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Sociological Studies of the Alpine Vegetation on Long Peak

Walter Kiener
University of Nebraska-Lincoln

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PREFACE

Born in Switzerland, Walter Bigler Kiener, a naturalized citizen of the United States, brought with him his great love of mountains, and their flora and fauna. Serving for five years as a United States Ranger in the alpine zone facing Longs Peak in Eastern Colorado, he had an opportunity to make extensive and critical investigations of its alpine vegetation.

Dr. Kiener's studies were directed, at the University of Nebraska, by Dr. Raymond J. Pool, a well known botanist. In 1940, the culmination of Kiener's work in the alpine region appeared as a doctoral thesis in partial fulfillment of the requirements for the Ph.D. degree in botany at Nebraska. His methods of investigation followed the European approach to ecological research in which he was greatly influenced by the works of such great scholars as Braun-Blanquet, Tansley, and C. Schroeter. Dr. Kiener's work was thorough and exhaustive. It represented the first extensive ecological research, based on European methods, in this country. It can rightly, therefore, be considered a pioneering effort in ecological research of the alpine area in the United States.

Because Dr. Kiener's research work was never published in a journal and because of numerous requests for loans of his thesis, it was proposed to the University of Nebraska Publications Board that his work be published and distributed. Members of the staffs of the Department of Botany and the University Museum were pleased when it was decided to publish the report in the *University Studies*. Several botanists read and edited the thesis, but no attempts were made to modernize terms or alter taxonomic entities because it was felt that Dr. Kiener's thesis, being a classic, should be as original as possible.

At the time of his death in 1959, Kiener willed his extensive collection of plants, catalogues, and notes, his research library, and other property to a long-time friend, Dr. Samuel I. Fuenning, now Director of the Student Health Center at the University of Nebraska.

Dr. Fuenning, in turn, presented all of these items to the University of Nebraska State Museum through the University of Nebraska Foundation. By far the largest part of his collection consisted of lichens. Between 15,000 and 20,000 lichen specimens from numerous localities, but mostly from Colorado and Nebraska, have been established as the WALTER KIENER MEMORIAL LICHEN COLLECTION in the Museum's Division of Botany-Herbarium. The Museum's lichen specimens have been added to the Kiener Collection. Other kinds of plants obtained by Kiener have been placed in the regular collections of the Herbarium in the Museum. A Walter Kiener Memorial Endowment Fund also was established in The University of Nebraska Foundation to help with the maintenance of the Kiener Collection and Library, and to encourage research.

It is our hope that the contributions made by Walter Kiener in his alpine ecological studies will stimulate further research in this fascinating field.

W. W. RAY, *Professor of Botany and Curator of the Museum's Division of Botany-Herbarium*

C. BERTRAND SCHULTZ, *Director of the University of Nebraska State Museum*

Acknowledgments

The writer is particularly indebted to Dr. R. J. Pool, Chairman of the Department of Botany, for the supervision of this work. He is indebted to Dr. Th. Just, of the University of Notre Dame for suggestions in the field and encouragement; to the late Dr. A. S. Hitchcock for the checking of the grasses; to Prof. I. W. Clokey, Pasadena, California, for aid in the identification of the carices; to Mr. E. J. Alexander of the New York Botanical Gardens for the checking of specimens with Rydberg's types. There are many more whose help the writer deeply appreciates.

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I / *Introduction*

General. On this continent no investigation is on record that had for its purpose the structural study of a whole unit complex of alpine vegetation. From Colorado several works are available that treat of the problem in part only. There was very little in the available literature on the biology, structure, and floristic composition of the complete vegetation when the writer, as a ranger for the United States National Park Service, was stationed for five summers on a ranger station located in the alpine zone facing Longs Peak. A desire to increase the knowledge of alpine vegetation led to this investigation, a desire that had its inception in a love for the mountains and all that dwells thereon, a love that was nurtured through long years of mountain climbing. An intimate acquaintance with high mountains proved of great help in the course of the investigation.

Location. The vegetation under study is that of the full area of the alpine zone on Longs Peak in Colorado. It includes all soil and rock surfaces from the timberline of the subalpine zone to the top of the peak. The altitudinal range is from about 11,000 to 14,255 feet. The area includes roughly four square miles and is crossed by latitude 40°15′ N and longitude 105°37′ W. Longs Peak is among the highest peaks of the United States. With regard to biology and climate it is complete and representative of the high mountains of Colorado. Its inclusion within the confines of a national park enhances the value of this study.

II / *Extent and Limitation of the Investigation*

In any study of vegetation, the first and indispensable requirement is a knowledge of its structure. The solution to practically all biological problems related to natural vegetation depends on the penetration and completeness of the study of structure. The study of structure does not in itself include the factors of the environment, but it is best understood when the climatic and edaphic conditions of the vegetation are also known. A knowledge of the latter becomes necessary in the evaluation of the causes of the pattern of distribution and succession. Factor data were collected whenever possible, but are included in this paper only insofar as they appear to help an understanding of the structure of the vegetation. It is proposed to treat the full data of the environment in a subsequent paper.

Geology and Physiography. The only direct influence physical geology has on the vegetation in our zone is that of the bedrock on the pH of the soils. All rocks are siliceous, consisting of pre-Cambrian metamorphic rocks, and younger granites and rhyolites. Indirectly the vegetation is affected by the mode of cleavage and jointing of the rocks. When this occurs horizontally and more or less at right angles, the mountain breaks up into ledges which provide a favorable substratum for the vegetation. But where the cleavage is in the form of exfoliation, the platy character combined with steepness of the slopes gives the vegetation small opportunity for a hold.

Geologic history, particularly that of the Pleistocene period, is closely bound up with the vegetational history, but this phase is not to be considered in this paper.

Physiography depends in the main on geologic structure. The great height of the mountain implies steep gradients of slope. The mountain is divided into the upper peak with very steep slopes on all sides and the main massif or base with generally gentler slopes. Rock weathering on the upper peak takes place almost entirely by physical disintegration; on the lower part chemical action also occurs. No two general slopes of any extent are uniform throughout as they bear smaller slopes on themselves. One might speak of a major relief to include the broader general slopes, and of a minor or micro-relief to include the smaller ones superimposed on the general system.

Physiography in this zone does not affect plant life directly, but the relief has a profound effect on the factors of the habitat which, interacting among themselves, act on the plants. Environmental effects of the major relief on plant life find their expression chiefly with regard to exposures such as north and south slopes and their intermediates. Usually a certain plant association dominates on a given exposure, but the micro-relief causes the presence of plants from other associations. Perhaps nowhere else are the contrasts of the micro-relief so prominent as in the alpine zone. One need only examine a rock standing one foot high above the general level to find radically different habitats around it. The strong alpine insolation is a master factor. Its absence on the shaded side will cause a constantly cold habitat with low water-vapor deficit, but the sunny side is a very dry and hot place causing a locally very high water-vapor deficit, often inhibitory to plant growth. Intermediate conditions occur on the other sides. All these physical contrasts with the correspondingly different plant responses are the expression of the varying environmental conditions, and may be found on areas smaller than a square meter in size. The principle of the varying conditions of environment and plant responses caused by the small rock described holds true in smaller as well as in ever-widening ecological wave lengths and amplitudes. It may be found in the pattern of lichen distribution on a small handpiece of rock lying on the ground, and be discovered again on a grand scale on the giant cliffs that form the summit. Once the effect of the micro-relief on the habitat is recognized, the orderliness and recurrence of the resulting pattern of plant distribution is found to be astonishing. Hence, knowing the relief, the pattern becomes predictable.

Environment and Growing Season. Temperature is usually given as the chief factor causing a timberline on mountains. The alpine zone lies above timberline where the average temperatures become increasingly lower with increase in altitude. The average decrease in temperature with altitude is usually given as 1 degree F. for every 300 feet. The altitudinal difference between the upper and lower borders of the alpine zone is over 3,000 feet, corresponding to a difference in average temperature of about 10 degrees. The recognition of this temperature gradient within the zone is of utmost importance in the field as well as in the synthesis of the vegetational distribution, since temperature affects plant life directly through its metabolism, and reacts on other factors of the habitat, notably evaporativity.

Wind enormously increases evaporativity, thus often becoming a critical factor in the distribution of plants. The importance of wind is often reduced because of the crouching habit and low stature of the plants, as well as the velocity-reducing micro-relief. A general wind reduction takes place during the summer months. Wind influence is most pronounced when it is concomitant with other factors such as lack of soil water on high ridges and steep slopes.

The effect the wind has on the distribution pattern of the vegetation, while remote, is probably most important during the winter months. It is well known to meteorologists and mountain climbers that during the winter the wind attains great average velocity. The most conspicuous result is the prevention of the formation of a continuous snow blanket over the whole mountain. The snow is drifted into the lees and down into the timber. Where such drifts linger into the growing season a different type of vegetation arises. The largest volume of snow comes to rest in the timberline belt, but some is often carried into the valleys, whence the people refer to this drift as "second hand" snow. As soon as drifts begin to form the vegetation underneath is protected from the desiccating effect of the wind, as well as from excessively low temperatures. But over the larger part of the area there is no continuous or effective protection by snow cover. A good many plants seem to depend on snow protection for their winter buds. The relative size and thickness together with exposure determine the duration of the snowdrifts, which in turn affect the type of vegetation.

The absence of a continuous cover sheet of snow in the alpine zone on the Rockies, due to wind, is a most striking difference from the general conditions on the high Alps. It is therefore not a mere coincidence that the main alpine plant association of the Southern Rocky Mountains is an Elynetum similar to the one long known from the high Alps where the Elynetum is restricted to wind-swept and snow-free slopes.

When in spring and summer the snowdrifts melt, the resulting cold water may inundate parts of the slopes for a considerable time and become inimical to plant growth by keeping the soil cold and deficient of oxygen. Later in the season such slopes may carry a xerophytic vegetation. It is not uncommon to find on the same slope close together xeric and hydric plants, but only one will be found in seasonal activity.

Two seasonal aspects of flowering occur through most of the zone. Plant activity usually begins about the middle of June and ends by the middle of September. If this be taken as the length of the growing season, however, no plant is found that uses for its seasonal activity the whole length of the growing season. This length is locally modified by snowdrifts, exposure, and temperature gradient.

Biotic Influences on the Vegetation. Relative inaccessibility and sparse settlement before the establishment of the national park area make it appear that commercial grazing never occurred in this zone. The national park status with its protection from grazing was established in 1915. But in 1925 a hostelry was built on the Boulderfield at an elevation of 12,700 feet. Since then, and up to 1935, every season two donkeys used in packing have been grazing regularly for part of the summer at that place, which is at the upper periphery of the vegetation carpet. As a matter of record it should be noted also that dogs were kept at the same place for a period of ten years. Since their presence may have had an influence on the wild animals, they may thus have exerted an indirect influence on the vegetation.

Additional grazing does occur when vacationists enter the zone with horses. It is a custom of the cowboy guides to turn the horses loose for grazing when stopping. There are thus certain places that are grazed regularly, and a certain amount of fertilizer with unwanted seeds is brought in. Trail building also causes disturbances of the vegetation. While all these interferences by man and his animals are not extensive, they are persistent from year to year and may become the cause of changes. The influence of the wild animals on the vegetation appears to be in balance as no disturbance was observed. Few burrowing animals were encountered within the alpine zone.

Earlier Investigations. During the summers of 1904 and 1906 Cooper (1908) made this area a part of a general survey of a larger area and published some of his observations. His study was concerned with broad successional relations over the large area and did not consider structure in particular. At the same time he was engaged in private topographic surveying, and by his work and enthusiasm he lastingly influenced some of the local naturalists. During the summers of 1928 and 1929, Cox (1933) investigated the alpine succession on James Peak, 30 miles to the south of Longs

Peak. This author has considered the vegetation of the timberline belt as alpine, thereby including practically every species known to be characteristic of the *subalpine* forest zone in his *alpine* succession. Of 294 species of vascular plants so listed, this author considers only 37 per cent of them as worthy of associational rank, but he does not give the status of the other 67 per cent. He further based his association partly on topography and partly on habitat, criteria that are not in themselves part of the vegetation, and therefore logically unsuited for the delimitation of vegetational units. The concepts used by Cox are different from those used by this writer. The works compare therefore only indirectly.

Other botanists have been in the area but with interests other than ecological studies of vegetation.

Methods of Investigation. The methods of Braun-Blanquet (1932) as expounded in his textbook on ecology formed the principal basis for this study. In addition the general works of Beger (1930), Lüdi (1930), Rübel (1922), Tansley (1923), Walter (1927) and Weaver and Clements (1929) were consulted, and valuable aid was obtained from them. Above all the writer is indebted to the classical work of Schröter (1926) for inspiration and suggestions. No one interested in the vegetation of the mountains can afford to overlook this great work of a lifetime of devoted studies by the dean of the mountain botanists.

At the beginning of the investigation large areas were first surveyed to list the species, together with notes on the habitat, time of flowering, vitality, and other features. After a general coherent picture of the floristic composition was gained, smaller areas were chosen for detailed analysis and the quadrat of one square meter in size became the standard for intensive studies. Sometimes several quadrats were arranged to form a transect; oftentimes four were taken together so as to form a single larger quadrat with a fifth one adjacent for statistical comparison, and some quadrats measured 10 meters on the sides. Several hundred quadrats surveyed were of a size of 1/25 of a square meter only, but these also were arranged in units to form larger squares. A large number of the surveys on cryptogamic vegetation was made in the laboratory from collections made in the field. Some quadrats were staked and mapped for permanency of record to facilitate long term observations. Most of the quadrat sites were selected, not at random, but for floristic or ecologic reasons in order to give a more valid description of the generally mosaic vegetation than could be obtained from sites taken at random. In taking the census of populations on nearly all surveys, the method of Braun-Blanquet (1932) was closely followed. Accordingly, the census consisted of the name of the species present, its estimated abundance and cover value, its degree of vitality, and its periodicity. From the survey lists, numbering in excess of one thousand, the association tables were compiled. They appear thus based on floristic composition only. But since most of the quadrat surveys were taken in typical, that is, floristically and ecologically uniform, vegetation the associations represent both floristic composition and ecological uniformity. They conform to the interpretation given by Nichols (1923) to the association concept, a work that proved otherwise helpful in this study.

Careful comparison of the association tables, obtained from the many quadrats, made possible generalizations regarding floristic composition which were more refined, both from the viewpoint of statistical reliability, and from the viewpoint of the concept of fidelity (Braun-Blanquet, 1932). Fidelity or, as it is often called, exclusiveness, however, had already been recognized in the early surveys in the field, and was in fact the clue that first led the writer to distinguish the different associations. In the final analysis the fidelity concept becomes an inseparable part of the association concept, though not without limitations. The resulting abstract associations synthetically conform with constant differences in environment and are therefore truly the indicators of the different environments produced by the same major climate but modified by the critical temperature gradient, the degree of local insolation, and the edaphic conditions as affected by the micro-relief.

Thermographs were located in different habitats and records were obtained for parts of five summers. In addition a sling psychrometer was carried on all field trips, and when feasible two-hour readings were taken of the temperature of the dry bulb and the relative humidity of the air. Livingston atmometer bulbs were used during one season to obtain data on evaporativity in different habitats. One wind meter was available, but was kept on the same station at timberline over parts of five summers, where frequent checks could be made.

For this one-man exploration, a tent camp was established in the timberline belt at an elevation of 11,100 feet, whence the field trips were made into the alpine zone. Much walking and rock-climbing and much back-packing of specimens, camera, and instruments were required, making all field work strenuous and time-consuming. The frequent lightning, rain, and hail storms did much to curtail the field trips. It was estimated that for one day's equivalent of actual field work, three days had to be spent in supporting labor, such as camp upkeep, packing, walking and climbing, and spoiled trips due to weather hazards. All supplies, apparatus, and specimens carried to and from camp had to be packed on horses or on the writer's own back. Commercial guiding, which was undertaken to help defray the cost of this research, also hampered it.

III / The Vegetation

The Vegetation at a Glance. A botanical observer making the ascent of Longs Peak, upon leaving the forest at timberline which is at about 11,000 feet altitude, would most probably notice the great abundance of rocks scattered all over the ground. Next he would be attracted by the bright colors of the multitudes of beautiful flowers close to the ground and scattered among the rocks. Then he might become conscious that while there is a carpet of vegetation interspersed with rocks and boulders, there are many places where small and inconspicuous plants grow out of a gravelly soil and are spaced so widely as to suggest a desert.

