FIRST HALF,

OPEN FILE REPORT

7954

UNITED STATES DEPARTMENT OF THE INTERIOR

U.S. GEOLOGICAL SURVEY [Reports - Open file series]

Influences of the soil on boreal and arctic plant communities

By

Hansford T. Shacklette, 1914-

1962

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS (continued)

LIST OF ILLUSTRATIONS (continued)

APPENDIX

CHAPTER I.

INTRODUCTION

A. Background of this Study.

A body of data is now available with which to examine the relationships existing between plants and their associated soils of boreal and arctic regions with more precision than has been possible formerly. These data consist of chemical analyses of many hundreds of plant tissue and soil samples that were collected by the author in an attempt to apply principles of biogeochemical prospecting to these regions where this method of prospecting for minerals had not been tested. This practical objective required a systematic study of the whole field of plant community-environment relationships that are found in these regions of Alaska. To this end, a five-year program of field and laboratory studies was begun in June, 1956, ~~under the direction of the Geochemical Exploration Section, Division of Mineral Resources, U. S. Geological Survey, Denver, Colorado in cooperation with the Branch of Alaskan Geology, U. S. Geological Survey, Menlo Park, California~~. This study was integrated with geochemical studies of soils, waters, stream sediments, and rocks being undertaken concurrently in Alaska by the same agencies. This arrangement resulted in much valuable corroborative information being available for a more accurate appraisal of plant species and plant community response.

The important background for a study of this sort includes a general familiarity with the plant species of the region, the factors determining plant community composition and structure, and the physical nature of the environment. It was therefore necessary to consider the phytogeography, geology, climatology and pedology of the region. In addition to discovering and presenting the responses of vegetation to these factors, an attempt is made to explain these relationships and to present concepts of the structure and unique features of these northern plant communities.

The practical application of these principles in deriving biogeochemical interpretations was to determine whether characteristics exhibited by plants and plant communities could be used as indicators of subsurface mineralization under conditions obtaining in geologically and climatically distinct regions of Alaska. Some of the results obtained by the use of this method have been already reported (Shacklette, 1958, 1960, 1961a; Chapman and Shacklette, 1960) and a complete account of geochemical exploration in Alaska is being prepared by the last-named authors.

B. Anomalies of High Latitude Plant Communities.

The vegetation of high latitudes at first presents a bewildering aspect to the ecologist accustomed to studies of temperate zone plant communities. When it is studied more carefully its relation to the environment appears to encompass a series of anomalies. Temperate zone vegetation is often easily visualized as being organized into rather discrete plant communities or associations that have a close coincidence with the variation in soil water, light, exposure, soil type, geologic formation or with other plant communities. Further, there is usually a general constancy of these relationships, so that one comes to associate a particular plant community with distinct environmental factor combinations.

In the high latitudes these relationships are often much less evident. One may see abrupt changes in vegetation that are not associated with an apparent change in environment; conversely, one may see abrupt apparent changes in environment having no marked effect on the plant community. One may also see environment change resulting in vegetation change, as would be expected to occur in temperate zone vegetation.

A particular plant community may occur on sites that appear to be quite different. A bog community, for example, is often in a depression, but it may occur in a stream valley, on an almost level area, a hill summit, or on the steep slopes of a hill. There may be zonation of the vegetation in a bog, or the species may appear to be randomly distributed. There are communities that appear to have dominant species, thus competition and succession is implied, or there may be communities having no species exerting a dominating effect on the community, and all stages of a postulated succession may be found intermixed in no logical order. Tree and shrub communities are often alternated with areas appearing "barren" that have only a thin covering of mosses and liverworts, although there may be no conspicuous differences in the topography and no apparent differences in the microclimatic factors.

The species of plants may likewise show apparently anomalous responses to the environment. In one small valley white spruce may occur only on the stream banks; in an adjacent valley this species may extend well up the slopes toward the crest of the hill. Steep slopes forested almost exclusively with white birch and aspen are found at places to have narrow bands of black spruce trees running vertically on the slope. The flat lands below the slope may be forested almost exclusively with black spruce, or the black spruce may occupy a steep slope, with no white birch and aspen present. In contrast to the vertical bands of vegetation on some slopes, other slopes may have narrow horizontal bands or zones of some conspicuous plant species. Pine trees may grow in bogs or on steep rock cliffs, but not on intermediate sites.

In high latitudes the total number of species in a vast region may be small, yet a high percentage of these will be found in a very small community. This condition is especially characteristic of arctic plant communities. This is in contrast to the communities of temperate zones where, although many species are available to become components of a community, the small plant communities are composed of only a low percentage of the total. This suggests two problems of high latitude plant community composition and structure--why are these regions so limited in species, and why is such a high percentage of these species present in the individual community?

The patterns of high latitude vegetation are often very striking, especially in aerial observation. The arctic tundra in places presents a repetition of quite uniform polygonal units of low vegetation. The bogs of the flat boreal regions have a complex pattern of vegetation zones, at some places related to the contours of the stream channels and at others to the margins of small lakes or bog pools. The mountains ordinarily display an altitudinal zonation of vegetation that somewhat duplicates, in a short horizontal distance, the change of plant communities over a long latitudinal range. The mountains often extend to a height at which no plant can grow. In Alaska this altitude varies within the general range of 2,000 to 4,000 feet for flowering plants, depending in part on latitude. In contrast, there is no land surface in the western hemisphere at or near sea level extending so far north that no species of flowering plant can grow on it.

The general picture of the high latitude anomalies, when using the temperate zone plant communities as a point of reference, is one of disorder--both in the relationship of the plant community to its environment, and in its species composition. Careful study reveals, however, that the picture is not one of disorder, but of complexity. The problem of the ecologist in studying this region is one of discovering cause-and-effect relationships of the plant communities and their environments to the end that the essential order, however complex, may become evident.

