncus trifidus* and *Scirpus cæspitosus* now appear and, with several mosses, make the Alpine Tundra complete. It was noticeable that as the mat developed *Diapensia* gradually disappeared, being entirely absent when it reached its characteristic development.

(d). *The Krummholz.* With the formation of a sufficient humus to support higher forms, trees encroach upon the Alpine mat. *Betula papyrifera minor* and *B. glandulosa* are the first to make their appearances. They show a high development of the *Krummholz* habit, lying prostrate upon the mat. Locally *Larix americana* and *Juniperus communis nana* are the pioneers, especially is this true upon the spurs. Following these pioneers comes the Picea-Abies combination. Islands of spruce and fir deploy as advance guards of the forest proper (Fig. 2). Which of these two trees is the pioneer, that is the more xerophytic, is problematical. The evidence is contradictory. Three possible theories may be presented: 1. *Picea* is the xerophytic pioneer, followed by *Abies* as the conditions become more and more mesophytic. The evidence from the Great basin, North basin, and clearing societies would favor this idea. 2. *Abies* may be the more xerophytic. This idea finds little support except in places where *Abies* is the dominant species. 3. Neither is to be considered as the pioneer. It is more a question of preoccupation. The first to appear stays and there is no question of succession. This theory seems to explain very satisfactorily all conditions, especially that on the "tableland" and "saddle," where we find *Picea* dominating in one place and *Abies* in another.

At the present time the *Krummholz* forest covers the upper slopes of the various spurs, a greater part of the "tableland," practically all of the "saddle," and extends far up toward the summits, scattered trees being noted within a hundred feet of the top (Figs. 2, 3). It is then only a question of time when the entire mountain, where physically possible, may be forest clad. That is, this possibility is not climatically excluded but only edaphically retarded.

The composition of the *Krummholz* is most astonishing. Associated with the *Picea* and *Abies* are *Betula papyrifera cordifolia, Pyrus americana,* and *Amelanchier oligocarpa.* On the forest floor *Cornus canadensis, Chiogenes serpyllifolia, Coptis trifolia, Linnæa borealis, Maianthemum canadense, Clintonia borealis, Trientalis americana, Oxalis acetosella, Gaultheria procumbens, Moneses grandiflora, Listera cordata, Aspidium spinulosum dilatatum, Streptopus roseus, Aster macrophyllus, Carex trisperma, Hylocomium splendens, Hypnum crista-castrensis, H. Schreberi,* and *Dicranum* all abound and in rich profusion. These forms, and many others which might be mentioned, are all common to the climax mesophytic forest of the region. Further, most of these forms are characteristic of the mesophytic forest of low altitudes. It seems then that the *Krummholz* forest is almost as mesophytic as the Picea-Abies combination of the Great basin and surrounding country, which very evidently is the climatic mesophytic forest of this district. The nature of this forest will be referred to a later discussion.

In other words, no true alpine conditions or climatic timber lines exist upon Ktaadn. The first is probably excluded by the excessive moisture, its happy distribution, and abundant retention, making the alpine conditions quite mesophytic. The so called timber line, a popular rather than scientific delimitation, is purely physical and not a climatic demarkation.

The conditions along the tension line between the *Krummholz* and the Alpine-Tundra are very suggestive. As the forest advances and takes possession of the mat, many forms are driven out, presumably by light starvation. Other forms are better able to adapt themselves and so remain as relicts of the Alpine mat.

Among these relict forms in the *Krummholz* may be mentioned *Vaccinium pennsylvanicum angustifolium, V. uliginosum, V. Vitis-Idæa, Kalmia angustifolia, K. glauca,* and *Ledum latifolium.* But as the forest advances and the conditions become mesophytic, these relicts gradually disappear, forced out by the other forms better adapted to the new conditions of soil and decreasing light supply beneath the canopy of thickly and almost impenetrably woven branches of spruce and fir.

Of the forest itself it is not the trees which first encroach upon the alpine mat, but rather the lower forms which, pushing out gradually advance the tension line before the forest which closely follows. This advance zone is never very conspicuous, but among its members *Cornus canadensis, Maianthemum canadense, Coptis trifolia,* and *Linnæa borealis* may be mentioned.

The North Basin. Under this discussion of the *Krummholz* it may be advantageous to introduce the conditions as they exist in the North basin. This amphitheatre of over 320 acres presents an appearance even more xerophytic and alpine than some of the upper limits of the mountain itself. A great morainic dump of granite boulders, forming kettles, completes the picture of chaotic desolation. All this is in vivid contrast with the Great basin whose altitude it approximates and which supports a well developed *Picea-Abies* mesophytic forest. The Alpine-Tundra here reaches an extreme yet characteristic development, the stages of succession being practically identical with those of the crest and summits. Here the *Krummholz* also reaches an excessive development, lying in most places perfectly prostrate and gnarled and twisted to a high degree. *Picea* is noticeably predominant, *Abies* being conspicuously absent.

At the mouth of the basin, as described above, is a moraine of medium size. The Alpine-Tundra mat and the prostrate *Krummholz* cover its northwestern side. The opposite face fronting southward is, on the other hand, well clothed by a *Picea-Abies* forest. Why has this basin and its slopes this extreme xerophytic condition? It will be recalled that in the discussion of the origin of the place it was stated that this basin with others was the seat of local valley glaciers, and a theory advanced suggesting that the North basin was perhaps the last to see glacial recession, hence the last to become vegetated. The highly alpine condition of this basin is then perhaps due not to climatic causes but to the recent disappearance of the local glacier retained within its walls. It is only a question of time when the record of glaciation in this basin will be deeply hidden by a *Picea-Abies* mesophytic forest as it is in the South basin to-day.