The observer following the trail would travel about a mile in a westerly direction along the slope of Mt. Lady Washington, a companion mountain of Longs Peak. On his left, on the northerly slope with its minimum of sunshine, he would observe that *Dryas octopetala,* a sedentary dwarf-shrub, is a dominant plant, covering large tracts on gravelly ground and giving the landscape its peculiar appearance. To his right and below is a broad trough, inclined toward the east, and known as Granite Basin. The middle or bottom of the trough reflects a lively green from locally dense vegetation, and is sprinkled with emerald pools that derive their water from melting snow-banks. The opposite slope that faces directly the noonday sun appears, however, as though barren of plant life, a desert above the forest region.

At Granite Pass, at about 12,000 feet elevation, there is some nearly level ground where the meadow carpet of alpine forbs is at optimal development. The botanical observer will have noticed the abundance of the grass, *Calamagrostis purpurascens,* along the trail, but if he be unaccustomed to climbing and therefore loath to leave the path, he will be fooled by this grass in his concept of the alpine meadow because the grass is abundant only along the trail as a result of soil disturbance created by the crew building the trail in the year 1925. Otherwise, the grasses are conspicuous by their near absence.

At Granite Pass, also, the trail passes a shallow basin where in early summer snow-water stagnates and where *Carex nelsonii* pioneers for the bog association, and where the little red *Elephantella groenlandica* has found the end of its invading power, or expressed differently, has reached the upper limit of its ecological amplitude.

The trail leads further up a steep north slope and through places where the vegetation is almost absent. The observer will have no difficulty in correlating the paucity of plant life with the severe environment, notably cold, wind, and drought.

At a bench mark reading 12,567 feet altitude, the observer enters upon the last half mile of established trail on the well known Boulder Field. The Boulder Field is another shallow basin, a half mile long with a dip of about 200 feet, extending roughly from south to north. At its far or southern end the basin has its inception in the steep slope of the upper part of Longs Peak known as the North Face. Flanked on the west by Storm Peak and on the east by Mt. Lady Washington, the basin forms a definite unit of topography and is aptly named, for it is essentially a field of boulders.

But the most remarkable feature of the Boulder Field is the fact that at its lower end there is a continuous carpet of vegetation among and around the boulders, and at the upper edge there is none. This carpet may be thin in places and very dense in others, particularly along the many streamlets. Before the end of this last half mile of trail is reached, the carpet of vegetation has dissolved itself imperceptibly, and at the end of the trail, at about 12,700 feet where stand the ruins of an infamous hostelry, flowering plants are scarce and widely scattered. Here in the middle of a nearly level "field" with apparently uniform environment occurs a distinct boundary of plant life. The only apparent change in environment is altitude.

At the upper edge of the Boulder Field, mosses on and among the rocks have become conspicuous as have also the lichens. In further ascending by the usual routes of the mountain climbers the botanical observer may climb directly up the North Face or he may go by way of the West Face. On either route he must travel over boulder-strewn slopes practically barren of flowering plants until he reaches an elevation of about 13,000 feet. Now again attractive flowers dot the mountainside but these are mostly different from those encountered farther down. These flowering plants seldom form a restricted carpet but grow after the manner of ruderals, that is, irregularly dispersed. Mosses and lichens come even more into prominence.

When an elevation of about 13,700 feet is reached, the observer still travels over extremely rocky areas where the flowering plants now are practically absent and where the cryptogamic plants hold sway in dominance and conspicuousness clear to the top of the mountain. On the summital plateau at an elevation of about 14,250 feet there is an abundance of cryptogamic plant life, although it is somewhat concealed among the boulders.

Altitudinal Subdivisions of the Vegetation. General observations and intensive survey work supply the evidence that based on the nature of the vegetation, and vegetation alone, the alpine zone represents three natural subzones.

On the upper part of Longs Peak, from 14,250 down to about 13,700 feet, cryptogamic plants only are permanently present and appear to be in harmony with the general as well as the particular environment. This vegetation differs considerably from that farther down and deserves to be recognized as an entity. It seems proper to call it the belt of cryptogamic vegetation, or, the high-alpine subzone. The vegetation of this subzone does not form a part of this study.

Next below this cryptogamic belt are found the vascular plants of the ruderal vegetation occupying the cliffs, ledges and crevices of the rocks. The vascular plants associate and compete with cryptogamic plants with which they are co-dominant over most of the area, but frequently the crypotgamic plants dominate the vascular. The presence of these vascular plants, as well as floral composition, characterizes this vegetation as an entity. Properly it is herewith called the belt of the plants of crevices and ledges, or the middle-alpine subzone. It extends roughly from 13,700 to 13,000, and extremely to 12,000 feet.

Below this ruderal vegetation there is usually a narrow strip of near barrenness and then the slopes become more gentle in steepness. Here the ground is more or less covered with a continuous vegetation, speckled with rocks and thinly spread on exposed slopes but forming a carpet on others. This is the belt of the alpine meadows, or the low-alpine subzone. It extends roughly from 12,600 to 11,000 feet and comes into contact with the timberline belt of the subalpine zone.

IV / *Method and Procedure*

For the analysis of the structure, sociology, and floristics of the plant life of the alpine zone, the association as proposed by Nichols (1924) and further elaborated by Braun-Blanquet (1932) was taken as the fundamental unit of vegetation. For the structural characterization of the communities, the methods also proposed by Braun-Blanquet offered several advantages. Inasmuch as this is the method of the so-called Swiss school of ecology, practically all the extensive ecological work on the vegetation of the Alps was done by this method. As there is great similarity between the alpine ecology of the Alps and that of the Rockies, the use of similar methods of investigation makes itself mandatory, for only thus can results be directly compared.

As has been stated in the introduction, the unit area of one square meter in size became the standard unit of detailed analysis, although many deviations and combinations were employed when a particular community seemed to recommend it. Small or peculiar communities were surveyed as wholes regardless of size. Whole slopes or other topographic units practically always were surveyed as wholes also, chiefly to check on the presence of species. In many instances this brought into the survey lists rarer species or invaders that on account of the broken and rock-strewn ground would not have come within any quadrat.

The analytic characters investigated were *periodicity, vitality, layering, sociability,* and *total estimate* or abundance and cover combined.

Periodicity. Because of the shortness of the seasonal cycle of nearly all species, and the variability of the micro-environment, the periodicity of most species is subject to great irregularity. For the whole zone three periods of flowering may be distinguished. The first occurs during the later part of June and the early part of July and is colorful and most attractive. It is comparable to the season of spring. The second period follows immediately with yellow flowers in dominance and lasts till early in August. This is the floral mid-season or summer time. The late summer or early fall season has only one species that is truly a late bloomer, namely, *Gentiana romanzovii*. The species comes into blossom by about the middle of August in favored places, and flowers are still found in September and even October when it may have already snowed several times. Periodicity, however, is more properly treated with the biology of the vegetation rather than with the structure.

Vitality. To estimate the degrees of vitality as given by Braun-Blanquet would presume that a thorough knowledge of the biology of the species was available at the outset of the investigation. Such was not the case. Efforts were made, however, from the beginning to estimate the vitality. It was found that on the whole a reduced vitality was a biological phenomenon of a particular habitat due to ecological conditions, rather than a structural characteristic. It was found advantageous to use simply the superscript $^{\circ}$ after the degree of the total estimate to note reduced vitality. The nature of it was then recorded in the field notes. In most cases reduced vitality would concern plants that are affected by climatic and edaphic factors of increased altitude, therefore plants that are not strictly at home in the alpine zone, or else, a factor or group of factors locally would reduce the vitality of the plants. The superscript $^{\circ}$ is used in this sense in the following tables of the associations.

Layering. Since the vegetation is made up of dwarf-shrubs and herbs of low stature, layering occurs only when mosses, lichens, and algae are present. This happens commonly. Because of the large number of species involved in this cryptogamic layer, their treatment is reserved for a subsequent paper. In the association tables the presence, abundance, and coverage of the cryptogamic layer is noted.

Sociability. After a good acquaintance with the vegetation was obtained, the degree of sociability was found to be dependent very largely on the life-form and the degree of abundance and coverage; therefore, the degree of total estimate would very nearly also express the degree of sociability. In the later surveys sociability was not entered in the notes, except when special occasions warranted it. Much time was thus saved. The species, as well as the individuals, are generally so well dispersed in the zone that the degree of sociability in 90 per cent of the surveys was 1. To simplify the tables, sociability was left out.

Total Estimate. The largeness of the area under study recommended that abundance and coverage of the species be combined to lighten the burden of the field work. For this, the six-part scale of Braun-Blanquet was used throughout the investigation. This

scale uses the sign and figures as follows:
x = sparsely or very sparsely present, cover very small.
1 = plentiful but of small cover value.
2 = very numerous, or covering at least 1/20 of the area.
3 = any number of individuals covering 1/4 to 1/2 of the area.
4 = any number of individuals covering 1/2 to 3/4 of the area.
5 = covering more than 3/4 of the area.

Braun-Blanquet states that: "It is plain that the smaller numbers have more to do with abundance, the larger with the cover." It happens that almost throughout the alpine zone the general rule is scattering of the individuals of the species of flowering plants. Only in the optimal stage of development of the Caricetum are the individuals of a species massed nearly regularly. In the survey lists the most common degrees of the scale of total estimate of abundance and cover are therefore x and 1. This type of dispersion is revealed with particular emphasis in those square meter quadrats of typical vegetation that were analyzed by means of 25 sub-quadrats. The results are found in the tables of the respective associations.

The Associations in the Field. It is easily seen in the field that the vegetation on a north slope differs from that of a south slope. Where the snow lingers the vegetation also differs from that surrounding it. Environmental conditions exert their influence on the vegetation and are usually observable in the field. Where the characteristics of an association extend over a fairly large area the association may easily be recognized, but in the alpine zone this is not the case. The associations occur mostly as small stands, often widely scattered, and in all stages of community development. The resultant pattern of distribution of small stands of various associations is a mosaic that implies that transitional areas must be as abundant as the pure stands themselves. This makes the survey work difficult and laborious, and requires a large number of surveys placed with discrimination.

The Associations in the Abstract. Tabulation of a large number of field surveys from as many stands as possible will show which ones must be relegated to transitional mixtures and which ones are representative of characteristic stands. Surveys of transitional areas may be of very great value for the illumination of biological phenomena and to ascertain the stage of development of the association, but in most cases must be eliminated to obtain the composition of the abstract association.

In a final tabulation of all the species in all the associations, as shown in table 8, it becomes numerically evident that some species occur in but one association, others in two, and so forth.

Fidelity. If the right hand results of table 8 are summarized as has been done in table 9, an insight is gained into the behavior of the species with regard to their range of ecological tolerance. This range may be expressed as the ecological amplitude of the species.

The table shows that 47 per cent of the species occur variously in but one association. These are species with a narrow range of ecological tolerance. When such a species also happens to be abundant it becomes an excellent indicator not only for ecological conditions but also for the association itself. In the sense of the Swiss school of ecologists this represents the highest degree of fidelity of a species to its association.

At the opposite end there are but two species that occur in all the associations present in the zone. Such a species has no indicator value and no fidelity for the association, but may have both for the alpine zone as a whole if the species in its distribution is restricted to this zone.

Between these two extremes are the species with intermediate degrees of fidelity. It seems obvious that the indicator value of a species, its sociological fidelity to the association, and its ecological amplitude are very nearly synonymous, at least so far as this work is concerned. It is believed that by the use of the concept of fidelity as presented in the association tables of this work, a much more profound understanding of all the interrelationships of the phenomena of plant life may be obtained.

For further discussion of this concept the reader is referred to Braun-Blanquet (1932).

The Associations as Indicators. It is axiomatic with ecologists to assume that characteristics of the environment are reflected by characteristics of vegetation. Every species to some degree reflects some condition of the environment in which it grows, and of which it is said to be an indicator. Environment itself, however, fluctuates over time and space as regards the effects caused by a factor, a group of factors, or all the factors of the environment. The ecologists speak of the uniformity of environment and mean that over a certain area the innumerable factors that make up the environment are with themselves and in their effect on vegetation, in a certain rhythm and long-time balance and near stability. Therefore, any areally limited uniformity of environment should find its reflection in a group of species, each of which has an ecological range that falls within the tolerance and the effectiveness of the factors of this environmental uniformity, whether this be large or small. This group of species, hence, should have some characteristics that are different from other groups of different environments. Such a characteristic is the particular combination of species of an association. The association then becomes the indicator of a particular environment, that is, a habitat. Such indicator groups of species of deductive reasoning are indeed the same as the associations listed in this study of inductive field work.

The Associations in Relation to Habitat. The alpine zone may be regarded as a major unit of environment, or a major habitat as concerns vegetation. It has been shown, however, that the zone, according to vegetation, has a three-fold subdivision. Each subzone shows further subdivision into the associations. An association must have a habitat, an environment to live in. Reciprocally, one might speak of an association of a certain habitat, or the habitat of a certain association. For the purpose of classification, each association must have a distinguishable character that is not possessed by any other. Such a character is the combination of species also known as floristic composition. If to this be added the consideration of ecological amplitude of the species, that is, fidelity, the characterization gains in distinctness. This has been done in this study.

It follows that the habitat of each association also must differ from every other. In the alpine zone there is one factor present in every association habitat which also varies in every habitat. This is the water balance.

The Associations Listed According to Water Balance. Differences of the water relations of the habitats are as a rule readily recognized in the field. In addition to field observations, many soil samples were taken to determine the water content. In the following the associations are listed according to decrease in water balance:

1) The Caricetum scopulorentis, the bog association.
2) The Saxifragetum chrysanthae, the ledge and crevice association.
3) The Salicetum petrophilae, the snowpatch association.
4) The Cirsiumetum scopulorentis, the rock-slope association.
5) The Elynetum bellardii, the meadow association.
6) The Dryasetum octopetalae, the north-slope association.
7) The Drosacetum carinatae, the south-slope association.

Within these associations are comprised all of the 118 species of vascular plants. But it must be emphasized again that these plants make up barely one half of the plant life of the alpine zone.

V / The Associations

The Nature of the Tables of the Associations. As in most other scientific work, tabulation of the results of the field surveys offers many advantages. Some of the outstanding features are as follows:

1. The table reveals the significant results at a glance.
2. The order of tabulation of the species by fidelity groups is in itself a characterization of the association.
3. The tabulation by individual stands, or unit areas, illustrates phases or stages of development of the abstract association as well as the manner of dispersion of the species.
4. Each stand or unit area is structurally analyzed by listing of the presence, the total estimate of abundance and cover, and the life form of the species. Each column reveals at a glance the combination of the species as well as the total number of easy comparison.
5. Each stand and unit area is listed with regard to altitude, exposure and angle of slope, and size of area surveyed.
6. The last column of each table tells of the species numerical presence with regard to the number of stands or unit areas surveyed. On table 6 is added a column for constancy which only differs from presence in that all surveys are of unit size of area, namely one square meter.

Each table is thus a penetrating analysis of each association with regard to its general life-form, its structure, its sociology and floristic composition, and the development of the association.

Because of differences of structure between the associations, the tables vary somewhat in the manner of their execution.

For explanation of the signs and numbers on the tables see page 17.

The tables as the Basis of the Report. It follows as a logical deduction from the preceding pages that these tables contain practically all the essential information regarding the structure of the alpine vegetation of the flowering plants on Longs Peak.

Further interpretation is centered around these tables.

The Caricetum Scopulorentis. The Bog Association. In Table 1 the stands surveyed are arranged in order of decreasing altitude. The elevation of 12,700 feet is the upper limit and only the initial or pioneer stage of this association is represented at this height. At the lower limit of the alpine zone the Caricetum does not stop but becomes invaded by subalpine shrubs and is transformed into a subalpine bog association. It is to be noted that this association occurs only on very gentle slopes or shallow level places.

Concerning the life-form of the species, practically all are hemicryptophytes. *Polygonum bistortoides* is sometimes classed as a hemicryptophyte and sometimes as a geophyte.