C. Unique Features of the High Latitude Environment.

The unique features of this environment having an effect on soil-plant relationships are all related to the qualities and quantities of insolation, which may exert a direct or an indirect influence. The direct influence is on both photoperiod and photosynthetic response. The light at high latitudes is characterized by its low intensity as compared to that of temperate regions, and the importance of diffuse light, as distinguished from direct light, increases northward. The quality of the light is also different from that of lower latitudes in that there is, toward the north, an increase in the proportion of short wavelengths to long wavelengths. The length of day during the growing season is perhaps the most striking feature of the arctic regions. North of the arctic circle there are at least a few days in summer having continuous sunlight and many days have continuous light of sufficient intensity for photosynthesis to occur. This is not only a photoperiod and photosynthetic factor of importance, but also one that contributes to a more continuously favorable temperature for plant growth.

The indirect effect of light on vegetation through its control of temperature is also of great importance in this environment. The total effects of temperature on any biotic community are outside the scope of this study, therefore only those of critical or unique importance in soil-plant community relationships or in the survival of plant species are considered. All plants are assumed to have a critical low temperature minimum for survival and reproduction; the singular quality of high latitude temperatures is in their selective effect on species having very low minima. Another temperature peculiarity, especially in continental areas, is the extreme range of fluctuation from summer to winter. In interior Alaska, for example, summer temperatures may exceed 80°F and winter temperatures may be as cold as -60°F or colder.

The length of the growing season is perhaps of even greater importance to vegetation than is the temperature range. The exact length is difficult to define for high latitude vegetation, for it includes much more than merely number of days in the uninterrupted frost-free period. It is better expressed as total number of hours during which the temperature is above freezing; that is to say that intermittent sub-freezing temperatures, especially at the beginning or end of the growing season, are of no critical importance to most high latitude plant species. At best the growing season is quite short at high latitudes, but there may be considerable differences in this respect between contrasting microhabitats in a relatively small area.

Soil instability is the outstanding feature of much of the ground surface of high latitudes. In contrast to soils of temperate zones, this instability is not restricted to slopes, although it is more intense there; the level soil surface may also be very unstable. This phenomenon is the result of freezing and thawing of the soil, which has been described in a number of detailed studies in respect to the physical processes that occur. When the soil is freezing intense heaving may occur, due to its expansion. While the soil is frozen most chemical and physical processes are immobilized, but on thawing (unless the ground is relatively level) the soil particles move slightly down slope before coming to rest. This process occurs not only annually, but may be repeated daily for short periods in spring and autumn, which intensifies the down-slope creep. Frozen soil will hold more water than unfrozen soil, thus when it thaws it becomes quite viscous with its excess water and the entire soil mass may flow a short distance down slope. Rocks imbedded in the soil are lifted by the freezing of the soil beneath them. When the soil thaws it flows around and under the rocks, therefore they do not settle as much as they were raised. This repeated process brings them to the surface of the soil, often in regular patterns that reflect the areas of greatest frost action.

Much of the area of high latitudes is underlain by perennially frozen ground (permafrost). This frozen layer, in addition to acting as a mechanical barrier to root penetration, also prevents percolation of water from the thawed layers of soil. This, with the low evaporation rate of a cool climate, often leads to the development of a very wet soil even in regions of low precipitation. The cycles of freezing and thawing that occur above the permafrost zone result in an intense "churning" of the surface layers of soil, and therefore great instability of the soil surface even in level areas. Characteristic microrelief features of the land surface are also developed in these regions by differential frost heaving. The depth of the seasonal thaw into the frozen subsoil is greatly influenced by the insulating or conducting qualities of the surface cover. If the insulating layer of vegetation is removed thawing extends into the permafrost, which may result in the formation of a small pool. This pool increases in size with time as the heat conducted into the underlying permafrost continues to thaw the frozen material. Conversely, as vegetation closes over a pool of water or over mineral soil, heat conduction into the permafrost is reduced and the level of permafrost rises. Thus there are a number of features contributing to soil instability that are very important in high latitudes. These are significant factors in the study of plant community-soils relationships.

Most high arctic regions are characterized by a low amount of precipitation. This lends greater importance to the degree of substrate permeability in determining water content of surface soils, for if it is relatively impervious, the soil may be saturated, whereas if free percolation is possible the soil may be excessively dry during the growing season. Sites having these contrasting qualities may be adjacent with the boundary between the two very abrupt. Another factor of low precipitation is the relatively light snowfall in many arctic and boreal regions. Snow cover thus varies greatly in an area as a result of drifts formed by micro- or macrorelief features alternating with sites of little or no snow cover. The depth of snow cover affects the vegetation directly (either favorably or unfavorably) and also indirectly through the differential effect on soil stability because of the reduced frost action under a snow cover.

An effect of the high latitude environment on the conversion of rock to soil is that here rock disintegration is mostly a process of mechanical action, which may be very intense and spectacular due to radical temperature change. Rock decomposition due to chemical action is greatly reduced because of the low temperature. In tropical climates these relationships are inverted, and in temperate zones the two processes may be approximately equal in importance. The relationship of the processes is reflected in the characteristics of the resulting soils.

The low level of the mean annual temperature of this environment results in reduced microbial activity. This prevents the complete decomposition of organic matter, therefore deposits of peat are continually forming wherever conditions are favorable for luxuriant plant growth. In much of Alaska the surficial deposits consist of peat, humus, or muck layers, all related to the climatic control of microbial decomposition.

Certain areas of the high latitudes are characterized by glaciers, which are evidence of ancient, recent, or present accumulations of snow in excess of the melt rate. In Alaska they are found best developed in the southeastern and central coastal ranges and in the Alaska Range; they are entirely absent from the most northern parts of the state. Their effect on plant community-soils relationships may be direct in that they influence the plants and soils in their immediate vicinity, or indirect in that the products of glaciation often constitute or contribute to the parent material from which soil is formed. Their effect on the formation of streams and rivers is well known.