(e). *The Picea-Abies Forest.* The theory has been advanced that the *Krummholz* is a mesaphytic combination and the evidence has been drawn from the *Picea-Abies* forest of the region. It may be well now to speak of this forest more in detail. In our discussion of climatic factors we have noticed that this combination, the resultant of a complex of factors, is the climax mesophytic forest type of this region. The principal trees are the black spruce, *Picea nigra,* and the fir-balsam, *Abies balsamea,* which form the forest stand. Associated, but largely confined to water courses, are *Betula papyrifera cordifolia,* and *Alnus viridis* which form threads of light green woven into the darker shade of the coniferous forest. The arbor-vitae, *Thuya occidentalis,* occurs sparingly along water courses at the outer border of the Great basin. It was recorded at an altitude of 2,800 feet.

The forest floor is covered with a dense and continuous mat of mosses consisting not of a multiplication of species but chiefly of three forms, *Hypnum Schreberi, H. crista-castrensis,* and *Hylocomium splendens* which recur continually in this thick moss carpet, covering rocks and logs alike with an uninterrupted mat of green. In this carpet also occur several liverworts, *Ptilidium ciliare* and *Bazzania trilobata* being the most prominent. On exposed rocks Dicranums are not uncommon. Through this moss carpet, arising from the rich humus below, extends a variety of forms. *Pyrus americana, Amelanchier oligocarpa,* and *nemopanthes fascicularis* are prominent, the abundance of seedlings of the former being especially noticeable. Other less common shrubs are: *Ribes prostratum, Viburnum pauciflorum* and *Aralia nudicaulis. Taxus canadensis* occurs abundantly and in its characteristic habit of growth. Other forms, which with the moss carpet constitute the forest floor, are: *Oxalis acetosella, Coptis trifolia, Maianthemum canadense,* *Cornus canadensis, Trientalis americana, Streptopus roseus, S. amplexifolius, Vaccinium canadense, Clintonia borealis, Lycopodium lucidulum, Phegopteris polypodioides, P. Dryopteris, Listera cordata, Moneses grandiflora, Goodyera tesselata,* and an abundance of *Monotropa uniflora* and *M. Hypopitys,* giving these woods a very mesophytic aspect.

This mesophytic forest covers the Great basin, South basin, the Northwest basin, most of the outer slopes and ridges, and extends far out into the lowlands about the mountain. Ascending the basins, the trees gradually become smaller until at the base of the last long precipitous ascent, the walls proper of the basins, there is an apparent tree line which skirts the base; especially is this noticeable in the Great basin. (Fig. 5). This "timber-line," so called, is more apparent than real and has its only delimitation in large trees. The walls of these basins are much subjected to slides of rock and gravel, and snow in spring, which rush down the slopes and strike at the base with tremendous force. In this plunge these avalanches sweep all before them being checked only by the larger trees at the base. The multitudinous repetition of these slides has thus formed a line of trees which represent not a climatic but an avalanche timber-line. Trees soon appear on these slides and within a few years they become reforested. The birch, *Betula papyrifera cordifolia,* is the most abundant on the slope trees. It seems, on account of its flexibility, particularly adapted to this precarious slope life. This very property of bending without breaking doubtless explains its predominance as a slope form. Mixed with it is the alder, *Alnus viridis,* and frequent spruce and fir. These trees form a continuous forest growth with the mesophytic forest of the lowlands and, gradually diminishing in size, extend up to the "tableland" and "saddle," there joining the *Krummholz* and reaching far up toward the summit. Most of the spurs, notably the Northern ridge, are also covered by this forest. Where slides are rare the composition is largely spruce and fir and would never suggest a timber-line, for the decrease in size is gradual. This same apparent "timber-line" exists upon the western and southwestern slopes. Harshburger[1] states that this timber-line is here at 3,700 feet and so maps it in a very diagramic way. Williams[2] says the timber-line barely averages

1. Op. cit.
2. Williams, E. F. Floras of Mt. Washington and Mt. Ktaadn. Rhodora 3: 1600 65. 1902.

3,100 feet in the great basin and 2,200 on the southern slopes; he adds: "this last being partly due, however, to their excessive steepness."

It would appear from the above discussion that this so-called "timber-line" is more apparent than real and has no relation to climatic conditions, as most writers have implied, but is largely determined by the steepness and the resulting avalanches on the slopes and is in reality the limit of large trees. It was shown above that the limit of the *Krummholz* upon the upper slopes was not climatic but that the question of time and edaphic conditions had alone retarded its further advancement. There is then no true climatic timber-line upon Ktaadn any more than upon the other mountains of Maine, Black Cap, Waldo, Desert, and others of far lower altitudes, and it is largely the element of time that retards the forestation of the very summit.