The exclusive species are not dominants except for *Carex nelsonii,* a pioneer species, almost wholly restricted to the initial stages of the development of the association. Two very small species are *Juncus triglumis* and *Juncus biglumis,* both of which also belong mostly to the pioneer stage of the association. Interestingly, *J. biglumis* also occurs higher up in the Saxifragetum of the middle-alpine subzone, forming a tie of relationship, but has not been found below the 12,000 foot level, where *J. triglumis* replaces it as far down as timberline.

The characteristic dominant of the association is *Carex scopulorum* which therefore properly serves to name the association. Co-dominant to a lesser degree is *Deschampsia caespitosa.*

Survey 32 is from a natural bowl, shallow at the surface, in which snow-water stagnates for most of the summer (Fig. 3). The area includes six square meters. The dominant is *Carex nelsonii; Juncus biglumis* is abundantly present but because of its smallness covers very little ground. Along the edges of the boulders mosses are abundant. With them grow some plants of *Claytonia megarrhiza* and *Lewisia pygmaea,* connecting this habitat with the Saxifragetum of the middle subzone. Within the quadrat only six species are present. Significant is the fact that *Sieversia turbinata* is represented by a few plants only; the habitat is too wet and probably too cold. But on the side where the ground slightly rises above the water table *Sieversia* is very abundant (Fig. 3) and forms a nearly pure stand, pioneering for the initial stage of the Elynetum. Thus, side by side, from almost the same spot, two different associations have their inception, the determinant being the quantity of water.

Survey 32 is very instructive. The community is a fine example of the pioneer or initial stage of the bog association. It needs only the entrance of *Carex scopulorum* to lead the stand to the beginning of the optimal stage of development.

The aggregate of 13 surveys of irregular sizes of areas along the streamlets of the Boulder Field is represented in the second column of Table 1. The association here is at the optimal stage of development and contains the largest number of species. The dominant is *Carex scopulorum*, closely followed by *Deschampsia caespitosa*. Of interest is the presence of the grasses *Poa arctica* and *Poa reflexa*, both of which are abundant but cover little ground. Because of the rhizome habit, these plants form tussocks and clumps and are thus very irregularly dispersed. Figure 4 shows the optimal stage of this association and the mode of dispersal of the plants.

Survey 501, at 12,000 feet at Granite Pass, also represents an initial stage of the association as indicated by the presence of *Carex nelsonii* and *Juncus biglumis*. Interesting at this height is the presence of *Elephantella groenlandica*, an invader from the montane valleys, which finds here its upper limit of distribution.

This stand apparently is kept in this stage by the seasonal depletion of the water supply in mid-summer.

Survey 502 in Chasm Gorge at an elevation of 11,800 feet represents within 10 square meters the initial as well as the optimal stage of development of the association. Because of locally more favorable humidity conditions in Chasm Gorge, subalpine shrubs invade to greater heights, and not far from this stand they have already invaded the Caricetum, transforming it to the subalpine phase.

Surveys 644, 645, and 646 comprise three surveys of one square meter each. The stand is located near the top of a northeast spur of the Longs Peak massif known as Battle Mountain. The water supply comes chiefly from snowdrifts and is limited to the early part of the summer. It is apparently not enough to permit the optimal development of the bog association; therefore the association stand is bound to remain in the initial stage. Interesting is the presence of *Caltha rotundifolia*, a non-alpine invader, reaching here its upper limit of distribution.

Survey 503 is located in Granite Basin, at the south base of Battle Mountain. The community in which this survey was made owes its presence to the all-season, underground seepage of a spring. In contrast with the pioneer stand 644-6, near the top of Battle Mountain, the stand of survey 503 has quantitatively all the water necessary for a luxuriant optimal development. In fact, in parts of the stand, subalpine shrubs have already invaded, initiating the transformation of the alpine bog into a sub-alpine bog. A comparison of the two columns on Table 1 will readily show the difference between the two stands.

Survey 67 is a part of a very small stand on a level place in the bed of an intermittent streamlet. The small number of species and their nature reveal the stand as a pioneer stage. The plants were small and covered almost one third of the area.

A comparison of this stand with stand 32 is instructive. The environment of the high altitude may keep stand 32 perhaps permanently in the pioneer stage. The stand is surrounded by a region nearly bare of flowering plants, thus reducing the possibilities of invasion by other plants. Its location forms the uppermost limit of the association. In contrast, the location of stand 67 is at an altitude where the association otherwise is optimally developed and may even be transformed into an association of a different life zone. The suggestion is obvious that if the streamlet were impounded to make the supply of water last for the whole summer the stand would develop toward the optimal stage. It is probable that periodic washings remove most immigrant plants, including the mosses, except the sturdily rooted pioneer *Carex nelsonii.*

The community function of *Carex nelsonii* is very definite. When in late summer the surface soil has become dry, simulating a dry habitat, the presence of this sedge is a positive indicator of the true condition of the habitat, namely, an intermittently inundated ground. The constancy of its indicator value makes this species very valuable to the investigator. One comes to love the sturdy pioneer. It is aptly named for Aven Nelson, a pioneer botanist of the Rocky Mountains. Names and qualities become inseparable and a tribute to *Carex nelsonii* is also a tribute to the botanical pioneer, Aven Nelson.

The Saxifragetum Chrysanthae. The Association of Crevices and Ledges. The Saxifragetum chrysanthae (Table 2) is of outstanding interest because of its unique status as the flowering plant association which occupies the highest altitudinal level on Longs Peak. As an association, it is a pioneer community doing outpost duty on the climatic frontier of the realm of the flowering plants. By its structural and floristic characters the Saxifragetum is readily distinguished from all the other associations. The distinction is so great that the association characterizes the belt of its occurrence as a recognizable subzone. This belt extends altitudinally above that of the other associations of flowering plants.

The habitat of this association includes the cliffs, ledges and steep slopes of the upper part of Longs Peak. Because of the high altitude, temperatures, chiefly of the soil, are lower than in the other associations. The substratum of nearly all places where plants grow is kept wet by the water from melting snow and ice. On the broader, sloping ledges or steep slopes, the soils may become dry toward the end of the summer. While the habitat on the whole is wetter than that of the other associations, it is not as wet as that of the bog association.

The optimal development of the association occurs on the so-called East Face (Fig. 5) which forms a precipice nearly 2,000 feet in height. The strike of the East Face, however, is 30 degrees west of north, which means that the giant wall really faces east-northeast. This is important to plant life with regard to insolation, which is here restricted to the morning hours. The granite wall in part is a plane or nearly so but with many crevices where the small saxifrages in large numbers find an uncontested home. However, the major part of the wall is a series of ledges, steep slopes, and walls (Fig. 6). It is on these ledges that plant life is found in greatest abundance. Bryophytes, lichens, and algae are present in great abundance also, at least as much so as the flowering plants. In places they are even more abundant. Frequently they occur together with the cryptogamic plants forming an inferior layer.

More than a hundred trips were made to the summit of Longs Peak, many of them as guide to mountain climbers. A number of trips onto the East Face were made as a solo climber, a practice considered dangerous in mountain climbing, but in most cases it was possible to join with fellow mountaineers in a safer, roped party. To explore the East Face for plant life, a knowledge of the technique of mountaineering is essential for safety. The results of the exploration are well worth the effort of long hours of arduous climbing together with the threat to life of mistakes in mountaineering.

It follows that a survey by quadrats in this area is impossible of physical achievement. The irregular and wide dispersal of the individuals would in itself not be well suited for survey by quadrats to give a comprehensive picture of the whole association. From the notes and observations of the many trips, Table 2 was compiled. The species are listed by fidelity groups and the rank or order of total estimate as estimated for the association considered as a single stand.

No single species of this association can be regarded as a dominant over the whole range of the association. Many dominate locally. Such species are indicated on Table 2 as being of the order of class 1 of total estimate of abundance and cover, and are really the important species. The generally low order of total estimate reflects the wide and irregular dispersal of the individuals, which usually are not in competition with one another. This manner of distribution is referred to as ruderal and is known from the high Alps and the Arctic.

It is a unique character of the association that one-half of the species rank in the two highest fidelity groups. Fourteen species alone rank as exclusive species of this association. This means that a large percentage of the species have a small ecological amplitude.

Concerning those that rank in fidelity 4 group, it could perhaps be argued that some of these too should rank in the higher groups. If they are found outside the area of the Saxifragetum, it is either on an inundated and nearly bare spot or on the shaded side of a boulder where evaporativity is reduced and the run-off from precipitation on the rock surfaces is concentrated. This manner of occurrence suggests that, when they are thus found within the area of other associations, they are really extraneous to the habitat of the respective associations, and should be regarded as relicts or invaders.

As may be seen from Tables 1 and 8, *Poa arctica* and *Juncus biglumis* occur only at the higher altitudes of the Caricetum and thus form a connecting link between the two associations. Their community function, however, is more important in the Caricetum than in the Saxifragetum.

Noteworthy is the distribution of *Claytonia megarrhiza*. Plants of this species have been found at as low an altitude as 11,300 feet, growing sheltered among rocks. Many more were found higher up, usually in the beds of streamlets. But at 13,000 feet, on a bouldery ledge, lives a small community, the individuals of which surpass in size by far any found at lower altitudes (Fig. 7).

A part of the group of species of fidelity rank 3 occur on localities where the soil becomes somewhat warmer and drier. Table 8 gives information on whether a species occurs also on the drier or on the wetter side of this association.

The invader species, *Draba crassifolia*, is a very small plant and is most often found in the upper subalpine zone. In the alpine zone it was found but once, at the Keyhole at 13,000 feet, where it was abundant.

Another invader, *Saxifraga rhomboidea*, occurs most abundantly in the foothills and the subalpine zone, but is also numerous in the alpine zone, where it has been found as high as 13,000 feet. With increase in altitude, its time of flowering occurs correspondingly later. Thus in the foothills it may blossom in May and on the East

Face it may blossom in August. Its vitality in the alpine zone does not seem to be reduced.

Concerning the life-form, practically all species are hemicryptophytes. The only exception is perhaps *Silene acaulis*, but the plants are so small in the Saxifragetum that they practically resemble the other plants in having the winter buds close to the ground. It might surprise the reader that the two species of Salix should be classed as hemicryptophytes. These are, however, true dwarf-shrubs, and the branches are so very nearly covered with soil and litter that the buds are found in the soil cover.

The seven species of Saxifraga are small and occur everywhere in the area of the association. Their physiognomy is the characteristic life-form of the association and it seems appropriate to name the association for the one species that is most common and at the same time exclusively restricted to this association.

The association should perhaps be classified with the snowpatch communities since it seems to depend on a good snow cover during the winter. The young buds of the plants are generally well developed in September when the first snow of the season begins to cover them up. When in June and July they become again uncovered they rapidly produce flowers and seeds. Although the snow-free season is very short, there are two aspects of flowering, and no species requires the full length of the growing season for its short cycle of seasonal activity. The adaptation of the plant life to the environment seems perfect. Natural selection seems to have had ample time for a perfect choice.

The Salicetum Petrophilae. The Snowpatch Association. Where in the low-alpine subzone the snow lingers into spring and summer, a different vegetation occurs. Such places are the lees of cliffs and boulders, secondary slopes and shallow depressions, wherever the dynamics of windflow permit the accumulation of snowdrifts. During the winter the snowdrifts serve as protection to the vegetation against cold and wind; but during the summer when the snow melts the drifts supply water for the vegetation. Such places also are suitable for the accumulation of precipitation by run-in, or may be the exit of seepage from higher slopes. Because such habitats are not in the direct path of the wind, the evaporativity is less than on the surrounding slopes. In addition, the snowdrifts catch dust and fine sand with much organic matter, such as pollen and insect remains, which upon melting settle on the ground and become incorporated in the soil. The resulting soil thus differs considerably from that of the other associations. It is to be expected that the vegetation of so distinctive a habitat should show equal distinctiveness.

The individual stands of the association differ according to the size of the snowdrifts and the time of their melting. The same stand may differ within its area depending on the factor of lapse of time between the beginning of plant activity at the periphery and the beginning in the center when the last snow has melted. Where this lapse of time is greatest the whole vegetational development of the stand may be found from the bare ground through the initial stage to the optimal stage.

Table 3 gives a summary of the structure of the association. Six of the species are exclusively restricted to this association. The dwarf-shrub, *Salix petrophila* (Fig. 8), is a strong dominant, but is not present in the primitive stands of the initial stage of development. It is fitting that the association should be named for this characteristic species.

Pioneer stands in the initial stage of development have *Carex pyranaica* as a dominant species, which is also an unfailing indicator of the snowpatch habitat.

Other excellent indicators of the snowpatch association are *Sibbaldia procumbens* and *Erigeron melanocephalus*. Both species are practically always found together, but they are apparently not true alpine species since they do not occur on the stands in the higher altitude, and in the others most often with reduced vitality.

As listed in Table 3, the stands occur from an altitude of 12,570 feet to 11,100 feet. The slopes where they occur are gentle and in a northerly direction. The stands range in size from about 10 to 100 square meters, with a few beyond these sizes.

Surveys 249 and 250 are located on the Boulder Field, whose altitude is the upper limit of the Salicetum stands. Survey 249 is in a slight depression, covered with cold snow water early in the season and turning dry soon after the snow has melted. This condition leaves the area half bare and the few plants show reduced vitality. Survey 250 is located on higher ground. The willow covers more than half of the square meter and bryophytes and lichens fill the area completely. As shown on the table there are only a few depauperate plants of two other species in this quadrat. The richness in bryophytes and lichens is typical of the higher altitudes. These two quadrats should be compared with the next two.

Surveys 68 and 235 (Fig. 9) are also of the standard size of one square meter. Both are representative of the optimal stage of development in which *Salix petrophila* is regularly and abundantly present with a scattering of some other species and a good layer of bryophytes and lichens. Competition in this stage has had a full trial, and by its dominance *Salix* has shown itself the master.

Surveys 662, 663, 664, 665, and 666 were each of one square meter but are listed on Table 3 as a stand of five square meters. The frequence with which the species occurred in the five quadrats is indicated in parentheses. The quadrats were chosen more or less at random out of a stand of about 1,000 square meters at an elevation of about 11,100 feet. Because of the lower altitude the stand is not located at the climatic boundary of the association. As shown in the table *Salix petrophila* occurs sparingly only in one quadrat. A perusal of the species listed in the table indicates that this is a primitive stand still in the initial stage of development. The stand is kept in this condition by the late melting snow-cover and subsequent quick drying of the soil.

A similar stand is represented by survey 123, located on top of Battle Mountain. Here, at 12,000 feet, is a more severe climate that helps to keep the stand in the initial stage.

Still more primitive is the stand of survey 94. The area is half bare and no *Salix* is found. In that part of the stand where the snow lasts the longest, *Carex pyrenaica* is locally dominant. The snowdrift regularly lasts into July and after its melting the gravelly ground soon dries.

In the last column in Table 3 is a summary of the number of stands surveyed in which the species occurs and its percentage of occurrence. This is called the degree of presence because the stands surveyed are not of unit area and therefore not strictly comparable for statistical analysis. If the prerequisites for a statistical analysis were attempted it would be necessary to survey by unit areas the whole stands and all the stands because the irregularity of development of the stands would not otherwise give a full picture.

Concerning the life-form of the species, the dwarf-shrub *Salix petrophila,* like the two other species of *Salix,* must also be considered a hemicryptophyte because of its buried branches. Several mat and cushion plants are listed as chamaephytes as is customary for such plants. In reality, however, they are intermediate between the two classes but closer to the hemicryptophytes. There are, thus, 85 per cent hemicryptophytes and 15 per cent chamaephytes in the association.

The Cirsiumetum Scopulorentis. The Rock-Slope Association. Rock weathering in the alpine zone is a slow process. From the precipitous slopes of the upper peak now and then a rock or boulder comes loose and tumbles down the side of the mountain. Where the slopes are less steep the rocks break up in place and slowly move downward by inches and feet, moved by gravity and water. In the subzone where the flowering plants grow, there are practically no gravel slides that are not stabilized by plant life. There are, however, slopes with angles of steepness from 10 to 40 degrees, covered with small to large sized rocks, and boulders. It is only within the area of the low-alpine subzone that rock-slopes are found with interstices filled to varying degrees.