Thus we see in the environment of high latitudes many unique factors having a potential effect on soil-plant community development. The anomalies presented by the vegetation of this region can be understood only by relating them to the peculiarities of this environment. Many aspects of these interactions could be studied. The emphasis chosen for this study is on the unique plant community-soils relationships that are found in this northern environment.

D. Problems of Plant Community-Soil Relationships in the High Latitudes.

Within a given area, with its particular climate, the development of plant communities is ordinarily controlled by (1) the species available, (2) the nature of the soil or other supporting substrate, (3) the interrelationships of these two factors, and (4) the time available. On this basis climate is accepted as the constant factor of an area, and the soil and plant species available are the variables. If all three were constant and sufficient time were available a uniform flora of very similar plant communities would be expected to develop. If the plant communities that develop and the soils that are formed are believed to be predominantly a function of climate operating in time, eventual uniformity would be expected in an end point of dynamic balance known as climax. Sections B and C above have suggested that high latitude plant communities are not regionally uniform; the assertion is made here that the soils also are not regionally uniform. The adequacy of the available time can only be estimated, unless we are ready to concede that certain present soils and plant communities are, in fact, "mature." The question arises if there is some factor or combination of factors of the high latitude environment, different from those of temperate zones, operating to interrupt unidirectional tendencies toward a terminus, and that, on the contrary, they direct these processes into cyclic repetition. In this matter the soils and the plant communities can be examined as separate entities insofar as their relative maturity is concerned.

Perhaps the most conspicuous anomaly of these high latitude communities of vascular plants is their indifference, in the majority of cases, to varying geologic formations. Since a plant community must reflect to some degree the characteristics of its component species, it is evident that the species as a whole are essentially indifferent to this factor. This results in communities of very similar structure and composition growing over a great variety of geologic formations. This does not, however, imply that there is a blanket of uniform plant communities covering vast areas--on the contrary, disjunction of communities is so frequent that it is the expected condition. The point is that there is no necessary correspondence between this disjunction and the underlying geologic formation. If it is accepted a priori that a positive relationship exists between plant communities and their supporting soils, the above anomaly can be extended to indicate that there is no general correspondence of soil type to bedrock type. If these soils, therefore, neither correspond to climate operating in time nor to underlying geologic formations, the question arises of just what is the predominant factor in soil genesis. It is in this context that the reciprocal action of plants on pedogenesis becomes an important consideration.

Many species of high latitudes are not restricted in their occurrence to a particular soil type. For example, white spruce (a commonly-recognized "dominant") can be found on residual lithosols, alluvial deposits of azonal soils, half-bog soils of an intrazonal nature, and on podzols having definite zonal characteristics. On the other hand, the associated species on each of these soil types may be quite different. In southeastern Alaska Sitka spruce may occupy the same range of soil types and likewise have different associated species with each type. The anomalous nature of these relationships may be contrasted with the much more constant relationships of more temperate zones. The uniformity of soil type (podzol) in the spruce-balsam fir forests of parts of northeastern United States and the relative uniformity of associated plant species from site to site illustrates this latter point. Even in the mixed mesophytic forest region of east-central United States where community species composition varies considerably from site to site the soil is of two general types--podzol to podzolic under pine trees of dry slopes and brown forest soil in the more mesophytic deciduous forests. Both types may occur in close proximity.

Thus in high latitudes the problem is presented as follows: Is genesis of a soil type independent of vegetation type, and to what extent are plant communities indifferent to soil type? A corollary of this question is this--is indifference to soil type the essential property of a "dominant" species that, in high latitudes, distinguishes it from the subordinate species of the community? We must keep in mind that the classification of soil "types," as used in this context, is based on their genesis.

On the other hand, we may observe in high latitudes a few flowering plant species and many bryophyte species that are particularly "sensitive" to a single property of a soil or rock type. They may be restricted to soils derived from limestone ("basic") rocks, or to soils originating from "acid" rocks. Certain species seem to require a high nitrate supply, and even some may have a requirement for a high copper concentration in the substrate. This raises the problem not only of this specific species-substrate relationship, but also the question of the origin and migration of these species in an area where the requisites are discontinuous. The extent and composition of communities of these peculiar sites and the role of the "sensitive" species in the community are also problems for investigation.

The most subtle of all relationships of plant communities and soils is that of community response to the geochemical regime that exists in high latitudes. In soils of temperate regions it has been established that many plant communities have a direct relation to the elemental content of the soils that support them which are, in turn, influenced by geochemical affinities to bedrock. These relations may be manifested in the inclusion or exclusion of species, in altered morphology of the plants, or in the chemical composition of the plant itself. These reactions in high latitudes have been, up to the present, but slightly investigated. The relation of the quantities of certain metals in the soil to the quantities in tissues of plants supported thereon suggests the degree of vital dependence of the plant on the particular zone of the substrate that is sampled. If metals not known to be useful in plant metabolism are absorbed, it is reasonable to assume that useful elements, if present, would likewise be absorbed. If the soil surface contains more of the metal in question than do the lower soil horizons the effectiveness of the plant community in biogeochemical cycling is demonstrated. The reverse of this proposition is also true. The depth of root penetration and the effectiveness of geochemical diffusion in a particular soil can also be judged by this method. Biogeochemical response is, in the end, the conclusive evidence of the degree of intimate association of plants and their substrate environment.

Regardless of how we may interpret the responses of a plant community we come inevitably to the problem of the ecological amplitude of its component species. The question arises as to the characterization of high latitude species in this respect--are there factors in their migration into an area and their establishment therein that have a selective effect on the species, making them different as a group in their ecological amplitude from those of temperate to tropical zones. The answer to this question is pertinent to an explanation of plant distribution in the far north.

In the final analysis, soil-forming processes and the resulting soils are determined primarily by the temperature regimen; high latitude plant communities are limited in response by the inherent ecological amplitudes of the component species. The response combinations that integrate to make possible the widespread occurrence of distinct communities in high latitudes are suspected of cancelling certain deterrents to mutual relationships between the two--that is to say there may be in operation compensating factors of a nature peculiar to this climatic area. This poses the question of just what these factors are and how they operate. If this can be answered satisfactorily, a better understanding will be had of the unique relationships of plant communities to the soils of boreal and arctic regions.