(f). *The Roches Moutonées Society.* In the Northwest basin are two rock hills rising some 20-25 feet above the general level of the shelf. With their sloping sides and flat glaciated tops they present a plant society most unique. Bare in places, they are almost entirely covered with a typical heath formation. The drainage is excessive and the conditions extremely xerophytic. The flat tops are dominated by *Kalmia angustifolia, Cassandra calyculata,* and *Ledum latifolium.* It bears a most striking resemblance to an old sphagnum bog. In places tussocks of sphagnum appear and associated with it is *Vaccinium Vitis-Idæa. Cladonia rangiferina,* and its less common variety *alpestris* are abundant. Around bare rocks *Vaccinium uliginosum* abounds. Little remains to tell of the early stages of this unique association. It is however clear that it has passed through the crustaceous-lichen and reindeer moss stages. The heath stage corresponds in sequence to that of the Alpine-Tundra which for some reason has failed to develop here.

Covering the steep sides of those *roches moutonnées* and the basin in general, is the mesophytic *Picea-Abies* forest with its characteristic undergrowth. Advancing from the edge of this forest to the flat glaciated tops are islands of *Krummholz* spruce and fir with single trees beyond. In several places the heath is thus completely spanned. The fusion of these islands makes the destruction of this heath in the near future a certainty. Why this rock society is so extremely xerophytic, perhaps even more so than the summits, can perhaps be explained by no other reason than by its excessive dryness, due to an almost perfect drainage. There is also little retention of water, and humus accumulation is necessarily slow. These conditions all contribute to extreme xerophytism at first, but once a soil is formed succession will follow as rapidly as upon the mountain.

B. THE ALPESTRINE MEADOW SOCIETIES.

This plant society furnishes one of the strongest evidences of the edaphic theory that has ever come under the writer's observation. On a substratum, otherwise very xerophytic and which would normally support an Alpine-Tundra society, occurs, by virtue of its location and exposure, a mesophytic Alpestrine meadow society. Situated at the base of the dripping west walls of the North basin, and so presenting a warm south and southeastern exposure, it possesses in these two conditions edaphic factors which determine its existence.

Passing out from the base of the cliff, several well defined plant zones are successively traversed. Situated at the base of a precipitous cliff and upon a sharp talus slope the soil is largely accumulated from the slopes above. By snow-slides and heavy rains a residual soil of gravel and humus is washed down and forms the substratum for these plant societies. Three very distinct stages or zones appear to-day. By a study of this horizontal zonation we may arrive at an understanding of the vertical succession.

(a). *The Pioneer Stage.* Upon the first accumulation of soil which lodges in cracks, crevices, gorges, on miniature shelves, and at the base of the dripping walls, *Scirpus cæspitosus* first makes its appearance, and often becomes very abundant. *Campanula rotundifolia,* forming vast beds, follows *Scirpus.* With it is associated *Solidago Virgaurea alpina.* (Fig. 6).

Potentilla tridentata next appears to work its way into this society. *Potentilla fruticosa* is often associated, but never abundantly enough to be dominant. *Arenaria grœnlandica, Carex scirpoidea, Luzula spadicae melanocarpa, L. spicata* and *Juncus articulatus* are less prominent but normally associated forms. This plant covering though sparce now acts as a retainer of soil and humus washed from above and also adds to it by its own decay. A humus and a power of hygroscopicity soon develop sufficiently to support a less xerophytic society and the next stage soon follows.

(b). *The Meadow Stage.* Determined by the increasing water content of the substratum the meadow encroaches with rapidity upon the pioneer society. In many places the meadow has entirely replaced it extending up to the very base of the walls themselves (Fig. 6). It is thus that the stage once dominant is now being gradually replaced by another of a higher ecological type: a more successful society in the struggle for existence. At the foot of the southwest wall of the Northwest basin the pioneer society is a feature of the past, the Alpestrine meadow entirely skirting the dripping face of this precipitous wall.

Among the first meadow forms to appear in the pioneer society are *Castilleja pallida, Prenanthes trifoliolata, Aster acuminatus, A. radula, A. umbellatus,* and *Anaphalis margaritacea.* Several of the grasses now appear. *Calamagrostis canadensis, C. Langsdorfii,* and *Bromus ciliatus* occur in great profusion, *Glyceria nervata, Agropyaum violaceum,* and *Agrostis rubra* are also common. With these grasses are associated *Heracleum lanatum, Habenaria dilatata, Arnica Chamissonis, Viola blanda, V. canina,* and *Solidago macrophylla.* As a whole this society presents a striking meadow aspect, and one which appears quite out of keeping with the surroundings. This society is quite extensive, occurring wherever these conditions are repeated. Here and in the Northwest basin, however, it reaches its typical development. In this meadow society accumulation from wash and decay are continually in progress. With fit conditions we have the advent of another society.

(c). *The Shrub Stage.* With higher food demands this stage follows only when, as in our lowland natural meadows, these conditions are fulfilled. In several places this stage has quite replaced the meadow, extending up to the very base of the cliff. The first form to appear in the meadow is *Diervilla trifida* which later becomes the character shrub of this stage. *Spiræa salicifolia latifolia* follows, often becoming very abundant. Associated but secondary forms are: *Rubus strigosus, R. canadensis, Lonicera cœrulea,* and *Ribes prostratum.* *Alnus viridis* soon makes its appearance and becomes the dominant bush. With it are *Cornus stolonifera, Nemopanthes fascicularis, Amelanchier oligocarpa, Prunus virginiana, P. pennsylvanica* and *Pyrus americana.* With these shrubs is associated a mesophytic undergrowth. *Phegopteris Dryopteris, Asplenium filix-foemina,* and *Aspidium spinulosum dilatatum* all occur in greatest profusion. Associated forms are *Streptopus roseus, S. amplexifolius, Clintonia borealis, Trientalis americana, Coptis trifolia, Galium triflorum, Viola blanda, and V. canina.* These forms precede the mesophytic forest which encroaches below. This latter society has been discussed above and need only be mentioned here. One fact seems very evident; whatever the pioneer stage, the ultimate is the climax forest of this region.