The rock slopes offer to plant life a habitat with characteristics of its own. On the soil material between the rocks, the plants may find a place to root and have the surface parts protected by the boulders. The wind velocity is reduced by the rocks and boulders and therewith also the evaporativity of the air between the rocks. Precipitation falling on the surfaces of the rocks concentrates in the interstices with the apparent effect of increasing the efficiency of precipitation for the plant life of this habitat. The peculiarity of the habitat implies a peculiar vegetation. Table 4 lists and classifies the species of the plant association that inhabits the rock-slopes.

Exclusive to this association are four species, one of which is the fern *Cryptogramma acrostichoides* (Fig. 10). This fern is practically always found on the protected side of a rock on southerly exposures. The dwarf columbine, *Aquilegia saximontana*, the two-flowered violet, *Viola biflora*, and the thistle, *Cirsium scopulorum*, have been found on southerly as well as on northerly exposures. While these species are exclusive to this association within the area of the alpine zone, it is known to the writer that a phase of the association continues its existence down into the subalpine zone where the thistle leaves the rocks and finds a similar shelter among the scrubby evergreens of the timberline belt. The thistle is a dominant as well as the largest-sized plant of the association and thus properly serves to name the association.

Of the species of fidelity rank 4, the two grasses, *Stipa lettermani* and *Agropyron scribneri*, are generally restricted to the warmer and drier, southerly exposures. The same is true for the distribution of *Lychnis drummondii*. The tall columbine, *Aquilegia coerulea, Senecio holmii, S. taraxacoides,* and *S. carthamoides,* however, are found only on easterly and northerly exposures. Exceptionally, some of these may be found on a south slope when a boulder forms a suitable habitat on its east or north side. The apparent requirement of the species of *Senecio* for a north exposure is better understood when it is remembered that these species also occur in the Saxifragetum. Hence, they are species of cold and moist habitats, preferring the higher altitudes.

Quite interesting is the occurrence of *Aquilegia coerulea* at this altitude. The highest occurrence is at about 12,000 feet. This columbine is best known from the aspen forest where it is abundant and where the individuals are largest in size. The distribution extends upward along the stream courses where the plants occur among shrubs and on rocky ground. In the meadows and the spruce-fir forest of the subalpine zone the species as a rule does not occur. It is found again among the willows at timberline. From timberline, the distribution extends over to the rock-slope and reaches an altitude of 12,000 feet, where, in the neighborhood of Granite Pass, among rocks and boulders, the species is not uncommon (Fig. 11). Within this distribution is an altitudinal difference of over 3,000 feet which in terms of climatic change is very great. But it must be noticed that in early summer when the columbine completes its seasonal cycle, the soil of the aspen forest is wet. Where willows grow the soil also is wet. As has been shown above, the soil on the rock-slope may also be wet. With regard to the water factor of the soil, the conditions in the different habitats are similar although the temperatures might be dissimilar. But concerning the aerial habitat, conditions differ markedly. In the aspen forest, as well as among the willows, the plants are at least partly shaded and the evaporativity of the air surrounding them is reduced. On the rock-slope in the alpine zone, however, the plants grow in full sunlight without a sheltering canopy of leaves and often without the immediate shelter of rocks. The contrast is certainly great and lends force to the theory of the replaceability of factors. The higher average temperature of the lower altitude seems to be replaced by direct insolation at the higher altitude where the average temperature is less. Also, the shade plant of the lower altitude becomes a sun plant at the higher altitude. As far as the plants are concerned, however, the climates of these widely divergent habitats as measured by man's instruments may have nearly identical effects. As an alternative explanation the suggestion is pertinent that while the plants are morphologically similar, their physiological inheritance may be dissimilar. Taxonomic experiments are necessary to solve the problem.

A habitat of such rocky nature makes it impossible for plants to form a carpet. The distribution is therefore very irregular. Although many stands were surveyed by quadrats of one square meter, these do not give a true picture of the association. A survey by stands seems to serve more adequately. In Table 4 are listed the floristic composition and total estimate for two stands of almost the same elevation, one on a north slope and the other on a south slope (Fig. 12). In the same table are also listed the presence values based on 15 stands.

Concerning the life-form, 94 per cent of the species are hemicryptophytes, and six per cent are chamaephytes.

The Elynetum Bellardii. The Meadow Association. It has been stated already that a more or less continuous carpet of vegetation with its own characteristics forms an entity, here called the low-alpine subzone. In the area of this subzone the major feature of topography is that of gentle slopes, frequently broken by locally steeper slopes and by depressions. The steeper slopes are inhabitated by the Cirsiumetum, and sometimes by the Salicetum, which also occupies depressions. Along the streamlets and on seepages, and in hollows where water collects, the Caricetum is at home. But all these appear as specialized associations, made to occupy special habitats, whereas the Elynetum so completely dominates the landscape that the average botanist untrained in alpine plant life would not suspect the presence of the others. The extensive habitat is strewn with boulders, but wherever the conditions are best for plant growth, a soil has been built up that covers all but the larger rocks. This happens mostly near the lower border of the area of the association where climate is most favorable for plants.

Concerning the water factor, this habitat ranks on the drier side of the middle between the wettest and the driest habitat. The species range from mesophytes to xerophytes, but the association as a whole is rather moderately xerophytic. Near the upper altitudinal boundary, which includes the initial stage of development of the association, there are more mesophytes, but near the lower border, which includes the declining stage, there are more xerophytes.

Of exclusive fidelity to the association are *Elyna bellardi, Erisimum nivale, Chondrophylla americana,* and *Campanula uniflora.*

The pseudo-sedge, *Elyna bellardi,* is dominant over the whole area of the association, except where the initial stage prevails. When soil parent material through plant activity is slowly converted to soil, the first occurrence of *Elyna* marks the threshold when the change to soil has taken place. The plants of *Elyna* depend on precursors of other species to prepare a soil for them to suit their fibrous root system, but in the final stage of the association, *Elyna* dominates almost to the exclusion of all other species.

Elyna reproduces centrifugally by short offset rhizomes; the center of the bunch dies, therefore circles of living culms are produced at the periphery (Fig. 14). In the center the dead culms leave stubbles that remain for great lengths of time, preventing the migrules of other flowering plants from entering, but offering a welcome habitat to lichens.

Present with *Elyna* is also its smut *Cintractia caricis.*

It is fitting to name the association for this important species. There is precedence for this in the fact that an Elynetum has been named from every major mountain range in Europe.

Of little importance is the exclusive species *Erisimum nivale.* It is not abundant and no community function is apparent.

A very abundant but small plant is *Chondrophylla americana.* This little gentian would escape notice if the vegetation were not examined carefully. The species is found only in the early stage of maturation and is therefore a true indicator of the optimal stage of development. In the initial or declining stage it has not been found.

The small bell flower, *Campanula uniflora,* occurs from the climatic initial stage of the upper altitudinal border to the optimal stage and is a trustworthy indicator of the association. It has not been found in the declining stage of the association. It is a small plant but is fairly common.

On Table 5 are listed the surveys of eleven stands, representing the initial, optimal, and declining stages of development of the association, as well as some modifications due to certain factors of the environment. A glance at the headings of the columns on the table shows that the stands surveyed range in altitude from 12,700 to 11,100 feet. The upper limit is coincident with the climatic boundary of the association, and the lower limit is where the association succumbs in competition to the higher life-forms of the subalpine forest. The table also indicates the generally low angle of the slopes.

Survey 27 (Fig. 13) represents a square meter of a stand that is typically a pioneer stage. The ground is rocky and gravelly, the substratum of the plants being soil parent material rather than soil. The aggressive *Sieversia turbinata* is abundant and dominant, but the plants are very small and do not cover much ground. Eight species participate in this stand, five of which are depauperate, and only three appear to be at home. The table also shows that these species, with one exception, are of low fidelity rank, and therefore of wide ecological amplitude. The lone exception is

Campanula uniflora, which thus relates the stand more definitely to the association. The general climate of this altitude is restrictive to the best development of the individuals, but the water factor must be even more limiting as the gravelly ground has little power for the retention of water. Nearby is the pioneer stand of survey 32 of the Caricetum (Fig. 3), where the *Sieversia* with a better water supply attains a much better development.

Survey 252 represents a gravelly area at 12,650 feet that was bared in 1925 by a trail crew to obtain the finer soil for trail cover. Ten years later there were only seven plants of three species present covering not more than one square decimeter. This survey is typical of many others and shows strikingly the reduced power of invasion and ecesis of alpine vegetation at this high altitude.

Survey 248 represents an advanced pioneer stage on a slope exposed moderately to the wind. Nearly half of the quadrat is filled with *Trifolium dasyphyllum,* which is a fairly good indicator of wind effect.

Survey 1 (Fig. 15) represents the dominance of *Sieversia* and the culmination of the initial stage. The area of the quadrat is on somewhat low ground and probably a little too wet for *Elyna.* This stage of development where *Sieversia* is dominant is widespread around the mountain in the upper half of the low-alpine subzone. The quadrat was surveyed by 25 subquadrats. On Table 5 the total estimate is listed for the species of the quadrat. The presence and percentage of presence for the subquadrats are also listed and give in detail the distribution within the quadrat.

Survey 34 (Fig. 16), like the preceding, has been surveyed by 25 subquadrats. It is but ten meters from survey 1 but is located on higher ground, where a good soil is present. The vegetation of this quadrat is in the beginning of the optimal stage of development. It should be noticed on the table that *Elyna* has entered the vegetation. *Elyna, Trifolium,* and *Sieversia* have the same rank of total estimate; all three are dominants. A comparison with survey 1 shows that *Polygonum bistortoides,* an indicator of moist ground, has a presence of 60 per cent in survey 1, but only 12 per cent in survey 34 on the drier ground. But new to survey 34 is a 100 per cent presence of *Polygonum viviparum.* While this presence is unusually high, yet it is a fact of constant observation that *P. bistortoides* nearly always occupies wetter ground than *P. viviparum.*

The presence of mosses and lichens over nearly half the quadrat of survey 1 is a significant as well as a typical difference compared with survey 34 where they are but sparsely present. The most significant difference, however, is the presence of *Elyna*. The development of the vegetation has passed that threshold that marks the difference between the initial and the optimal stage. A further difference is found in the number of characteristic species, that is, the species of the two highest fidelity classes. In the stand of survey 1 there are but three species of fidelity 4 and 5, but in survey 34 there are six, twice as many. There are, however, many resemblances which are readily reflected by Table 5, notably in the number of species per square meter, namely 15 and 16, respectively. It is in these two stages as represented by the two surveys that the association attains the largest number of species. The two quadrats are typical of the Elynetum vegetation found on Longs Peak from a little below the altitude of 12,000 feet to about 12,600 feet.

Survey 257 represents in one square meter the type of a pioneer stand of about 1,000 square meters. The location is a north slope where insolation is at a minimum and where the wind has full access on the open slope. The soil is gravelly with small power to retain water and is more like parent material than soil, an indication that plant life on this area always was scant, never being abundant enough to form a soil. One glance at Table 5 reveals the paucity of this vegetation kept in a near-permanent stage of primitiveness.

Surveys 709 to 713 represent five square meters forming a transect of a south slope in Chasm Gorge at an elevation of 12,000 feet. These are aggregated into one stand on Table 5. Much snow accumulates in this gorge, and on the north slopes stands of Salicetum dominate. But on the south slope the soil dries soon after the snow has gone and no Salicetum develops. The gorge, however, is on the east side of the Peak and thus sheltered from the steady westerly winds. During cyclonic weather disturbances, warm, moist air from the south becomes undercooled in contact with the cold East Face of Longs Peak and the moisture condenses. Chasm Gorge is well known as a fog hole.

In the first quadrat near the top of the slope, where the snow lasts longest, a few plants of *Sibbaldia procumbens*, the snowpatch indicator, are present. Otherwise *Selaginella densa* is the dominant, and a few plants of the xerophytic invader *Solidago decumbens* are also present. *Sieversia* is a subdominant, and the ubiquitous *Festuca* is also present. At the first glance, this is a queer assemblage of plants in one square meter of vegetation, but it is readily explained. The *Sibbaldia* of the snowpatches revives quickly when the snow has melted and the soil is still cold and wet. It completes its seasonal cycle before this south slope dries. During July and August this square meter become a habitat for xerophytes such as *Selaginella* and *Solidago,* and naturally the top of the slope would be driest.

The next succeeding quadrats down-slope have *Sieversia* becoming dominant and present in all five quadrats. This definitely shows that the affinities are with the Elynetum, but the list on Table 5, and the associational distribution on Table 8, show that there are also affinities with the Drosacetum and the Salicetum, and, through the invading shrub *Desiphora fruticosa,* with the subalpine zone. The peculiar conditions of environment of Chasm Gorge as sketched above, when compared with the rest of the alpine zone, account for the jumbling of extremes as found within five square meters of vegetation.

Surveys 706, 707, and 708 are located in Chasm Gorge also, not far from the preceding survey. The particular location, however, is at the base of a huge cliff on a stabilized rock-talus slope. The stand slopes to the southwest but is on the top of a larger, general south slope (Fig. 17). Where the slope faces south, the vegetation is that of the Cirsiumetum. Two associations are here very close together and overlap to some extent, but the Cirsiumetum is in its stage of optimal development, while the Elynetum is represented by the initial stage only.

On Table 5 the three quadrats are listed separately and reveal the primitive stage of the stand.

Aggregate A in Table 5 is composed of surveys 235, 236, 707, 708, and 715, each of one square meter. The total estimate of abundance and cover is listed for all five quadrats together, but a second cipher indicates the number of times it occurred in these five quadrats. The stand is located on the east shore of Chasm Lake, in the moist Chasm Gorge, but is here subjected to some wind effect. The area is several thousand square meters in size and much diversified by bedrock exposures, and by rocks and boulders. It follows that the vegetation is also much diversified. A survey of the stand as a whole showed the presence of representative species of several associations. Although snow lingers long at Chasm Lake a Salicetum has not developed in spite of the fact that the characteristic *Salix patrophila* is present. The bog association is represented by *Deschampsia caespitosa,* but it does not form a stand. On small exposed areas plants of the very xeric Drosacetum are present but neither forms a stand. To top it all the subalpine invader shrub *Dasiphora fruticosa* is not uncommon and scrubby conifers are here near their maximum elevation. On the whole, however, the stand is representative of the initial stage of development, reaching here and there the optimal stage. The quadrat of survey 236 had nearly half its surface covered with *Elyna bellardi*, beautifully illustrating the optimal stage.

This stand resembles much those of aggregates 709–713 and 706–708.

In summarizing, it is of interest to note that in the narrow Chasm Gorge with its increased humidity, all associations are represented. The increased humidity has its effect in a reduction of the area of the Elynetum, the main association of the alpine zone. Expressed differently, a more favorable water balance enables the subalpine pioneer invaders, including shrubs and trees, to reach higher elevations at the expense of the area of the alpine zone. The water factor shows itself again as of prime importance.

Survey 140 (Fig. 18) represents a quadrat surveyed by 25 subquadrats as indicated on Table 5. The stand is on an area denuded by water and wind. It is comparable to survey 252 with which it shares a similar origin, but due to difference in elevation the environment differs considerably. The stand is still occasionally flooded by water, a condition that has existed for some time and probably will continue for a long time. The lichen *Lecidea cyanea* is a reliable indicator of intermittent flooding. This lichen is abundantly present on rocks and pebbles on the ground, and it covers some of the ground that appears bare on the photograph of Figure 18.

Aggregate B of Table 5 represents 20 surveys of one square meter each of the final or declining stage of the association. The quadrats are from representative stands ranging in elevation from 11,300 to 11,800 feet. On the table are listed the combined total estimate for all the quadrats, and the presence in the twenty quadrats, listed by cipher and percentage.