E. ACKNOWLEDGMENTS

The author wishes to express gratitude to Dr. William S. Benninghoff, University of Michigan, Ann Arbor, Michigan, who has guided the entire development of this paper with many helpful suggestions, stimulating conversations, and critical reviews. He also wishes to acknowledge the invaluable assistance given by Mr. Robert M. Chapman, ~~who was Party Chief, Geochemical Exploration~~ of ~~Alaska,~~ U. S. Geological Survey during three field seasons when data were collected for this study. The services of the analytical laboratory of the Geochemical Exploration Section, U. S. Geological Survey, Denver, Colorado were indispensable, and this help is gratefully acknowledged. HTM

Special thanks are due Dr. Herman Persson and Dr. Eric Hultén of the Naturhistoriska Riksmuseet, Stockholm, Sweden for their assistance in plant identification and for their hospitality while the writer was at their museum. The facilities and services of several institutions were freely put at the writer's disposal, and he wishes to express appreciation for this courtesy extended by The Herbarium, University of Michigan, Ann Arbor, Michigan, and the Biology Department, Georgetown College, Georgetown, Kentucky.

The support of the Office of Naval Research, U. S. Navy in providing funds for an expedition in 1948 by a party (including the writer) from the University of Michigan to Northwest Territories, Canada is acknowledged. This party was directed by Dr. William C. Steere, present Director of the New York Botanical Garden; he is thanked for his advice and help in this study.

CHAPTER II.

METHODS

A. Sources of Observations in Alaska.

The field studies in Alaska were planned in such a manner that the principal metallogenic provinces could be sampled in order to consider the geochemical relations of soils, streams, and plants to the principal metals. This plan included, at the same time, areas of the principal geologic formations, major vegetational regions, and areas of occurrence of most of the recognized soil types of the state. The Arctic Slope, Arctic Sea area, and Seward Peninsula were not included in the detailed biogeochemical survey, but areas in each were briefly studied by the writer. The Aleutian Islands were not included in any of this work (Figure 1).

The soil that supports vegetation is generally related to the inorganic surficial deposits of an area. The látter, however, are not necessarily derived from the underlying geologic formations, but may be composed of materials transported by glacial action, wind, or water. Residual soils are scarce in Alaska; most soils were derived from a surficial deposit that had been brought into the area and deposited over the bedrock. However, in areas of strong relief and active erosion the soils and other surficial deposits usually lie over the bedrock from which they were derived, or are only slightly displaced down slope. Karlstrom (1960, p. 334) presents a sketch map of Alaska on which seven major regional groups of surficial deposits are outlined as follows: (1) glacial and other deposits associated with heavily glaciated alpine mountains, (2) glaciolacustrine deposits of larger

Figure 1.--Map of Alaska showing areas of this study.

Pleistocene proglacial lakes, (3) undifferentiated deposits associated with generally unglaciated uplands and lowlands of the interior and North Slope, (4) fluvial deposits, (5) eolian deposits, (6) coastal deposits of interbedded marine and terrestrial sediments, and (7) deposits associated with volcanic peaks and flows of Quarternary and Tertiary age. Areas in which this study was made (Figure 1) together include all these deposits. The map of Karlstrom is quite generalized and of such a scale that local differences cannot be shown, therefore it is necessary to determine the surficial deposits of each small area of study by ground reconnaissance.

The geologic map of Alaska (Dutro and Payne, 1957) shows the occurrence of formations of sedimentary, metamorphic and igneous rocks ranging in age from Precambrian to Recent in which all the principal rock types are found. It was possible in this study to find some plant species intimately associated with each major rock type. A great variety of rock types are often found in close association near the ore deposits because metal concentrations are frequently found in veins of intrusive magmas and plutonic rocks, or in zones of contact metamorphism between the veins and the country rock. In such situations it was often difficult or impossible to associate soils and plants with a particular rock type. To circumvent this difficulty some of the locations for soil and plant studies were deliberately chosen to include only a single rock type.

The kinds of soils of Alaska as defined by Kellogg and Nygard (1951) have very little relation to the kinds of their underlying formations as presented by Dutro and Payne (ibid.). This is partly explained by the fact that the classification of soils used by the former authors is based on genesis and morphology of the soils--not on their mineral constituents. It is therefore not accurate to state that the soils are never actually related to their underlying or associated rock types; it is only that the existing relationships are not expressed by the nomenclatural grouping. Kellogg and Nygard (ibid.) identify and describe ten Great Soil Groups found in Alaska as follows: (1) Subarctic Brown Forest soils, (2) Arctic Brown soils, (3) Ground-water Podzols, (4) Alpine Meadow soils, (5) Tundra soils, (6) Half-bog soils, (7) Bog soils, (8) Alluvial soils, (9) Lithosols, and (10) Regosols. The present study sampled numerous occurrences of each of these soils (with the exception of Ground-water Podzols, which were not identified with certainty). All these kinds of soils are widely distributed throughout Alaska, with the exception of Arctic Brown soils, Subarctic Brown Forest soils, and Podzols, and may be encountered in any region of the state from the extreme southeastern to the extreme northern part (Alpine Meadow soils will not, of course, be found on the northern part of the Arctic Slope).

In planning this geochemical study of Alaska, consideration was also given to selecting sample sites in such a way that the principal types of vegetation could be sampled. Hultén (1941, p. 4-7) divides Alaska into eleven districts "which as far as possible represent approximate phytogeographical units." Sample sites in the present study were located in seven of these districts, as follows: (1) Eastern Pacific Coast district, (2) Central Pacific Coast district, (3) Alaska Range district, (4) Lower Yukon River district, (5) Central Yukon River district, (6) Bering Strait district, and (7) the Arctic Coast district. Sigafoos (1958) recognizes three major vegetational regions in this state, as follows: (1) Coastal Spruce and Hemlock region, (2) Interior Spruce and Birch Forest region, and (3) the Treeless region. Most of the detailed sampling was done in the first two regions listed above, but numerous sample sites were in arctic alpine and tundra regions of mountains, which are in fact "treeless."