C. THE POND-BOG SOCIETIES.

The scene of general and local glaciations, the environs of the mountains are dotted with ponds whose origin is unquestionably morainic. A marked variation in size and depth presents a variety of conditions which closely control the plant life of these upland ponds. The low mean temperature of the water and the destructive spring freshets preclude an abundant acquatic vegetation in those ponds, Cowles, Davis, and Chimney, which are situated at the base of the slopes and receive the brunt of these spring devastations. In the ponds this zone is the mesophytic climax forest. Sometimes an inter-removed from these destructive agents, a slight aquatic vegetation sustains itself.

(a). *The Pond Societies.* The shores of these ponds are rock strewn and slope off to some depth. A narrow zone of alder and birch, *Alnus viridis* and *Betula papyrifera cordifolia,* fringe the ponds, coming in many localities to the waters edge. Behind vening zone of amphibious forms borders the water's edge. Again a heath formation may fringe the shores. Some of the ponds, located several miles from the mountain, are bordered by a bog-like zone in which *Cassandra calyculata, Kalmia angustifolia, Ledum latifolium, Myrica Gale, Sphagnum* in profusion, *Drosera rotundifolia, Sarracenia purpurea,* and *Pellia epiphylla* abound. The presence of this sphagnum bog flora, characteristic with the exception of *Pellia,* under such excellent conditions of drainage, would seem to have its explanation in a temperature factor, as suggested by Kihlman[1] and not by the accumulation of humus acids as Schimper claims.[2] Similar short features obtain at Davis and the two small ponds of the Northwest basin.

1. Kihlman, A. O. Pflanzen biologische studien aus Russich-Lappland, acta. soc. pro Fauna et Flora Fennica 6: 1890—abstract Flora 75.
2. Schimper, A. F. W. Pflanzen geographie auf Physiologische Grundlage. Jena 1898.

Lake Cowles shows perhaps the highest development of an aquatic flora, yet it is much limited as to species and individuals. In the shallow water of the rocky shores grow *Isoetes heterospora,* its highest and most northern station, *Isoetes echinospora Braunii, Potamogeton confervoides, Lobelia Dortmanni, Zizania sp., Nuphar odorata minor,* and *Nymphæa Kalmianum.* These forms are never in enough abundance to be a potent factor in the life history of the pond.

Chimney pond, on the other hand, has, as far as the writer was able to observe, no acquatics yet it is bordered by an interesting zone of amphibious forms. Among these may be noted *Pellia epiphylla* which covers all available space at the water's edge. *Scirpus cæspitosus, Carex saxatilis,* and *Carex scabrata. Sphagnum* is present, but occupies a zone farther from the water's edge. In this fringing meadow-like zone also occurs *Vaccinium oxycoccus, Kalmia glauca, Aster radula, A. acuminatus* and several species of violets. Intermediate between this zone and the mesophytic forest occurs a belt of *Spiræa salicifolia latifolia* and *Alnus viridis.* The life history of these ponds is doomed to be long, leading doubtless to the sphagnum bog. Their destruction will be largely due to detritus washed from above.

A small pond in the Northwest basin, situated at the base of heavily wooded slopes, and receiving some residuum, is now nearing its temporary climax. Its life history will be comparatively short, leading to a small natural meadow. The shores are now bordered with a fast encroaching meadow, and similar islands almost spanning the pond make its future very evident. Upon the islands spruces have already appeared. In this meadow society grow *Scirpus cæspitosus, Carex rigida Bigelovii, Aster radula, Aster umbellatus, Lycopodium inundatum,* and many other less prominent forms.

(b) *The Sphagnum Bog Society.* In the great basin, near the outlet of Lower Basin pond, is located a small sphagnum bog. In a deep morainic depression, and isolated from the receipt of much detritus, its life history has doubtless been of great length. With the exception of a few open spots (Fig. 9) the once rocky shored pond is completely captured by sphagnum and its associated forms. By a study of these open places we are able in a measure to interpret the past order of succession, for we have here in miniature what presumably took place in the bog as a whole. The *Sphagnum* advances from the edge, dying down below. As it grows above it continually opens the way for further encroachment. The opening is finally spanned and a soil is formed. Upon this *Scheuchzeria palustris* appears, even before the substratum reaches the surface. As the soil reaches the surface *Drosera rotundifolia* and *D. longifolia* come in. As the *Sphagnum* continues its growth and the condition becomes drier *Sarracenia purpurea* appears. Associated with it are *Vaccinium oxycoccus* and *Smilacina trifolia.* With still drier conditions *Eriophorum gracile, Carex trisperma,* and the characteristic *Carex pauciflorum* become constituents of the bog flora. The heaths next appear: *Cassandra calyculata, Kalmia angustifolia, Kalmia glauca,* and *Ledum latifolium* are abundant, occurring in the order named. With these, *Pyrus arbutifolia* and *Viburnum cassinoides* are common. Other forms whose place in this succession was undeterminable but which are very significant are *Empetrum nigrum, Vaccinium uliginosum,* and *V. Vitis-Idaea.*