It has been stated above that *Elyna* possesses a fibrous root system which requires a certain prepared soil bed for growth and successful competition. As the fibrous roots in great numbers extend in the surface soil, they absorb the water from precipitation for their use and thereby prevent it from percolating to greater depth, to the detriment of the plants with the deep taproots. Competition thus takes place very largely under ground and consists of the well-known struggle between deep taproots and shallow fibrous roots. Since there is no ground water in the alpine zone, *Elyna* becomes the winner, other circumstances of the environment being favorable. The chief competitors are *Sieversia* and *Elyna*. *Sieversia* has a taproot which may be short and thick on moist ground, or five feet long and thin as twine. There is thus a certain plasticity which explains partly the aggressiveness of this species. The following may illustrate this: On a certain area where *Sieversia turbinata* and *Salix petrophila* were densely intergrown, an intense competition was suggested. Upon digging out the root systems it was found, however, that only *Salix* was occupying the shallow soil, but the *Sieversia* roots extended almost horizontally five feet under a boulder where they obtained water from silt washed in. There was no competition by roots at all.

In the course of development of the meadow association the roots of *Elyna* starve out those of *Sieversia*. On the surface this process is aided in favor of *Elyna* by increased evaporativity of the environment. With decrease of altitude and consequent increase of temperature, the evaporativity increases. *Elyna* is of more xeric structure than *Sieversia*, hence *Sieversia* also loses out above the surface. In fact, the whole hereditary equipment of *Elyna* is superior to that of any other species in a well aerated soil. Such a soil is possible only where the slopes are nearly level so as not to allow too much runoff. On such places, *Elyna* becomes the exclusive dominant. While *Selaginella densa* and the lichens may become very abundant, they largely occupy the stubble of the dead parts of the *Elyna* plants (Figs. 19 and 20).

This stage of development has been called the final or declining stage because it is obviously the end of the development of the association, and declining since the number of species per unit area becomes reduced as well as its carbohydrate production. On September 3, 1935, three quadrats of one square meter each from the initial, optimal and declining stages were clipped close to the ground and the plant material air dried. The sample of the optimal stage became spoiled by packrats at the timberline camp. The two remaining samples were later brought to the laboratory and dried in an oven at 105 degrees Centigrade to a constant weight. The sample of the initial stage of survey 1 produced 136.6 gm. of plant material and that of survey 138 produced 104.5 gm. or only 75.67 per cent of the amount produced in the initial stage. Observations suggest that the optimal stage produces the largest amount of plant material per unit area.

Under aggregate C on Table 5 is the percentage of occurrence of each species in the group of 100 units of one square meter each.

These are scattered more or less uniformly over all stages of the association and may therefore be spoken of as the normal spectrum of distribution of the species within the association. It offers interesting opportunities for comparison of the distribution among the different surveys, and is particularly significant in the differences of percentage in comparison with aggregate B, the surveys of the declining stage.

Concerning the life form, more than 90 per cent of the species are hermicryptophytes.

The Dryasetum Octopetalae. The North-Slope Association. In the low-alpine subzone extensive slopes with an angle of 10–30 degrees facing north occur on which a minimum of insolation is received and the soils therefore are never warmed to the same degree as a level or south-facing soil. Not being warmed means that the layer of air immediately adjacent to the soil is not unduly warmed and therefore the evaporativity of this layer of air remains at a more favorable level in terms of plant life. This fact is tremendously important, as will be shown below, but the effect of insolation is variously modified by the micro relief.

The steepness of these slopes causes much run-off of precipitation and the slopes are therefore a rather dry habitat. This predisposes a certain paucity of plant life on the slopes and in turn a slow progress in soil formation. Thus the soils are mostly gravelly. That the water factor is again the controlling determinant of plant distribution is shown by the fact that, where seepage occurs, *Sieversia* initiates an Elynetum, and where snowpatches form, a Salicetum comes into being. But the largest area on these slopes is inhabited by the Dryasetum.

The Dryasetum is an association poor in the number of species. Nearly all of the species occur also in the Elynetum; however, the composition differs with regard to abundance and fidelity. The only species of exclusive fidelity is the dwarf shrub *Dryas octopetala* (Fig. 21), which never occurs in typical Elynetum or any other association. One might be inclined to consider the Dryasetum as a mere phase of the Elynetum, which it floristically is, but the near-constant dominance of *Dryas* and the poor representation by other plants give the vegetation a very different character, sufficient to make it stand out as an entity. If the rock-inhabiting lichens were added to the list, to which they properly belong, the nature of the entity would be more strongly emphasized. By way of contrast, the south slopes also show separate characters of their vegetation;

hence, a certain uniformity of ecology is expressed by the different vegetation of the two kinds of slopes.

Survey 64 represents the vegetation of a square meter typical of a much larger area. The whole quadrat is covered with plants of *Dryas* and the other species are scattered among them leaving no bare area. The elevation of 12,100 feet is very nearly the upper limit of the distribution of *Dryas*. It is near this elevation also that this species reaches its best development, growing out into places fully exposed to the sun, thus demonstrating that the plant is tolerant to sunlight and is found on north slopes for reasons other than intolerance to light. This is an important observation. It is also in this stand, of which survey 64 is representative, that *Dryas* was found in competition with invading *Elyna* on a well developed soil (Fig. 22).

On Table 6 are listed the surveys of five widely scattered stands, each represented by five quadrats of one square meter each. The stands resemble one another, with the exception that with decrease in altitude there is an increase in bare area as well as an increase in the peculiar *Dryas* terracing.

As a pioneer plant, *Dryas octopetala* has a worldwide reputation. Schröter (1926) gives an excellent account of the ecological functions of this species in the alpine zone of the Alps and summarizes accounts from outside the Alps. On page 273 of his work, Schröter gives details of the genesis of the terraces in which the plants of *Dryas* arrest creeping soil and gravel masses and thus cause the terracing by stopping the soil flow. The terracing is a common occurrence on Longs Peak (Fig. 23) but significantly occurs only on the gentler slopes where there is no evidence of any creep of the substratum. The origin of the terracing is therefore different, but from careful observation over the large area the following explanation fits the observed facts.

Ecesis of any plant on the gravelly ground is difficult because of dryness. If sunlight impinges directly on the gravel, raising its surface temperature, the layer of air above it becomes excessively dry and still further inhibits the growth of plants. But on the side of a rock where water locally concentrates, and insolation is absent or reduced, a plant may ecise and develop a root system which penetrates the spaces among the deeper rocks where there is more moisture. The plant then will support a better growth of the woody branches trailing on or partly in the ground. The growing plant will modify its own habitat by forming a mulch of fallen leaves and holding dust between its branches, which will insure greater retention of water from precipitation. The spreading shoots cannot survive the dryness of the bare gravel. Where this gravel is heated in the sun, the evaporation of the air layer next above will be so high as to exceed the transpiring power of the young shoots, causing their death. At the same time the north slopes are open to the westerly wind that keeps the sand and fine gravel in motion, blowing them out from among the larger rocks wherever they are exposed. The *Dryas* plants with their branches as well as their roots form a protective network holding the soil particles in place. The processes of plant growth and wind erosion go on together, but are limited in scope. Once a level is created it becomes subject to greater heating by insolation, and the plants cannot invade the hot and dry area. Terracing by *Dryas* has been observed only where the environment of the habitat appears critical to plant life. This criticalness is indicated by the half-bareness of the area (Fig. 23). Terracing thus is an aid to plant life in the conquest of the habitat.

The Dryasetum is a pioneer association in the sense of being able to invade a bare area, where the environment is critical with regard to the water factor.

Concerning the life form, *Dryas octopetala*, a dwarf shrub, is usually considered a chamaephyte, but in our habitat is more nearly a hemicryptophyte, as are nearly all of the other plants.

The Drosacetum Carinatae. The South-Slope Association. As on the north slope, there is a paucity of plant life on the south slope, giving it the character of desert vegetation. The vegetation on the south slopes also depends largely upon the summer's precipitation. But in contrast with the north slope there is no vegetation carpet on the south slopes as formed by *Dryas* on the north slopes. All plants are small and widely spaced. All are xerophytes, with the exception of such species as *Polygonum bistortoides*, which may grow on a drainage line.

There are two species of exclusive fidelity, namely, *Eriogonum xanthum* and *Senecio werneriaefolius*, both extremely xerophytic plants of sparse occurrence.

Survey 97 (Fig. 24) as shown on Table 7 is a typical quadrat of a stand of marked paucity in number of individuals. The slope faces directly south and the surface is mostly coarse rock with smaller soil particles between. The quadrat was surveyed by 25 subquadrats and the distribution within the quadrat is listed on Table 7.

Survey 200 (Fig. 25) as shown in Table 7 represents the optimal development of the association. This quadrat was also surveyed by subquadrats and permits direct comparison with survey 97. A somewhat gentler slope and better soil development seem to account for the much better development of the vegetation.

Survey aggregate A represents 25 quadrats of one square meter of widely scattered localities. The total estimate was averaged and is given on the table for all the quadrats. The presence is given by numbers and by percentage to make it available for comparison with other associations.

Survey aggregate B represents six large stands surveyed only as wholes. Interesting is the fact that more invader species appear on these lists. It illustrates the chief mode of invasion, mainly by the occupation of disturbed areas, such as result from burrowing, an overturned rock, and so forth.

In the column under presence on Table 7 is given the number of times a species occurred in any of the stands listed. It gives a fair approximation of distribution and frequency. It was not converted into percentages because all the areas were not of unit size. A comparison of these figures with those of aggregate A of unit areas shows a constant increase in presence with the number of surveys, which is an indication of the entity of the association.

The Drosacetum also is a pioneer association that settles on bare areas. But here too the water factor keeps the vegetation so thinly spread that it does not form a carpet. The vegetation much resembles that of a desert.

Concerning the life form, nearly all the plants are hemicryptophytes.

SUMMARY

1. Structural analysis of the vegetation of the alpine zone on Longs Peak in Colorado reveals a threefold altitudinal subdivision: (1) a high-alpine subzone where only cryptogamic plants are at home; (2) a middle-alpine subzone, where the vascular plants of the ledge and crevice association vie with lichens, bryophytes, and algae for dominance; and (3) a low-alpine subzone in which the vascular plants are dominant over the cryptogamic plants.

2. Seven unit groups of vascular plant species, here called associations, dwell in the alpine zone in seven distinct habitats each with a characteristic environment. The water balance is a dominant factor present in all associations and varies in a decreasing order in a characteristic manner for every association. Listed in the order of this decreasing order, the associations are:

1) The Caricetum scopulorentis, the bog association.
2) The Saxifragetum chrysanthae, the ledge and crevice association.
3) The Salicetum petrophilae, the snowpatch association.
4) The Cirsiumetum scopulorentis, the rock-slope association.
5) The Elynetum bellardii, the meadow association.
6) The Dryasetum octopetalae, the north-slope association.
7) The Drosacetum carinatae, the south-slope association.

In addition, but not treated in this paper, there are many communities of lichens, bryophytes, and algae.

3. The seven plant associations have a combined number of 118 species of vascular plants. Tabulated for every association in the order of ecological amplitude, here called fidelity, and listed by divers stands, the species indicate their function with regard to community and environment and reveal the life history of the association itself. Thus the association tables presented give a graphic summary of the floristic composition, the structure, and the ecology of the associations.

4. A tabulation (Table 8) of all the vascular species listed in phylogenetic order with their occurrence in the associations, the associations arranged in the order of decreasing water balance, gives a graphic summary as well as a cross reference of the ecological amplitude of the species over the whole alpine zone. It is also a comparison of the floristic composition of the associations. This tabulation also shows that the wetter associations contain more

species from the lower end and the drier associations more from the upper end of the phylogenetic series.

5. The analysis presented is the result of an investigation extending over seven years and is based on over a thousand single surveys in the field.

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TABLE 1. CARICETUM SCOPULORENTIS. THE BOG ASSOCIATION.

Number of Survey		32	Aggreg.	501	502	644/5/6	503	67	
Altitude in Feet of Stand		12,700	12,500	12,000	11,800	11,800	11,400	11,300	
Exposure and Angle of Slope, Degrees		0	0–2 N	0	0	0	0–2 E	0	Presence
Aeral Size of Survey in Square Meters		6	100	10	10	3 (1, 1, 1)	10	1	/7
Fid. 5. Exclusive	Life-form								
Carex nelsonii	H	3	x	1	x	1		1	6
Juncus trigumis	H				x	1	x	1	4
Juncus castaneus	H		x°		x		x		3
Sedum rhodantum	H		1	x	1		1		4
Fid. 4. Selective									
Deschampsia caespitosa	H		2	x	2	1	2	1	6
Poa arctica	H		1						1
Poa reflexa	H		1		x		x		3
Carex scopulorum	H		3	x	3		3		4
Carex ebenea	H			x					1
Juncus biglumis	H	1	1	x					3
Saxifraga rivularis	H		x		x				2
Chionophila jamesii	H		x					x	2
Fid 3. Preferential									
Carex capillaris	H		x	x		x			3
Carex albo-nigra	H		1	x					2
Carex chalciolepis	H		x	x			x		3
Stellaria umbellata	H		x	x	x		x		4
Sedum integrifolium	H	1	x	x	1		x		5
Fid. 2. Companion									
Festuca brachyphylla	H		x	x		1			3
Luzula spicata	H	1	x	x		1	x		5
Lloydia serotina	H		x	x	x		x		4
Polygonum bistortoides	G		1	1	1	1	1	1	6
Polygonum viviparum	H		x	x	x	x	x		5
Sieversia turbinata	H	x	x	1	1	1	1		6
Gentiana romanzovii	H	x	x	x	1		x	x	6
Fid. 1. Invader									
Caltha rotuntifolia	H				x	x	1	1	4
Elephantella groenlandica	H			1			x		2
Mosses, lichens, algae		3	2	2	2	2	2		
Bare soil, exclusive of boulders		1/10				1/8		2/8	
Number of species per survey		6	22	19	16	10	17	7	

TABLE 2. SAXIFRAGETUM CHRYSANTHAE. THE ASSOCIATION OF CREVICES AND LEDGES.

Altitudinal range: 13,500 to 12,500, extremely to 12,000 feet.
Exposure: East to north to west, optimal northeast.
Slopes: From horizontal ledges to vertical rock surfaces.
Size of area: Many thousand square meters, extending beltlike around the Peak, equal to the middle-alpine subzone.
Distribution of plants: Widely dispersed.
Habitat: Cold and humid. Soil: Skeleton to mature micro soils.

Fid. 5. Exclusive sp.

Poa leptocoma	H	x
Poa lettermani	H	1
Carex misandra	H	x
Salix nivalis	H	x
Salix saximontana	H	1
Ranunculus pygmaeus	H	1
Saxifraga cernua	H	x
Saxifraga delicatula	H	1
Saxifraga chrysantha	H	1
Trifolium nanum	H	x
Polemonium viscosum	H	x
Polemonium speciosum	H	1
Polemonium grayanum	H	x
Synthyris alpina	H	1

Fid 4. Selective sp.

Poa arctica	H	x
Juncus biglumis	H	x
Claytonia megarrhiza	H	1
Lewisia pygmaea	H	1
Lychnis montana	H	x
Saxifraga flagellaris	H	1
Primula parryi	H	1
Chionophila jamesii	H	1
Senecio taraxacoides	H	x
Senecio carthamoides	H	x

Fid. 3. Preferential sp.

Carex ebenea	H	x
Carex albo-nigra	H	x
Oxyria digyna	H	1
Cerastium beeringianum	H	x
Sagina saginoides	H	1
Saxifraga debilis	H	1
Saxifraga rivularis	H	1
Oreoxis alpina	H	x
Androsace subumbellata	H	x
Primula augustifolia	H	1
Mertensia viridis	H	1

Fid. 2. Companion sp.

Festuca brachyphylla	H	1
Luzula spicata	H	1
Silene acaulis	Ch	x
Stellaria umbellata	H	x
Arenaria sajanensis	H	x
Draba streptocarpa	H	x
Sieversia turbinata	H	1
Gentiana romanzovii	H	x
Erigeron simplex	H	x

Fid. 1. Invader sp.

Deschampsia caespitosa	H	x
Carex pyrenaica	H	x
Draba crassifolia	H	x
Saxifraga rhomboidea	H	x
Artemisia scopulorum	H	x

Lichens, mosses, algae, and fungi are co-dominant over the whole area, and dominants locally, numerically far exceed the flowering plants.
Bare areas are extensive.
The number of species in the association is 49.

TABLE 3. SALICETUM PETROPHILAE. THE SNOWPATCH ASSOCIATION.