B. Field Studies.

The large size of Alaska, the lack of public living accommodations in by far the greater part of the state, and the limited highway system necessitated the establishment of field camps in most areas of study. Access to the areas was sometimes by means of motor vehicle, but most commonly was by airplane, boat, or helicopter. Travel within the areas was generally on foot or by boat. In addition to the usual supplies and equipment for camp life and field work, a portable geochemical laboratory was taken into the areas and put in operation in the base camps (Figure 2). From these camps excursions of one or more days were made into the surrounding territory. Facilities for drying soil and plant specimens were maintained at base camps. The personnel of the field parties usually consisted of a geologist, an assistant geologist, a chemist, and a botanist.

When the study of an area was begun a general reconnaissance was made of the geological and botanical features in relation to known mineralized deposits and also to non-mineralized areas. Field notes on the composition and structure of the plant communities as influenced

Figure 2. Field laboratory at Mahoney Creek, Revillagigedo Island, Alaska, in an abandoned cabin. This laboratory was equipped for copper, lead, and zinc quantitative determinations. June 14, 1957.

by environmental factors were started, and continued in more detail as the study progressed. Plant lists were made and herbarium specimens were prepared in each area in an attempt to provide a rather complete account of the species of vascular plants and bryophytes that were present. Ordinarily the locations of mineralized veins and outcrops were known in each area from published accounts or from past or present mining and prospecting activities. Traverses were established by Brunton compass to cross these mineralized zones and to extend into non-mineralized zones on either end of the traverse. Sample sites were next selected along the traverses, usually at regular intervals if terrain and vegetation made this possible, spaced 25 to 300 yards apart, as determined by the intensity of sampling that was desired. At each sample site a hole was dug in the soil extending to the parent rock material, where possible. Samples of the soil from the various horizons were selected, temperature readings of the soil horizons were made, and the soil profile was described in detail, including the nature of the C or D zones. These holes were numbered and marked with a pole and flag to facilitate finding them if additional study was desired later after chemical tests of the soil had been made at base camp. The pH of the soils from the different horizons was determined at camp in the evening of the day they were collected while they still had practically the original field moisture content. Both a Beckman pH meter and a Lamotte soil testing kit were used; it was found that the results obtained from the two methods were in close agreement, and that the Lamotte kit was somewhat easier to use.

The botanical studies at each sample site included a description of the plant community present and the selection of species of plants to be collected for chemical analysis. In choosing plant species to be sampled it was desirable that the species chosen should occur at each sample site on the traverse, in order that comparisons of chemical content might indicate the relation of the plant to the mineral deposit. This was not always possible, however; some traverses had so few species of plants suitable for biogeochemical analysis that it was necessary to take interrupted series of samples and base the interpretation of their analyses on standard median values. Standardized collecting techniques were established for each species to be used in biogeochemical studies, which varied with the morphology of the species being collected. These techniques were rather arbitrarily developed, in view of no or inadequate precedents, practicability of the method being an important consideration.

Plant species to be collected for analysis were identified in the field. In addition, herbarium specimens were made of each species for later verification of the field determinations. The plants selected for analysis were those growing as near as possible to each soil sample site. In most instances the plant was within a six-foot radius of the site, for the smaller plants, to a somewhat greater radius for large shrubs and trees, but in all cases sufficiently near the soil sample site to be reasonably presumed to have root extensions into the soil sample. This is in essential agreement with the principles of Warren, Delavault and Fortescue (1955). The desired plant parts were excised with a knife, the excess parts removed, and the samples placed in plastic bags (Figure 3). A field number was assigned the sample which corresponded with the soil sample taken from the same site. At base camp the plant parts were chopped up with shears for compact packing, placed in polyethylene bags and sealed, then packed in quart-size freezer cartons for air shipment to the Geochemical Section laboratory in Denver. Plant samples were not ordinarily analyzed in the field because it was considered impractical and excessively time-consuming to ash or chemically digest the organic matter in the samples with the limited equipment that could be easily transported.

Soil samples collected at each site were taken to base camp for drying. The samples were then pulverized and sifted through 80-mesh silk screen and the minus-80 fraction analyzed by field colorimetric methods. Based on the results of these field analyses, the sampling of an area could be extended or intensified to correspond more closely to the pattern of geochemical anomalies. If the exact location of the mineralized zone was unknown, reconnaissance sampling of sites spaced 200 to 300 yards apart followed by analysis of the samples would often indicate the area of mineralization and could be followed by more intensive sampling. The minus-80 fraction was obtained in sufficient quantity for later analysis in the laboratories in Denver.

In most areas the scope of geochemical studies was increased to include the collection of stream sediment samples, water samples, and samples of the rock outcrops for later chemical analysis. In this way a more complete understanding could be had of the origin, dispersion, and accumulation of the geochemical elements.