Upon the bog, trees now make their encroachment. *Picea nigra* is the pioneer. Associated with it, but coming later and less abundantly, are *Thuya occidentalis* and *Larix Americana.* In places this advancing forest zone is strongly *Thuya* and seems to be associated with the old rocky inlet. The remaining four-fifths of this border zone is dominantly *Picea.* When this zone closes in upon the bog, as it already has for some distance, the conditions within are constantly made more and more mesophytic and we have a mesophytic undergrowth advancing from the surrounding mesophytic climax forest. Among these mesophytic forms which closely follow the advance of the spruce are *Coptis trifolia, Trientalis americana, Clintonia borealis, Cornus canadensis, Chiogenes serpyllifolia, Trillium undulatum,* and *Osmunda cinnamomea.* The characteristic mesophytic shrubs *Nemopanthes fascicularis* and *Amelanchier oligocarpa* are also present.

The entire absence in the bog of orchids such as *Calopogon pulchellus, Arethusa bulbosa, Pogonia ophioglossoides,* and *Habenaria hyperborea,* so characteristic of sphagnum bogs of lower altitudes in Maine, seems a peculiar fact of distribution. Isolation has doubtless precluded their appearance.

The future of this bog is very evident. With the continual advance of the mesophytic forest, the bog will gradually disappear and the climax forest will one day blot out its history.

The strong mountain affinities of this bog flora may be now noticed. The possession, in common with the mountain flora, of the majority of the typical bog forms, especially *Vaccinium uliginosum, V. Vitis-Idaea,* and *Empetrum nigrum,* would seem to strongly indicate an identity of physiological conditions and suggest a common cause. We have already shown that the vegetation of the higher slopes was probably subjected to a high "transpiration ratio" due to a minimized absorption and an accentuated transpiraton. Similarly this high "transpiration ratio" exists in the bog and in the Arctics, and in all these varied habitats there is a striking identity not only specifically but ecologically, thus demonstrating the physiological similarity of these habitats. Such soils are said to be physiologically dry, in other words xerophytic.

The exact cause of the low absorption in the sphagnum bog is yet problematical. Two theories are in vogue. Schimper claims[1] that the lack of drainage and aeration causes the

1. Op. cit.

abundant accumulations of humus and humic acids. These act upon the roots inhibiting absorptive power. Similarly these acids preclude nitrifying bacteria, thus making the soil poor in nitrogen. In all the absorption is reduced to a minimum.

The other theory, advanced by Kihlman[1] and applied to the sphagnum bog by Ganong,[2] would refer the cause of low absorp-

1. Opp. cit.

2. Ganong, W. F. Upon raised peat bogs in the province of New Brunswick. Trans. Roy. Soc. Canada 3: II, 131-163. 1897.

tion to the low temperature, making this strong ecological and specific resemblance of Arctics, mountains, and sphagnum bogs due to an identical factor. A set of readings by the writer substantiate the latter theory. We have also shown in some preliminary experiments that the low temperature of the bog is sufficient to reduce the absorption to a minimum.

The striking Arctic and Alpine affinity of the sphagnum bog and the border flora of mountain ponds, as noted above, leads to a very significant consideration, the question of their origin. It has been shown above that the Alpine flora is glacial in origin. In view of this fact and the floral similarity between the above plant associations and the Arctics, we are led to suggest a similar explanation. Whether these ponds have received their border floras through local and valley glaciation and avalanche action or by general glaciation, is of course entirely problematical. The former mode would, however, seem more probable and must, at least, have been a source of subsequent introduction of the Arctic-Alpine forms.

This hypothesis may be extended to extra montane ponds; in these, however, general glaciation must have been the source of this relict flora. Such a condition as described for Sandy Stream pond might well be taken as an example of the initial stages of such a plant society. The centripetal encroachment of this border zone would eventually develop a typical sphagnum bog, not unlike the one described above and quite identical with a multitude of others scattered over the New England States. If we hold to the glacial relict theory to explain the Arctic affinity of the sphagnum bog flora, we are frequently confronted with this condition: that ponds presumably similar, i. e. glacial, and synchronous in origin, in the same region and subjected to identical general influences, have passed through the natural meadow on the one hand and the sphagnum bog on the other. It has been shown above that a difference in the duration of the life history may be called upon to explain this seeming contradiction. We must presume, however, the initial stage in both classes of ponds to have been similar if not quite identical to the condition characteristic, to-day, of the shores of Sandy Stream pond. The divergence was subsequent to the pioneer stage.

A rapid development, a short life history, made possible by the relatively quick distruction of a pond, favors the introduction of forms, which, in the struggle for existence crowd out the glacial relicts and result in a natural meadow. A slow succession, an extended life history, for opposite reasons, supports the development and extension of the glacial relicts and the consequential formation of the sphagnum bog.

VII. Conclusions.

In the preceding discussion we have traced the origin and genetic development of the Ktaadn flora and studied the various factors operative in determining the present plant physiognomy. An attempt has been made to show that the accepted principles of physiographic ecology hold in general in Alpine as well as in lowland regions. The discussion has necessarily been rather general; but it is hoped that it will lay the foundation for further and more critical study along similar lines. While most of the ideas presented are not new, some of them, perhaps, appear in a new relation and others, so far as the writer is aware, have here their first expression. The conclusions of the study may be summarized as follows:

1. The flora of Mt. Ktaadn is glacial in origin, adventive from Arctic Eastern Europe, by way of a former land connection, through Iceland, Greenland, and Arctic Eastern America.