Number of Survey		249	250	66	123	235	751	68	124	94	95	662/6			
Altitude of Stand in Feet		12,570	12,570	12,100	12,000	12,000	12,000	11,900	11,900	11,800	11,800	11,100			
Slope Angle and Exposure in Degrees		2° NW	3° NW	5° N	0°	3° NE	5° NE	5° NE	7° NE	3° NE	2° NE	5° NE		Presence	
Areal Size of Survey in Square Meters		1	1	20	100	1	10	1	50	20	30	5(5x1)		15/	%
Fid. 5. Exclusive sp.	Life-form														
Agrostis rossae	H			x					x	x	x			4	26
Carex pyrenaica	H				1		1	x	x	1	x	1	(4)	10	66
Juncus drummondii	H							x	x		x	x	(2)	5	33
Salix petrophila	H shrub	3	4	3	1	3	3	3	3		2	x	(1)	10	66
Sibbaldia procumbens	H			x	x	x°	x°	1	1°	x	1	1	(5)	13	86
Erigeron melanocephalus	H			x	x	1°	x°	1	1°	x°	x°	1°	(5)	13	86
Fid. 4. Selective sp.															
Poa reflexa	H			x	x	x	x		x			x	(2)	7	46
Carex scopulorum	H			x	1	1	1	x		x	2			7	46
Castilleja occidentalis	H			x	x							x	(2)	4	26
Fid. 3. Preferential sp.															
Carex albo-nigra	H			x	x				x					3	20
Carex chalciolepis	H			x			x		x					3	20
Oxyria digyna	H			x					x					2	13
Paronychia pulvinata	Ch cush.			x					x			x	(1)	3	20
Sedum integrifolium	H	x°	x°						x					3	20
Chionophila jamesii	H	x		x					x					3	20
Fid. 2. Companion sp.															
Selaginella densa	Ch mat			x								1	(4)	5	33
Festuca brachyphylla	H			x		x	x	1	x			1	(5)	10	66
Luzula spicata	H			x	x				x	x	x	1	(4)	9	60
Polygonum bistortoides	G	x°			x									2	13
Polygonum viviparum	H				x	x	x	x	x		x			6	40
Silene acaulis	Ch cush.	x°		x				x	x	x	x			6	40
Stellaria umbellata	H				x				x		x			3	20
Arenaria sajanensis	Ch mat			x	x	x	x	x	x		x	1	(5)	12	80
Sieversia turbinata	H	x°	x°	1	1	1	1	x	x	3		1	(5)	14	93
Gentiana romanzovii	H	x°			x			x	x					4	26
Fid. 1. Invader sp.															
Mosses, lichens, algae		1	3	3	2	2	3	2	2	1	3	3			
Bare area. (Rocks, gravel, etc.)		1/2		1/20	1/2	1/10	1/10	1/20	1/3	1/2	1/10	1/10			
Number of species per survey		7	3	18	15	9	11	12	21	8	12	13			25

TABLE 4. CIRSIUMETUM SCOPULORENTIS. THE ROCK-SLOPE ASSOCIATION.

Number of Survey Altitude in Feet of Stands Exposure and Angle of Slope in Degrees Areal Size of Surveys in Square Meters		287 11,900 45 S 10	510 12,000 20–45 N 10	Presence in 15 Surveys 11,400–12,000 10–45 S–N 1–100	
Fid. 5. Exclusive species	Life-form			15/	%
Cryptogramma acrostichoides	H	1		8	53
Aquilegia saximontana	H	x		4	26
Viola biflora	H	x		3	20
Cirsium scopularum	H	1	1	10	66
Fid. 4. Selective sp.					
Stipa lettermani	H			1	6
Agropyron scribneri	H	x		2	13
Lychnis drummondii	H	x		3	20
Aquilegia coerulea	H		x	6	40
Senecio holmii	H		x	2	13
Senecio taraxacoides	H	x	x	3	20
Senecio carthamoides	H		1	8	53
Fid. 3. Preferential sp.					
Calamagrostis purpurascens	H	x		3	20
Trisetum spicatum	H		x	6	40
Carex chalciolepis	H	x	x	8	53
Avena mortoniana	H	x		4	26
Oxyria digyna	H	x	x	8	53
Trifolium dasyphyllum	H			2	13
Oreoxis alpina	H			4	26
Androsace subumbellata	H			2	13
Mertensia viridis	H		x	6	40
Fid. 2. Companion sp.					
Festuca brachyphylla	H	x		5	33
Polygonum viviparum	H			2	13
Silene acaulis	Ch cush.	x		4	26
Arenaria sajanensis	Ch mat			2	13
Sieversia turbinata	H			2	13
Fid. 1. Invader sp.					
Carex festivella	H	x		4	26
Arenaria fendleri	H			4	26
Sedum stenopetalum	H			1	6
Phacelia sericea	H	x		4	26
Pentstemon whippleanus	H	x		6	40
Solidago decumbens	H	x		3	20
Erigeron compositus	H			2	13
Erigeron trifidus	H			2	13
Erigeron simplex	H	x		7	46
Synthyris alpina	H		x	3	20
Lichens, mosses, algae		1	1	1	
Bare area		4/5	4/5	4/5	
Number of species per survey		19	11	35	

TABLE 5. ELYNETUM BELLARDI. THE MEADOW ASSOCIATION.

Analysis of "total estimate" and "presence" of several stands in different stages of development.

Number of survey		27	252	248	1			34			257	Aggregate 709–713		706–708			Aggregate A		140			Aggregate B			Aggregate C
Altitude in feet of stands		12,700	12,650	12,550	12,567			12,567			12,200	12,000		11,900			11,850		11,300			11,300/800			11,100–12,500
Exposure and angle of slope in degrees		0–2 W	0	2 N	0			0			5 N	10–20 S		20 SW			0–2 W		0			0–5 E			
Areal size of surveys in square meters		1	1	1	1 (25x1/25)			1 (25x1/25)			1	5 (5x1)		1	1	1	5 (5x1)		1 (25x1/25)			20 (20x1)			100 (100x1)
Fid. 5. Exclusive sp.	Life-form				T.E.	P.	%	T.E.	P.	%		T.E.	P.				T.E.	P.	T.E.	P.	%	T.E.	P.	%	P.&%
Elyna bellardi	H							2	25	100							1	1				3	20	100	36
Erisimum nivale	H																								2
Chondrophylla americana	H				x	3	12	x	3	12															14
Campanula uniflora	H	x						x	3	12															12
Fid. 4. Selective species																									
Poa rupicola	H											x	1	x			x	1							6
Carex capillaris	H			1°													x	1	1	22	88				6
Drosace carinata	H											x	3									x	5	25	17
Castilleja occidentalis	H				x	4	16	x	7	28															6
Tonestus pygmaeus	H							x	1	4															10
Actinella lanata	H																					x	12	60	12
Rydbergia grandiflora	H				x	1	4	x	2	8												x	7	35	19
Fid. 3. Preferential sp.																									
Calamagrostis purpurascens	H																					1	12	60	19
Trisetum spicatum	H														x		x	2				x	4	20	6
Agropyron scribneri	H																					x	2	10	2
Carex rupestris	H			x	1	22	88	1	24	96	1	x	4				x	2	1	25	100	x	7	35	57
Carex albo-nigra	H	x°						x	17	68															6
Lloydia serotina	H			x																					11
Stellaria umbellata	H	x	x												x										4
Paronychia pulvinata	Ch cush.			x							1	x	1												24
Sedum integrifolium	H				x	4	16																		6
Trifolium dasyphyllum	H			3	2	21	84	2	18	72	1	x	4									1	7	35	45
Oreoxis alpina	H																					x	2	10	2
Primula augustifolia	H	x		x	x	4	16	x	4	16									x	1	4				14
Phlox caespitosa	H mat																					2	2	10	2
Eritrichium argenteum	H											x	1									x	4	20	6
Castilleja brachyantha	H																					x	4	20	6
Artemisia scopulorum	H																								8
Artemisia pattersoni	H																					x	5	25	9
Fid. 2. Companion sp.																									
Selaginella densa	H											1	4			x	x	1	1	10	40	2	15	75	35
Festuca brachyphylla	H	x°	x°		x	5	20				x	x	4	x			x	4							40
Luzula spicata	H	x°			x	3	12				x				x		x	2							24
Polygonum bistortoides	G or H			x	1	15	60	x	3	12				x								1	13	65	30
Polygonum viviparum	H			x				1	25	100							x	4	2	25	100	x	2	10	20
Silene acaulis	Ch cush.	x°	x°		x	1	4	x	5	20		x	3	x		3	x	2	x	3	12				34
Arenaria sajanensis	H mat				x	1	4				x	x	2				x	1				1	17	85	47
Sieversia turbinata	H	1°		1	2	25	100	2	25	100	1	2	5	1	1		2	5	x	5	20	1	14	70	69
Gentiana romanzovii	H			x	x	7	28	x	6	24							x	2	x	5	20				16
Erigeron simplex	H													x			x	1				x	1	5	13
Fid. 1. Invader sp.																									
Danthonia intermedia	H											x	1												2
Carex scopulorum	H				x	4	16	x	7	28															4
Arenaria fendleri	H																					1	12	60	30
Saxifraga rhomboidea	H																					x	2	10	2
Sedum stenopetalum	Ch shrub																		x	7	28	x	3	15	3
Dasiphora fruticosa	Ch shrub											x	2				x	1				x	5	25	4
Pedicularis parryi	H																								2
Campanula rotundifolia	H																					1	9		18
Chrysopsis pumila	H																					1	8		8
Lichens, fungi, mosses, algae		2		2		3			x		2	2		(2) 1	(2) 1	(1) 1	3		3			2			
Bare area		3/4	99/100	1/3		1/10			1/10		4/5	2/5		3/4	3/4	3/4	1/2		1/2			1/3–2/3			
Number of species per surveys & aggregates		8	3	10		15			16		7	13		8	6	3	15		9			26			47

Table 6. DRYASETUM OCTOPETALAE. THE NORTH-SLOPE ASSOCIATION.

Number of survey Altitude in feet of stand Exposure and angle of slope in degrees Areal size of survey in square meters		63/4,503/6 12,000 30 N 1	2995/9 11,650 15 N 5	725/29 11,500 10–15 N 5	720/24 11,400 15-30 N 5	3300/4 11,300 10–15 N 5	667/9/71/3/5 11,200 10–15 N 5	Presence p. stands 6/	Constancy p. quadr. /25/	%
Fid. 5. Exclusive sp.	Life-form									
Dryas octopetala	Ch woody	5	4	2	2	2	2	6	24	96
Fid. 4. Selective sp.										
Carex rupestris	H	x	1	1	1	1	1	6	25	100
Paronychia pulvinata	Ch cush		x			x		2	2	8
Sedum stenopetalum	H				x			1	1	4
Phlox caespitosa	H mat						x	1	1	4
Eritrichium argenteum	H					x		1	3	12
Castilleja brachyantha	H	x	x		x	x	x	5	12	48
Actinella lanata	H		x			x		3	5	20
Fid. 3. Preferential sp.										
Calamagrostis purpurascens	H		x	x		x	x	4	12	48
Trisetum spicatum	H		x	x	x			3	4	16
Draba streptocarpa	H						x	1	1	4
Trifolium dasyphyllum	H		1					1	5	20
Primula augustifolia	H						x	1	1	4
Erigeron simplex	H	x			x			2	2	8
Artemisia scopulorum	H		x					1	2	8
Artemisia pattersonii	H		x	x	x	x		4	7	28
Fid. 2. Companion sp.										
Selaginella densa	H mat		x		x	x	x	5	10	40
Festuca brachyphylla	H	x		x	x		x	4	6	24
Polygonum viviparum	H			1		x		2	6	24
Silene acaulis	Ch cush.			x			x	2	4	16
Arenaria sajanensis	H mat	x	x	x	x	x	1	6	16	72
Arenaria fendleri	H		x		x	x	x	4	10	40
Sieversia turbinata	H	1	x	x				3	3	12
Fid. 1. Invader sp.										
Lichens on rocks		..	1	2	1	2	2			
Bare area		..	1/4	1/10	3/4	2/3	2/3			
Number of species per survey		7	14	10	11	12	13			

TABLE 7. DROSACETUM CARINATAE. THE SOUTH-SLOPE ASSOCIATION.

Analysis of "total estimate" and "presence" of four survey aggregations.

Number of survey		97			200									
Number of aggregates		25			25			25			6			Total Presence
Altitude in feet of stands		11,050			11,300			11,100–11,900			11,100–12,000			
Exposure and angle of slope in degrees		26 S			16 S			15–35 S			10–35 S			
Areal size of surveys in square meters		1/25			1/25			1			5–1,000			
Fid. 5. Exclusive sp.	Life-form	T.E.	P.	%	T.E.	P.	%	T.E.	P.	%	T.E.	P.	%	/33
Eriogonum xanthum	H										x	3		3
Senecio werneriaefolius	H							x	5	20	x	4		9
Fid. 4. Selective species														
Stipa lettermani	H							x	3	12				3
Avena mortonianae	H										x	2		2
Poa rupicola	H				x	6	32	x	4	16	x	1		6
Agropyron scribneri	H							x	6	24	x	2		8
Drosace carinata	H				1	17	68	1	11	44	1	3		15
Tonestus pygmaous	H				x	8	32	1	12	48	x	2		15
Actinella lanata	H	x	1	4	1	15	60	1	20	80	1	6		28
Fid. 3. Preferential sp.														
Calamagrostis purpurascens	H							1	15	60	x	1		16
Trisetum spicatum	H	x	8	32	1	5	20				1	5		7
Carex rupestris	H	1	15	60	1	25	100	1	23	92	1	5		30
Lloydia serotina	G							x	1	4				1
Paronychia pulvinata	Ch cush.	1	12	48				x	21	84	1	5		27
Draba streptocarpa	H				x	6	24	x	1	4	x	2		4
Trifolium dasyphyllum	H							1	9	36	x	2		11
Phlox caespitosa	H							x	2	8	x	3		5
Eritrichium argenteum	H				x	1	4	x	5	20	1	4		7
Castilleja brachyantha	H	x	1	4				1	18	72	1	3		20
Erigeron simplex	H							x	1	4	x	2		3
Artemisia scopulorum	H				1	11	44	1	21	84	1	4		26
Artemisia pattersoni	H							1	7	28	x	2		9
Rydbergia grandiflora	H							x	5	20	x	1		6
Fid. 2. Companion sp.														
Selaginella densa	H mat				1	25	100	1	11	44	x	2		14
Festuca brachyphylla	H							x	1	4				1
Luzula spicata	H				x	1	4	x	5	20	x	2		8
Polygonum bistortoides	G							x	4	16				4
Polygonum viviparum	H				x	3	12	1	9	36				10
Silene acaulis	Ch cush.							x	2	8	x	1		3
Arenaria sajanensis	H mat	x	4	16	1	12	48	1	22	88	1	6		30
Sieversia turbinata	H				1	12	48	1	23	92	1	5		29

Table 7. DROSACETUM CARINATAE. THE SOUTH-SLOPE ASSOCIATION. (Continued)

Number of survey			97			200								
Number of aggregates			25			25			25			6		
Altitude in feet of stands			11,050			11,300			11,100–11,900			11,100–12,000		Total
Exposure and angle of slope in degrees			26 S			16 S			15–35 S			10–35 S		Presence
Areal size of surveys in square meters			1/25			1/25			1			5–1,000		
Fid. 1. Invader Sp.	Life-form	T.E.	P.	%	T.E.	P.	%	T.E.	P.	%	T.E.	P.	%	/33
Arenaria fendleri	H				1	20	80	1	20	80	1	5		26
Heuchera parvifolia	H										x	3		3
Heuchera bracteata	H										x	3		3
Sedum stenopetalum	H				x	8	32				x	2		3
Dasiophora fruticosa	Ch shrub							x	6	24	x	2		8
Potentilla nivea	H				x	6	24				x	3		4
Pedicularis parryi	H				1	13	52				x	3		4
Campanula rotundifolia	H				x	4	16	x	4	16	x	3		8
Chrysopsis pumila	H				x	1	4	1	16	72	x	3		20
Solidago decumbens	H										x	2		2
Erigeron compositus	H	1	12	48	x	4	16	1	8	32	1	4		14
Erigeron pinnatisectus	H							x	2	8	x	2		4
Lichens, mosses, algae		2	25	100	2	24	96							
Bare area			4/5			3/4			1/5–3/5			2/5–4/5		
Number of species per survey aggregate			7			20			34			38		

TABLE 8. ANALYSIS OF THE ASSOCIATIONAL DISTRIBUTION OF THE VASCULAR SPECIES.