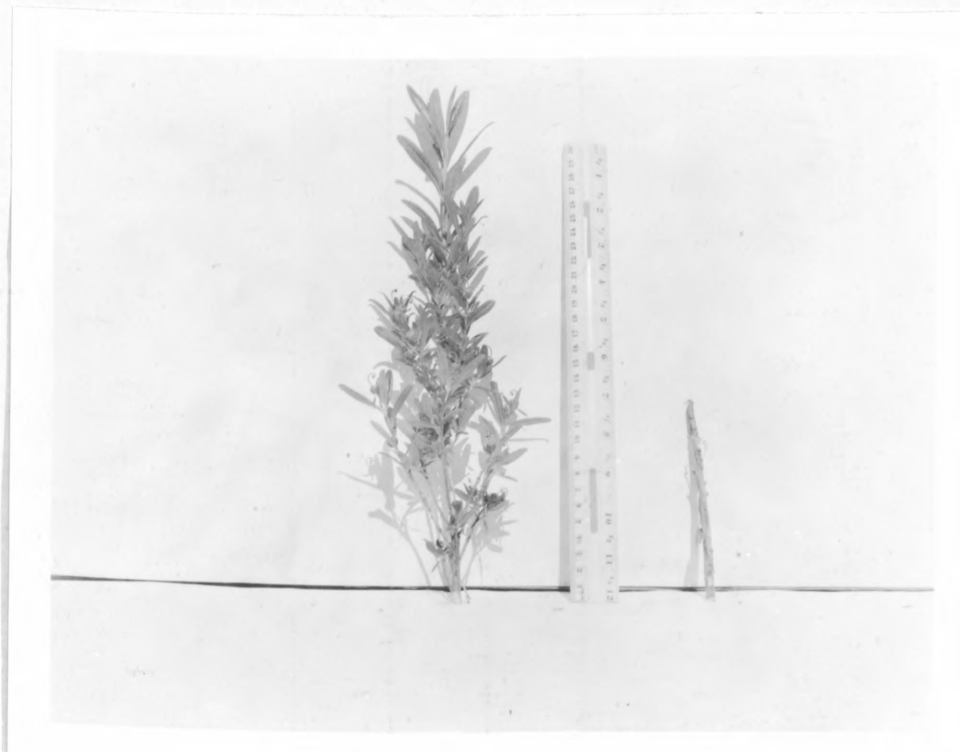


Figure 3. Cladothamnus pyroliflorus collected for chemical analysis. The specimen on the left has one- and two-year-old portions of the stem, with one-year-old side branches. All parts less than two years old were removed from the sample, and the older stem section (right) used for analysis. Approximately twenty such stem sections were included in each sample, in order to obtain adequate residue when ashed for chemical analysis. August 1, 1957.

C. Laboratory Studies.

The analysis of plant tissues was done by the staff of the Geochemical Section laboratories in Denver. The plant samples were first oven dried and then pulverized by grinding in a mill. The resulting powder could be then stored until analyzed, which was often done several months afterward. Approximately 2,146 samples were prepared in this manner. The first step in analysis was to remove the organic matter, which was ordinarily done by burning. The ash was then analyzed for content of the particular metals being investigated, using slight modifications of the methods developed for soil analysis as described by Bloom (1955), Lakin, Almond, and Ward (1952), Ward and Lakin (1954), and Canney and Hawkins (1958). The authors of the above-cited publications were all staff chemists of the Denver laboratories, and many of the tests were developed and modified while working with the samples described in this report. Determinations of mercury and antimony content of plant tissues required chemical digestion of the organic material rather than burning, because these elements are readily volatile and would be lost in burning. Great difficulty was encountered in digesting the dry powdered plant tissues because of the violent reaction with the reagents. A method of pelletizing this powder was devised that slowed the reaction sufficiently to obtain satisfactory results. Extreme care was necessary in all stages of preparation and chemical analysis to prevent contamination of the samples from any source, because the very low metal content of most plant tissues would be obscured or greatly exaggerated by even trace contamination.

Some of the plant samples were analyzed by semi-quantitative spectrographic methods to determine the content of all elements that can be detected by these methods. The samples were prepared as for ordinary chemical analysis and the ash was formed into pellets that were placed on the target electrode. This work was also done by the chemists of the Geochemical Section laboratories in Denver, using methods and equipment devised or modified by these chemists and described by Canney, Myers, and Ward (1957) and Oda, Myers, and Cooley (1959). With those elements that could be compared, the analyses by spectrographic methods corresponded closely to those made by the more usual colorimetric methods. Some analyses were also made by paper chromatographic methods, after the procedure of Hunt, North, and Wells (1955) and were found to correspond closely with those made by the other methods.

Analysis of all soil samples was also made at the Denver laboratory, although many of the samples had been previously analyzed in the field. Field and laboratory analyses ordinarily agreed closely, but in this study only the laboratory analyses are used because they are believed to be more nearly accurate.

Although most specimens of vascular plants were tentatively identified in the field, reference specimens of all sampled species were collected for later critical determination in the laboratory. Specimen identification of these plants was done by the author largely at the Herbarium of the University Museums, University of Michigan, Ann Arbor, Michigan, although some was done at Georgetown College, Georgetown, Kentucky and at the offices of the U. S. Geological Survey, Denver.

The first set of herbarium specimens is deposited at the University of Michigan; sets of duplicate specimens have been sent to the U. S. National Herbarium, Smithsonian Institution, Washington, D. C. and to the Naturhistoriska Riksmuseet, Stockholm, Sweden. The bryophytes were often identified in the field or later in the laboratory by the writer, but all specimens were sent to Dr. Herman Persson, Paleobotaniska Avdelning, Naturhistoriska Riksmuseet, Stockholm, who has made critical determinations of the entire collection (Persson and Weber, 1958; Persson and Shacklette, 1959). Dr. Eric Hultén of the Naturhistoriska Riksmuseet has examined all vascular plant specimens, and has named some species of the more critical genera and corrected identifications of some other species.

D. Organization and Analysis of Data.

After the critical determinations of species were made the names were entered in the field note books to corroborate or correct the field identifications. In this manner the species of plants were assembled according to geographical occurrence, and the plant lists made in the field could likewise be verified or amended. The separate collections of bryophytes, with full label data, were entered on individual species cards, which gave a ready presentation of the ecological relationships of each species. Soil profile diagrams were drawn either in the field, or in the laboratory from the field descriptions of profile characteristics. When the plant releves were combined with the soil profile data of a traverse, soil-plant relationship diagrams could be constructed (Figures 22 and 27).