2. The flora is determined by local climatic conditions repre-

senting not only ecologically but specifically the climatic societies of regions far to the north.

3. This striking ecological and specific similarity of the floras of high mountains, the Arctics, sphagnum bogs and borders of cold ponds, is probably caused by a physiological identity of the various habitats, a physiologically dry soil, a xerophytic soil. Such habitats are characterized by a high transpiration-ratio due to an identical cause, minimized absorption, probably determined, in part at least, by the retardative effect of low temperature.

4. The *Krummholz* of the "tableland," "saddle" and upper slopes is a depauperate mesophytic forest determined by the high precipitation, its happy distribution, and abundant retention.

5. There is no true climatic timber-line upon Ktaadn. The demarkation between Alpine-Tundra and *Krummholz* forest upon the higher slopes is merely edaphic. At the base of the precipitous lower slopes the so-called "timber-line" is in reality an avalanche line.

6. The length of the life history of a pond determines its temporary climax; if short the natural meadow, if long the sphagnum bog is the result.

7. Whatever the pioneer stage and the order and rate of succession, all the plant societies are progressing toward a common end, the *Picea-Abies* combination, the climax mesophytic forest of the region.

8. The glacial relict theory may be extended to account for the Arctic affinity of the sphagnum bog flora of extra montane pounds; while in local and valley glaciation may be sought the origin of the Arctic-Alpine flora which borders the shores of ponds and forms the sphagnum bogs within the Mt. Ktaadn region.

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EXPLANATION OF PLATES.

Fig. 1. Relief drawing of Mount Ktaadn as seen from the south.

Fig. 2. A view on the "Saddle" showing the Alpine-Tundra in the foreground and the *Krummholz* islands beyond. The height of the trees is shown by the camera case standing upon the crown of a prostrate spruce. The xerophytic structure of the *Krummholz* is clearly shown. The rocks rising through the mat are covered with lichens.

Fig. 3. The "Saddle," North Mountain, and the Northern Ridge beyond from the north slope of West peak. The covering of the Central Mountain by the *Krummholz,* its extension far up toward the northern summits, and its encroachment upon the Alpine-Tundra, are clearly shown. The conditions along the east brow of the "Saddle" are to be noted (cf. Fig. 2).

Fig. 4. General view on the "Saddle" showing the extension of the *Krummholz* passing without interruption down the west slope. View looking northwest from north slope of West peak. The point of the Northern Ridge is seen at the right and the Sourdnahunk Mountains beyond.

Fig. 5. "Avalanche-timber-line" at the base of the precipitous east wall of the South Basin. Chimney Pond in foreground.

Reprinted from Rhodora *3:* 1902.

Fig. 6. At the base of the northeast wall of the North Basin are seen the Alpestrine meadow societies. At the right is the "pioneer-stage" in which *Campanula rotundifolia* is dominant. At the left is the "meadow-stage" which follows the pioneer society. It has here reached up to the very base of the dripping walls.

FIGURE 2.