The arrangement of the associations shows decrease in water balance.

	Caricetum	Saxifragetum	Salicetum	Cirsiumetum	Elynetum	Dryasetum	Drosacetum	Amplitude
	Hydrophytic					Xeroph.		
Cryptogramma acrostichoides R. Br.				x				1
Selaginella densa Rydb.			x		x	x	x	4
Stipa lettermani Vasey				x			x	2
Agrostis rossae Vasey			x					1
Calamagrostis purpurascens R. Br.				x	x	x	x	4
Deschampsia caespitosa (L.) Beauv.	x	x						2
Trisetum spicatum (L.) Richter				x	x	x	x	4
Avena mortoniana Scribn.				x			x	2
Danthonia intermedia Vasey					x			1
Poa arctica R. Br.	x	x						2
Poa reflexa Vasey & Scribn.	x		x					2
Poa leptocoma Trin.		x						1
Poa rupicola Nash.					x		x	2
Poa lettermani Vasey		x						1
Festuca brachyphylla Schult.	x	x	x	x	x	x	x	7
Agropyron scribneri Vasey				x	x		x	3
Elyna bellardi (All.) C. Koch					x			1
Carex pyrenaica Wahl.		x	x					2
Carex festivella Mack.				x				1
Carex ebenea Rydb.	x	x						2
Carex rupestris All.					x	x	x	3
Carex capillaris L.	x				x			2
Carex misandra R. Br.		x						1
Carex nelsonii Mack.	x							1
Carex albo-nigra Mack.	x	x	x		x			4
Carex chalceolepis Holm	x		x	x				3
Carex scopulorum Holm	x		x		x			3
Juncus drummondii E. Meyer			x					1
Juncus triglumis L.	x							1
Juncus biglumis L.	x	x						2
Juncus castaneus J. E. Smith	x							1
Luzula spicata (L.) DC	x	x	x		x		x	5
Lloydia serotina (L.) Sweet	x				x		x	3
Salix petrophila Rydb.			x					1
Salix saximontana Rydb.		x						1
Salix nivalis Hook.		x						1
Erigonum xanthum Small							x	1
Oxyria digyna (L.) Camptera		x	x	x				3
Polygonum bistortoides Pursh	x		x		x		x	4
Polygonum viviparum L.	x		x	x	x	x	x	6
Claytonia megarrhiza (Gray) Parry		x						1
Lewisia pygmaea (Gray) Robins.		x						1
Silene acaulis L.		x	x	x	x	x	x	6
Lychnis montana Wats.		x						1
Lychnis drummondii Wats.				x				1
Stellaria umbellata Turcs.	x	x	x		x			4
Cerastium beeringianum Cham. & Schlect.		x						1
Sagina saginoides (L.) Brit.		x						1
Arenaria sajanensis Willd.		x	x	x	x	x	x	6
Arenaria fendleri Gray				x	x	x	x	4
Paronychia pulvinata Gray			x		x	x	x	4

TABLE 8. ANALYSIS OF THE ASSOCIATIONAL DISTRIBUTION OF THE VASCULAR SPECIES. (Continued)

	Caricetum	Saxifragetum	Salicetum	Cirsiumetum	Elynetum	Dryasetum	Drosacetum	Amplitude
	Hydrophytic					Xeroph.		
Aquilegia coerulea James				x				1
Aquilegia saximontana Rydb.				x				1
Ranunculus pygmaeus Wahl.		x						1
Caltha rotundifolia (Huth) Greene	x							1
Draba crassifolia Graham		x						1
Draba streptocarpa Gray		x				x	x	3
Erysimum nivale (Greene) Rydb.					x			1
Sedum stenopetalum Pursh				x	x		x	3
Sedum integrifolium (Raf.) A. Nels.	x		x		x	x		4
Sedum rhodantum Gray	x							1
Heuchera bracteata (Torr.) Ser.							x	1
Heuchera parvifolia Nutt.							x	1
Saxifraga flagellaris Willd.		x						1
Saxifraga chrysantha Gray		x						1
Saxifraga debilis Engelm.		x						1
Saxifraga rivularis L.	x	x						2
Saxifraga cernua L.		x						1
Saxifraga delicatula Small		x						1
Saxifraga rhomboidea Greene		x			x			2
Dryas octopetala L.						x		1
Sibbaldia procumbens L.			x					1
Dasiphora fruticosa (L.) Rydb.					x		x	2
Potentilla nivea L.							x	1
Sieversia turbinata (Rydb.) Greene	x	x	x	x	x	x	x	7
Trifolium dasyphyllum T. & G.				x	x	x	x	4
Trifolium nanum Torr.		x						1
Viola biflora L.				x				1
Oreoxis alpina (Gray) C. & R.		x		x	x			3
Primula augustifolia Torr.		x			x	x		3
Primula parryi Gray		x						1
Drosace carinata (Torr.) A. Nels					x		x	2
Androsace subumbellata (A. Nels.) Small		x		x				2
Chondrophylla americana (Engelm.) A. Nels					x			1
Gentiana romanzovii Ledeb.	x	x	x		x			4
Phlox caespitosa Nutt.					x	x	x	3
Polemonium viscosum Nutt.		x						1
Polemonium grayanum Rydb.		x						1
Polemonium speciosum Rydb.		x						1
Phacelia sericea (Graham) Gray				x				1
Eritrichium argenteum Wight					x	x	x	3
Mertensia viridis A. Nels		x		x	x			3
Chionophila jamesii Benth.	x	x	x					3
Synthryis alpina Gray		x		x				2
Pentstemon whippleanus Gray				x				1
Elephantella groenlandica (Retz.) Rydb.	x							1
Pedicularis parryi Gray					x		x	2
Castilleja brachyantha Rydb.					x	x	x	3
Castilleja occidentalis			x		x			2
Campanula uniflora L.					x			1
Campanula rotundifolia L.					x		x	2
Chrysopsis pumila Greene					x		x	2
Tonestus pygmaeus (T. & G.) A. Nels.					x		x	2

TABLE 8. (Continued)

	Caricetum	Saxifragetum	Salicetum	Cirsiumetum	Elynetum	Dryasetum	Drosacetum	Amplitude
	Hydrophytic				Xeroph.			
Solidago decumbens Greene				x			x	2
Erigeron melanocephalus A. Nels			x					1
Erigeron simplex Greene		x		x	x	x	x	5
Erigeron compositus Pursh				x			x	2
Erigeron trifidus Hook.				x				1
Erigeron pinnatisectus (Gray) A. Nels							x	1
Actinella lanata Nutt.					x	x	x	3
Rydbergia grandiflora (T. & G.) Greene					x		x	2
Artemisia scopulorum Gray		x			x	x	x	4
Artemisia pattersoni Gray					x	x	x	3
Senecio holmii Greene				x				1
Senecio taraxacoides (Gray) Greene		x		x				2
Senecio carthamoides Greene		x		x				2
Senecio werneriaefolius Gray							x	1
Cirsium scopulorum (Greene) Cockerell				x				1

TABLE 9. SUMMARY OF ECOLOGICAL AMPLITUDE OF THE SPECIES. (From Last Column of Table 8)

Number of associations	1	2	3	4	5	6	7
Number of species	56	26	17	12	2	3	2
Percentage (approx.)	47	22	14	10	2	2	2

FIG. 1. LONGS PEAK. Flanked on the left by Mt. Meeker and on the right by Mt. Lady Washington and Storm Peak, and Chasm Gorge in front of Longs Peak. Note the alpine zone with snowpatches above the subalpine spruce belt.

FIG. 2. BOULDER FIELD and NORTH FACE. Midway on the "field" ends the low-alpine subzone; the high-alpine subzone is nearly coincident with the uniform slope including the summit. Elynetum of the initial stage shows in foreground. There are practically no flowering plants near the upper end of the "field."

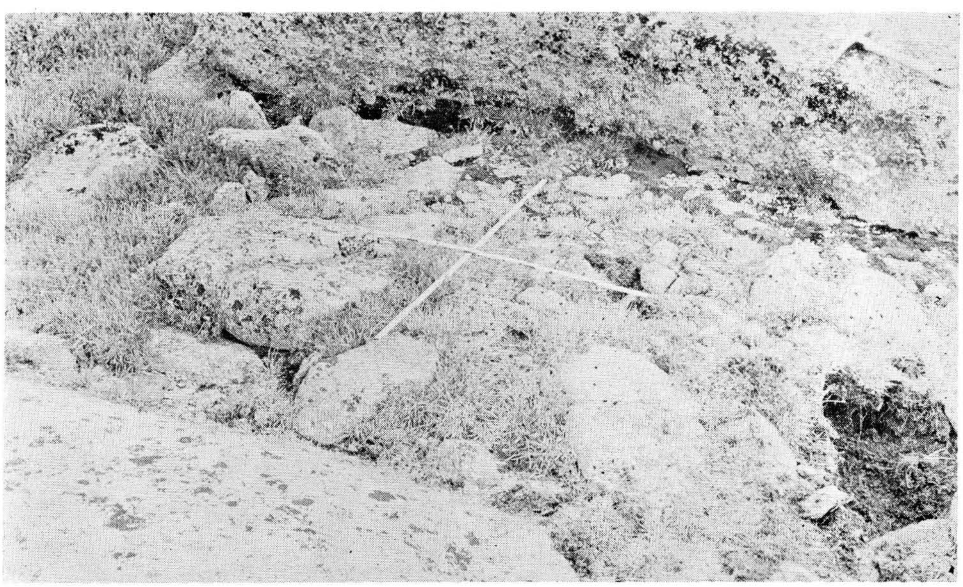

FIG. 3. CARICETUM, SURVEY 32. The dominant is *Carex nelsonii*. At left, on higher ground, *Sieversia* initiates an Elynetum stand. Cross sticks are one meter long.

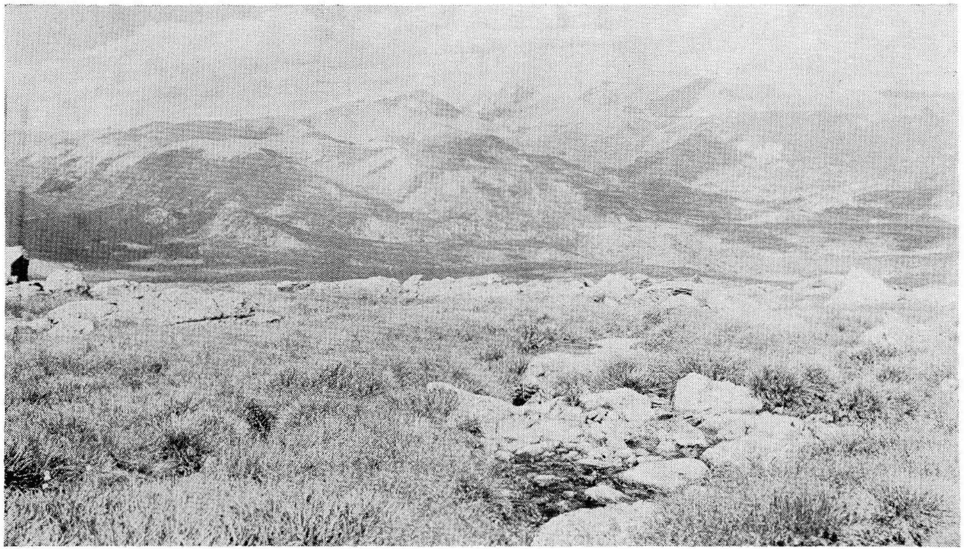

FIG. 4. CARICETUM, AGGREGATED SURVEYS. Shows optimal stage, and the tendency of species to dominate locally; also the bunch habit of the plants.

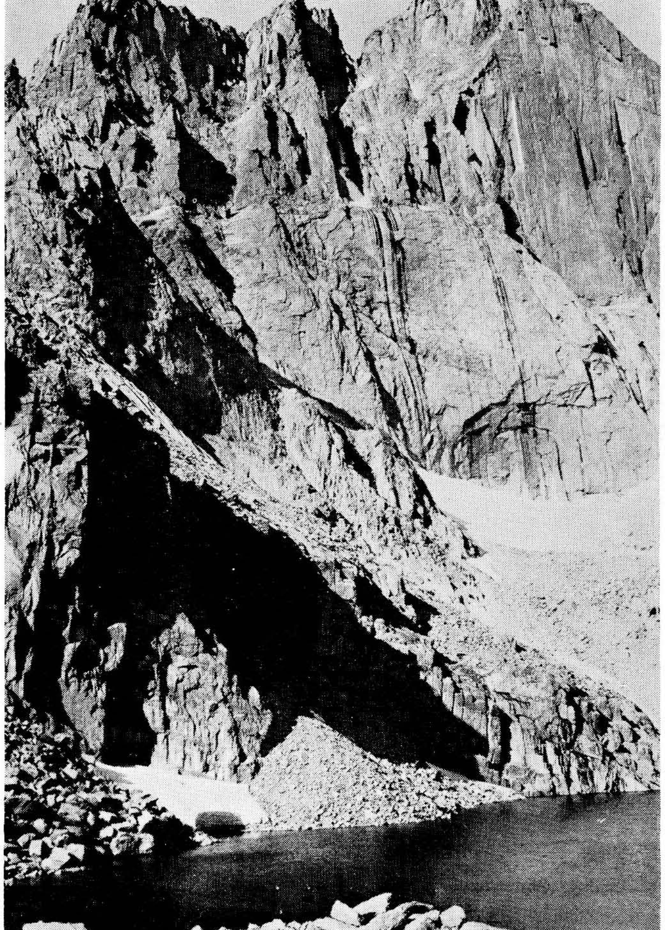

Fig. 5. EAST FACE. Shows Chasm Lake and a part of Chasm Gorge. The middle-alpine subzone begins at lake and extends to within 700 feet of the top. To the right of the lake, but not shown, on the southerly slope 150 feet above the lake, occurs the Elynetum stand of surveys 709-713.

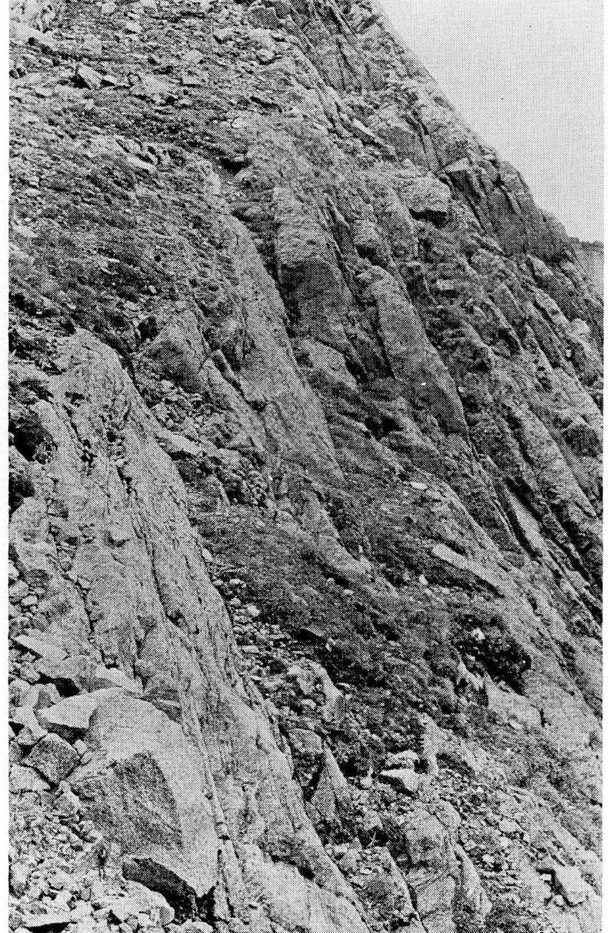

Fig. 6. SAXIFRAGETUM. Shows the distribution of plant life on ledges and in crevices of the rocks.

FIG. 7. CLAYTONIA MEGARRHIZA. Colony of large plants at an elevation of 13,000 feet on the East Face. In the distance is the south slope of Mt. Lady Washington.