The laboratory analyses of plant tissues yielded over 7,000 separate values, which were classified by species of plant, chemical element, traverse designation and sample site number, and the area of Alaska where the specimen grew. These results were first arranged in tables to show, for each species of plant, the high, low, mean, and median values in element content. Then the ratios of high to low values for each species and each element were tabulated. The traverses were plotted separately as bar graphs to show the values, for each element, of each species of plant found at a sample site. The values for the soil at each sample site were superimposed as line graphs in such a manner that the relative values were easily compared. The results of analyses were then arranged according to the element tested so that the characteristics of the elements in relation to their absorption by plants could be readily compared.

In the studies of the Mahoney Creek area, southeastern Alaska (Shacklette, 1960) the unique control of the exact location of the sharply-delimited ore vein (because it could be examined in surface outcrops as well as from a mine adit that permitted underground inspection of the vein) allowed a statistical appraisal of the analyses to be made and the standard deviation and standard error computed. At other sites the samples could not be so accurately arranged into "background," "halo," and "ore vein" groups for statistical comparison.

CHAPTER III.

THE EFFECTS OF SUBSTRATE FACTORS ON VEGETATION

Within a given area, with its particular climate and topographic relief, the development of plant communities is governed by (a) the species present, (b) the nature of the substrates, (c) the interrelationships of these two factors, and (d) the time available. The origins and distributions of plant species are not the principal topics of discussion in this chapter; however, certain of these aspects will be presented as they arise. Interpretation of plant distribution must include consideration of the features of environment characteristic of the area under consideration. It is believed that the significance of the extreme physical environment is especially pronounced in plant distribution and speciation in the more northern regions of the world. The conclusion of these studies presents some principles of these relationships with suggested interpretations and applications.

The emphasis of this study is on the unique nature and properties of the substrates of northern plant communities as they influence plant community development. These substrate properties, reflected in the features of the plant communities occupying them, may then readily be determined if they can be shown to have identifiable and more or less constant effects on the vegetation. This forms the basis of terrain evaluation by means of vegetation analysis (Benninghoff, 1953).

A large portion of Alaska is mantled with surficial deposits, as has been mentioned earlier, and the gross composition of these deposits often bears no relationship to that of the bedrock beneath it. The study of plant-substrate relationships therefore requires a consideration of (a) the relationship of plants to bedrock formations, (b) the relationship of plants to surficial deposits overlying bedrock, and (c) the effect of bedrock on the geochemical nature of surficial deposits as revealed by soil and plant analysis and the correlation of the two.

A. Bedrock Type.

For many years it has been generally recognized that plant species distribution often coincides with the areal extent of a particular geologic formation or bedrock type. Many botanists and geologists have demonstrated that in certain instances the occurrence of one of these factors indicates the simultaneous occurrence of the other; thus geologists have used known areal vegetation distribution as an indicator of specific rock types, and botanists have used the known distribution of rock types to predict the occurrence of certain plant species or plant communities. A few citations will amply demonstrate this fact.

Cuyler (1931) gives a general evaluation of vegetation as an indicator of geologic formations. Fernald (1942) in discussing the Coastal Plain flora cites drastic changes in floristic assemblages of ravines where erosion has cut through non-calcareous deposits into the ancient calcareous marine deposits. McInteer (1941, 1947) has shown the usefulness of plants as indicators of the occurrence of limestone as opposed to sandstone formations in Kentucky. Nasvetailova (1955) cites many examples of species as indicators of the nature of the substrate (both bedrock and surficial deposits) in central Russia and elsewhere. Victorov (1955) lists three plant species whose occurrence is definitely related to iron ore deposits in New Caledonia. Duvigneaud (1958) reports a species of flowering plant of Katanga, South Africa "whose resistance to copper toxicity appears to be infinite." Meijer (1960, p. 15) in describing the vegetation of Kinabalu Mountain, North Borneo says, "De struktuur van de vegetatie op ultrabasische formaties maakt het mogelijk voor de geologen om deze met behulp van luchtfoto's in kaart te brengen." The list of similar observations could be extended much farther.

Because most correlations of this nature have been made in temperate or tropical zones where positive relationships are frequent, there is the tendency to assume that this relationship may be established as a general phenomenon of all climatic zones if one is alerted to the possibilities. This was the assumption of the writer when beginning the examination of Alaskan plant communities. The expected correlations were not at once apparent. Other factors of environment were assumed to be masking this effect, and it was thought that if enough sites were examined this selective effect of rock type on vegetation would somewhere express itself. After examining many plant communities under many different conditions of environment the majority of differences of plant community distribution was most logically explained by the differences of factors other than rock type. The examination of relevés (lists of plant species) over similar and different rock types failed to establish a significant number of species as "exclusive" or even "preferential." It was generally impossible to differentiate between oxylophilic and calcicolous species, from their relation to bedrock deposits, except with some bryophytes and a few vascular plants. Not only did "presence" or "absence" generally fail to establish this relationship, but morphological and physiological expressions of this difference were also lacking.

The few communities of plants that were controlled by the chemical nature of the bedrock were of very restricted extent but of widespread occurrence. Other than those communities (mostly bryophyte) confined to limestone substrates, all communities showing such coincidence were found also to have tolerance to unusually high concentrations of lead, zinc, copper, iron sulfate, magnesium sulfate, and possibly nickel, beyond the tolerance limits of other species of the region (Shacklette, 1961a). Outcrops of these minerals in Alaska are, of course, quite rare--therefore the importance of these very limited plant communities as components of the total vegetation is extremely slight. They are, however, of great interest in relation to geochemical prospecting and will be considered in detail in Chapters IV and V.

In seeking an explanation for an apparent lack of correlation between rock type and vegetation type we may first consider the properties of rock which may affect the association of plants with it. A discussion of these properties follows.

a. Kind, amount, and availability in the rock of elements known to be nutritive requirements of plants. In a temperate zone having adequate rainfall the supply of nutritive elements is frequently the limiting factor in plant growth, not only in determining the vigor of growth, but of including or excluding certain species from community composition based on their absolute requirements for these elements, or their competitive ability in obtaining them. The elements that most commonly are limiting are, in order of importance, nitrogen, phosphorus, and potassium. The supply of nitrogen is not directly related to rock type, therefore it will be discussed in a separate section.