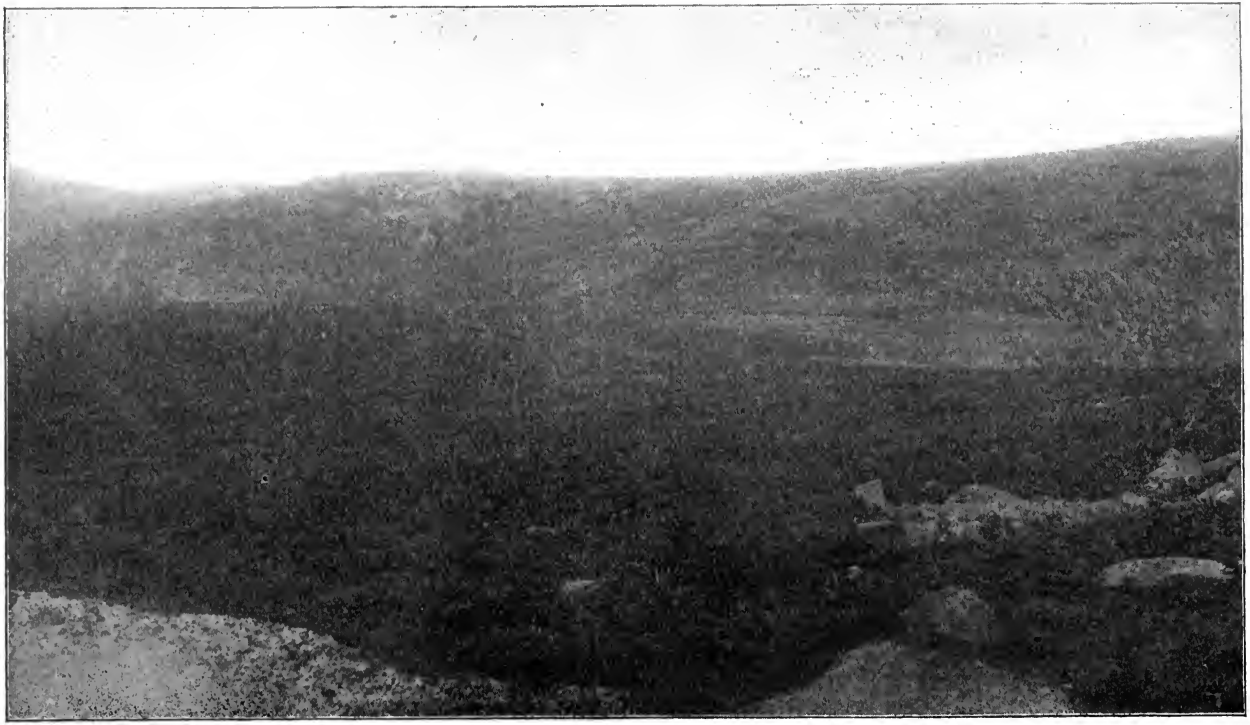

FIGURE 3.

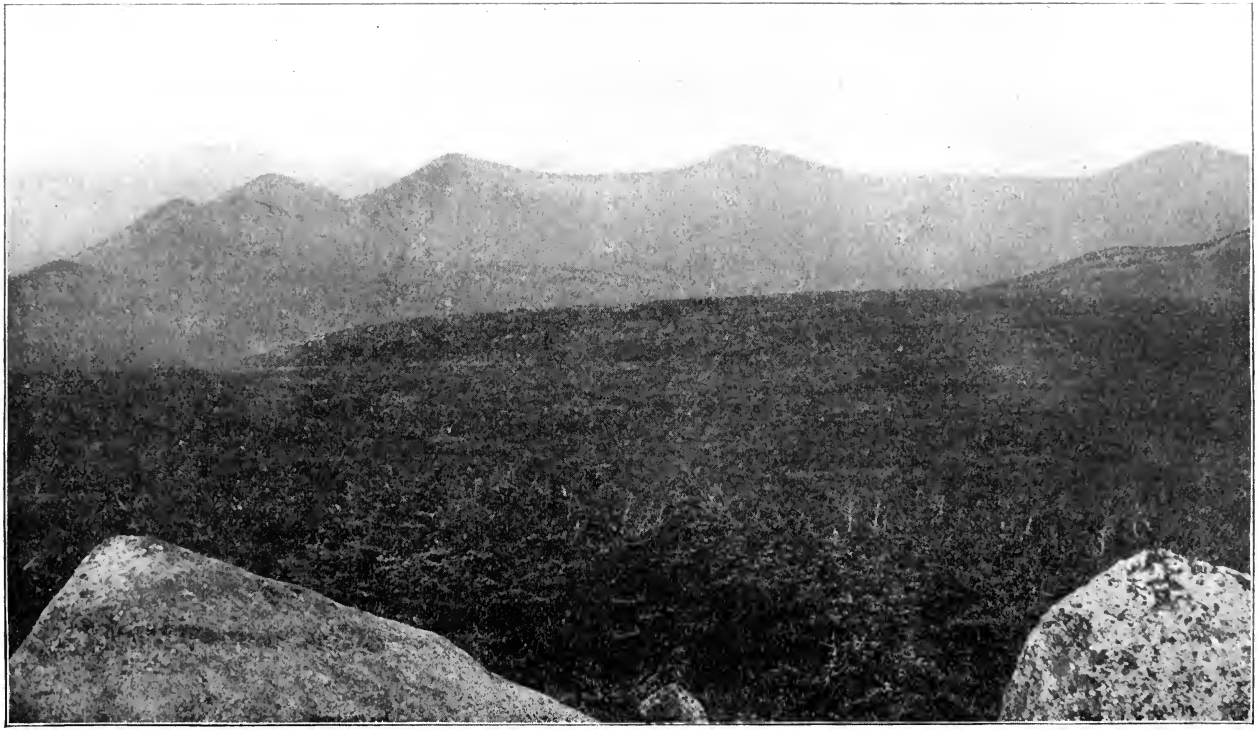

Figure 4.