FIG. 8. SALIX PETROPHILA. The woody stems are nearly buried in soil showing only the leaves and the catkins. On the left is *Carex pyrenaica* and to right *Carex scopulorum.*

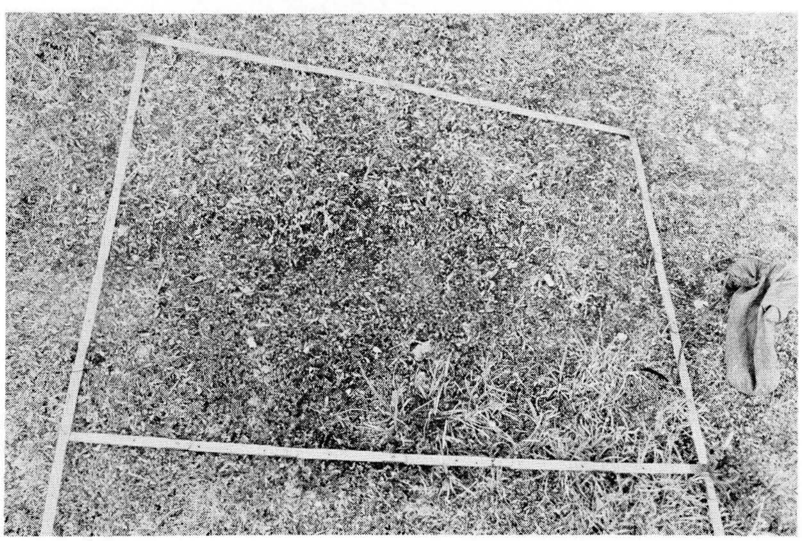

FIG. 9. SALICETUM QUADRAT 235. The dominant is *Salix*. In the lower right corner is *Carex scopulorum.*

FIG. 10. CRYPTOGRAMMA ACROSTICHCOIDES. Note shelter afforded by boulder on southerly slope. The scale is in inches.

FIG. 11. AQUILEGIA COERULEA. Note shelter of rocks and the large number of seed-bearing follicles. The plants are in full sunlight on northeasterly slope.

FIG. 12. CIRSIUMETUM. Showing *Cirsium*, *Phacelia*, and some grasses.

FIG. 13. ELYNETUM STAND 27. Small plants of *Sieversia* are the dominants in this pioneer stand. Note the lichens on the rocks.

FIG. 14. ELYNA BELLARDI. Shows the centrifugal growth with the dead center. Scale is in inches.

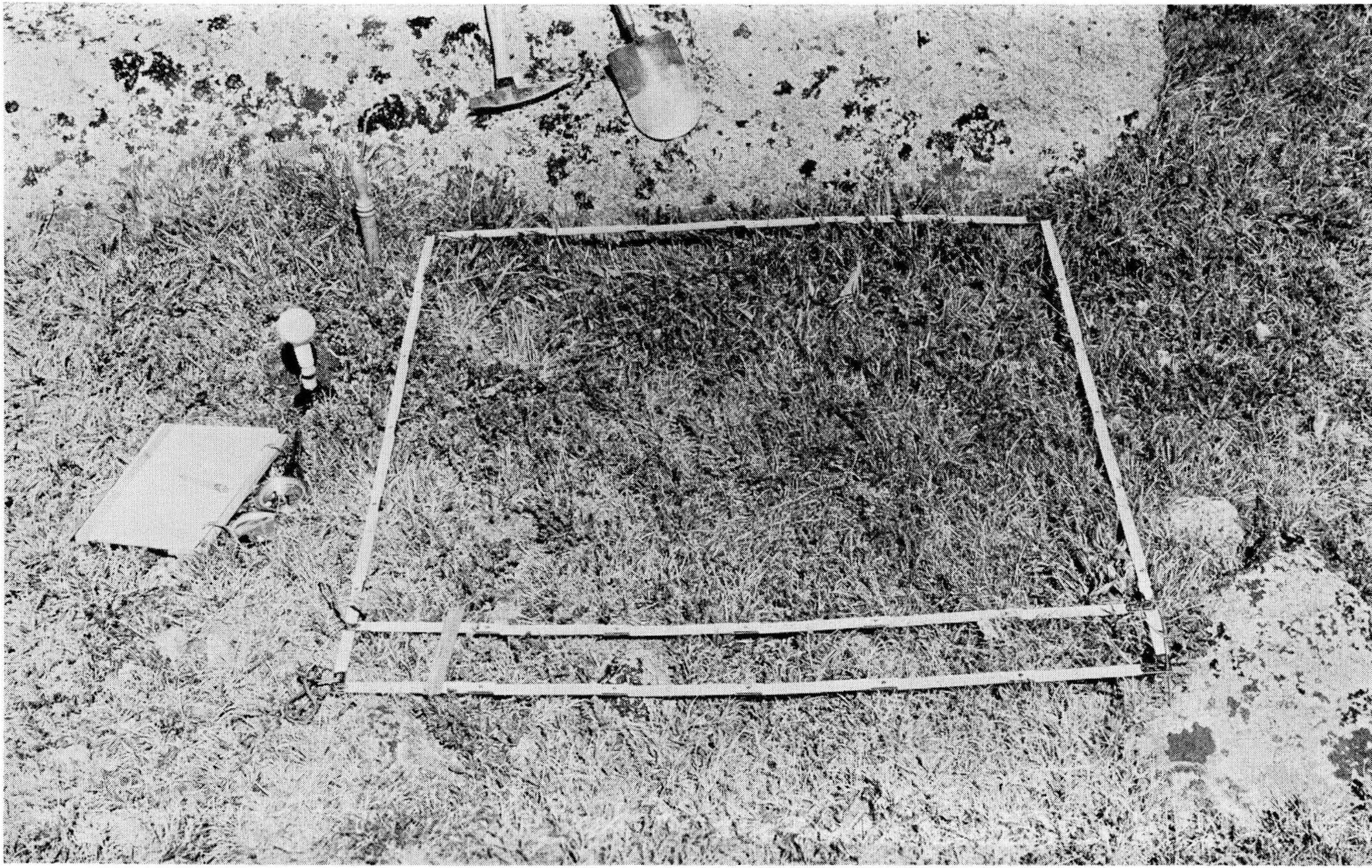

FIG. 15. ELYNETUM SURVEY 1. This stand represents the culmination of the initial stage and shows the dense vegetation but is without *Elyna*.

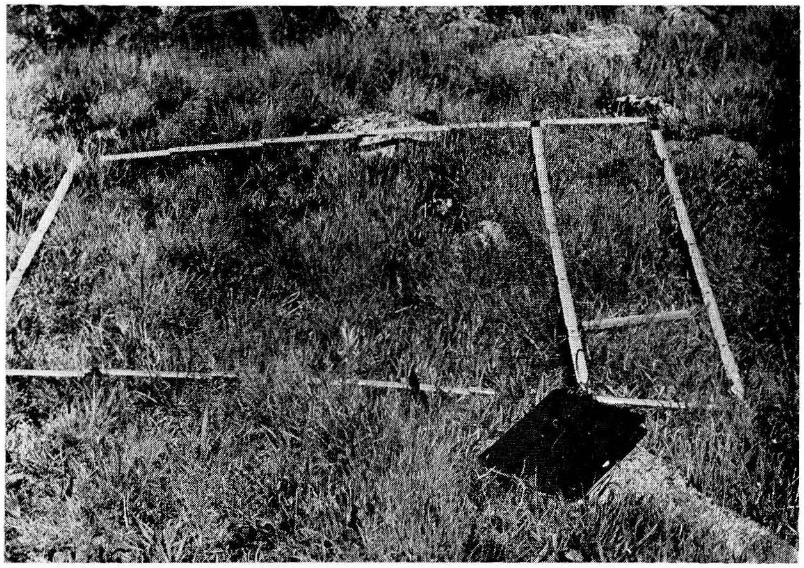

FIG. 16. ELYNETUM SURVEY 34. The quadrat represents the optimal stage of development of the association. One of the dominants is *Elyna*.

FIG. 17. ELYNETUM / CIRSIUMETUM. Primitive Elynetum of surveys 706–708 on top of slope. Where the slope faces directly south the Cirsiumetum occurs.

FIG. 19. ELYNETUM, DECLINING STAGE. Quadrat 138. *Elyna* is the only dominant and forms a pure stand, with a rich layer of lichens and bryophytes.

FIG. 20. ELYNETUM, DECLINING STAGE. Quadrat 138a. This is a subquadrat of only 20 cm. on the sides of survey 138.

Fig. 21. DRYAS OCTOPETALA. This species often forms extensive pure stands. Note *Rhizocarpon* on the rock.

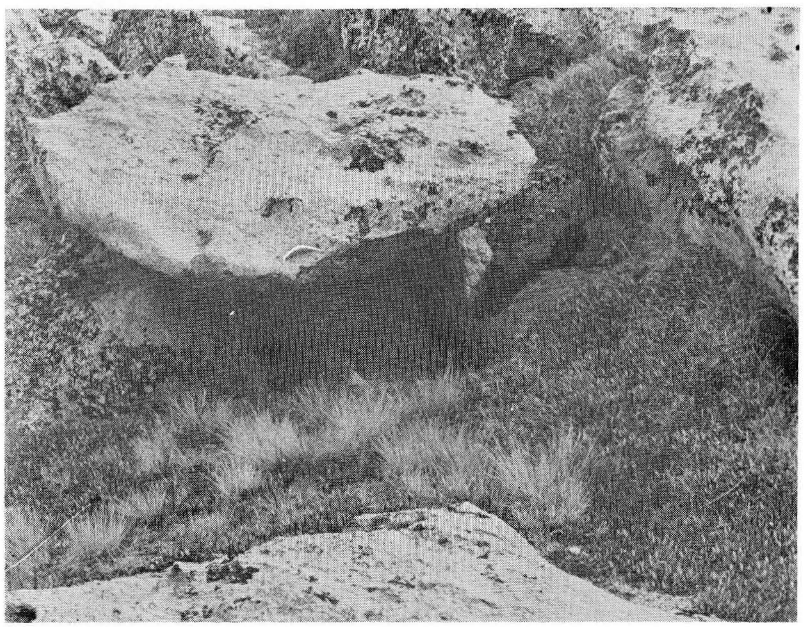

FIG. 22. DRYASETUM / ELYNETUM CONTACT. Competition here takes place on well developed soil.

FIG. 23. DRYAS TERRACING. The more level places are near-barren of flowering plants. *Dryas* grows on the terrace slopes.

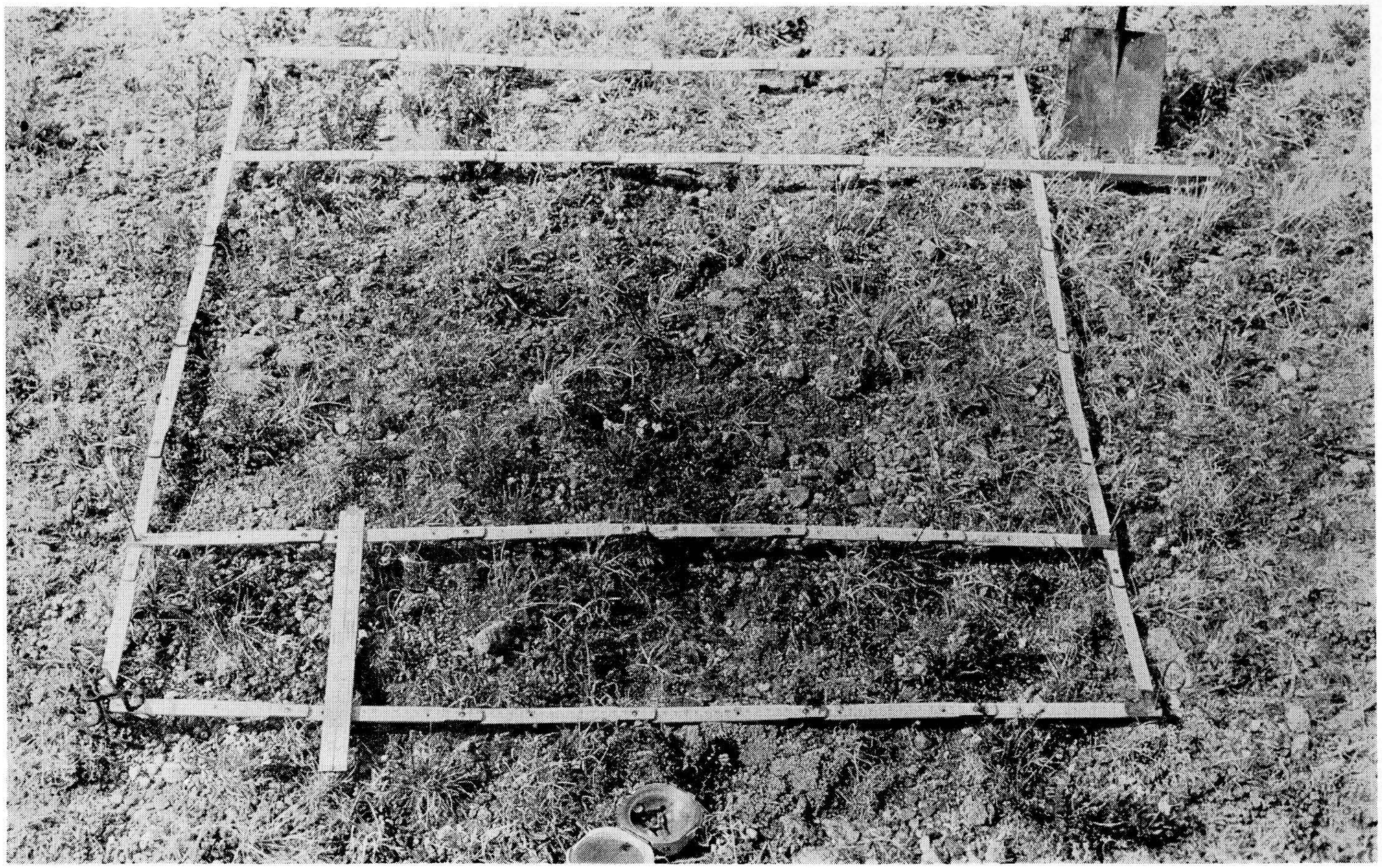

FIG. 25. DROSACETUM, OPTIMAL STAGE. Survey 200 on southerly slope.

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Brief Biography of the Author

Dr. Walter Bigler Kiener was born on October 18, 1894, in Berne, Switzerland. In November 1922, at the age of 28, he came to New York City. Later he moved to Denver, Colorado, because of his love for mountains.

In January 1925, he was involved in a mountain tragedy. In a sacrificial attempt at rescue, parts of his fingers and feet were lost. Several months later he was employed as a United States Ranger in the Rocky Mountain National Park. It was during this time that many professional people became acquainted with him and encouraged him to continue his thirst for education.

Walter Kiener entered the University of Nebraska as an adult special student. He received his A.B. degree in 1930, his M.S. in 1931, and his Ph.D. in 1940—all from the University of Nebraska. He then established his home in Lincoln. It became a workshop for natural history studies. In addition, he assembled an extensive herbarium of lichen specimens.

Dr. Kiener was known for his significant studies of (1) ecology of alpine vegetation of the Rocky Mountains, (2) limnology of Nebraska, and (3) ecology and taxonomy of cryptogamic vegetation.

Several species of plants have been named after Dr. Kiener. During a trip to Mexico in 1945, he visited high altitudes on both Popocatepetl and Ixtacihuatl. His moss collections, which were obtained on these trips, were published by E. B. Bartram (1949. The Bryologist 52: 23–27) and included two new species, *Pleuridium kieneri* and *P. exsertum*. A moss collected on Longs Peak in 1932 was described by R. S. Williams (1936. The Bryologist 38: 92–94) as *Splachnobryum kieneri*. Another species named in honor of Dr. Kiener was described by Fay Kenoyer Daily (*Chara kieneri, a New Species from Nebraska*. 1949. Butler University Botanical Studies 9: 127–130).

Dr. Kiener has been credited with founding the Nebraska State Game Commission's Fisheries Research Department. He was a noted writer and lecturer on subjects ranging from aquatic biology to alpine vegetation. Those who knew Dr. Walter Bigler Kiener regarded him highly for his professional work.

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