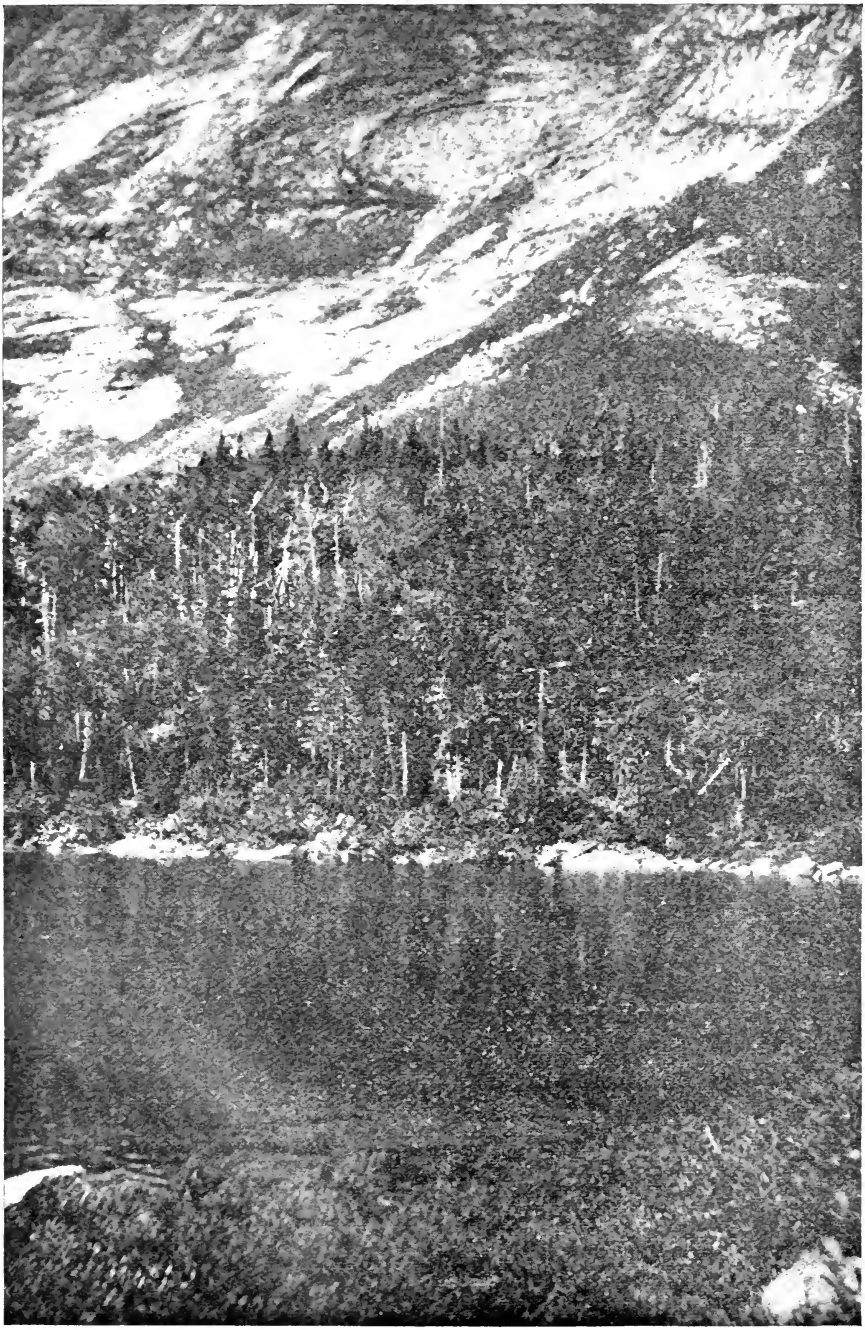

Figure 5.

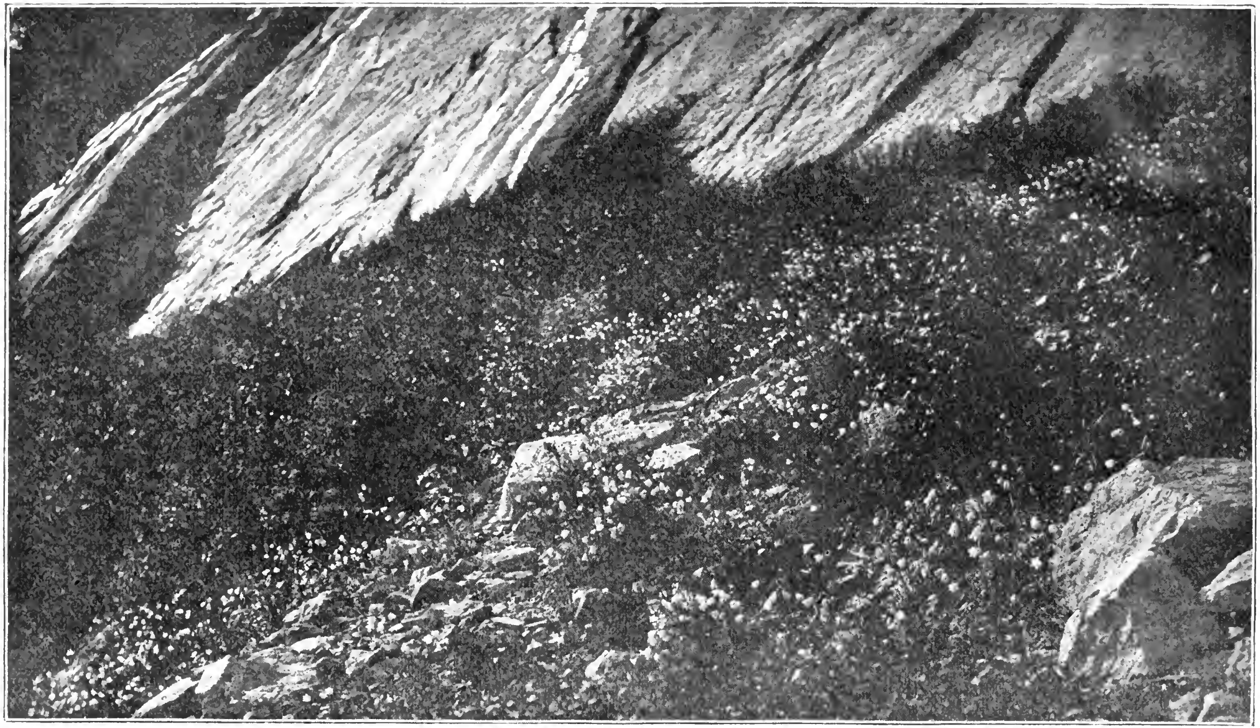

FIGURE 6.