1. Phosphorus. The supply of phosphorus in Alaskan soils is generally extremely low in relation to requirements for agriculture (Laughlin, 1958, p. 24) but deficiencies apparently are not so evident in relation to site occupancy by native vegetation. The explanation of this latter observation is to be found in Liebig's law of the minimum--it is the other environmental factors that are limiting (Rübel, 1935, p. 336). The length of growing season, for example, inhibits vegetational productivity to a level at which small amounts of the nutritive elements meet the plant requirements. Plant species comprising a community are not competing among themselves for the mineral supply that may be areally variable and related to the rock type, but are adjusting to other environmental factors that are less distinct areally and unrelated or less closely related to rock type. This

limits or prevents the use of distinctive plant communities as indicators of the areal extent of geologic formations in arctic and boreal regions as contrasted to the indicator value of more temperate zone plant communities. From the standpoint of Liebig's law of the minimum, one may say that limited vegetational productivity because of other environmental requirements compensates for the low supply of some of the essential substrate elements. In temperate or tropical zones the other factors of environment may favor a vegetational production rate at which the nutritive elements become limiting factors. The overall requirements for these elements is a function of vegetational productivity per unit of area. Several investigators are making quantitative studies of native vegetation productivity in arctic Alaska, but the results have not yet been published; however it is obvious from inspection that productivity there is much less than in temperate zones.

Another indication of the sufficiency of rock-derived essential elements in the substrate was found in the studies of relevés made on serpentine colluvial slopes as compared to those of adjacent schist and limestone slopes. It is commonly recognized that a substrate derived from serpentine is usually deficient in the supply of phosphorus (Walker, 1954) and often potassium, and in addition, may have certain elements in toxic amounts, particularly nickel. Floras on serpentine soils are usually quite distinctive in species composition, and often have endemic species. Such soils are often sparsely vegetated. The south-facing serpentine outcrops on the West Fork of the Tolovana River, near Livengood, although burned over at least once since 1900, still are as completely vegetated as are neighboring schist and chert slopes having similar exposure, relief, and fire damage. The charred remains of large white spruce trees on the serpentine slopes indicate a former cover of well-developed forests, and young spruce trees are slowly occupying the site (Figure 4). Frost action on the soil near the summit of the slopes apparently has been intensified following the destruction of the forests and is retarding occupancy by plants.

Relevé of serpentine outcrop on the West Fork of the Tolovana River near Livengood, Central Yukon district, Alaska.

Line transect begins at the base of the serpentine cliffs and extends 1,500 yards up the slope to the plateau near the summit. Observed June 14, 1960.

Species	Abundance-Cover and Sociability Values 1./
Bryophytes:	
Abietinella abietina	+.2
Aulacomnium palustre	+.2

1./ Scales of Abundance-Cover and Sociability (after Braun-Blanquet):
Abundance-Cover —
- 5 = covering more than 3/4 of the sampled area
- 4 = covering 1/2 to 3/4 of the sampled area
- 3 = covering 1/4 to 1/2 of the sampled area
- 2 = with any number of individuals covering 1/20 to 1/4 of the sampled area, or with very numerous individuals but covering less than 1/20 of the area
- 1 = numerous, but covering less than 1/20 of the sampled area, or fairly sparse but with greater cover value
- + = sparse and covering only a little of the sample area
- r = very rare and covering only a very little of the sampled area (usually only 1 example)

Sociability—
- 5 = in large solid stands; very dense populations
- 4 = in small colonies or larger mats; rather dense populations
- 3 = in small patches or polsters; distinct groups
- 2 = in small groups or clusters
- 1 = growing singly

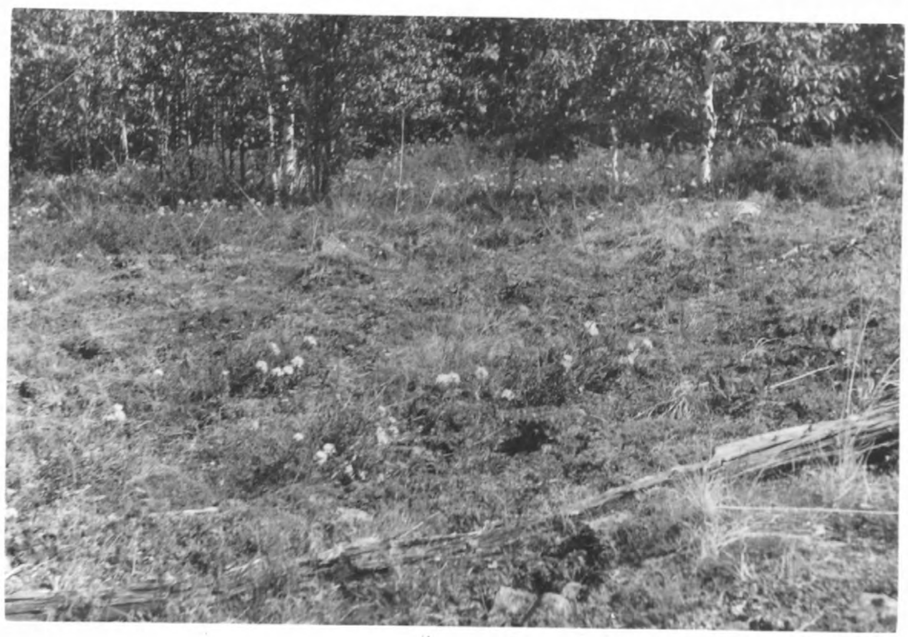


Figure 4. Vegetation of the serpentine "barrens" at West Fork near Livengood, Alaska. Conspicuous in the foreground are the fruiting inflorescences of Anemone patens subsp. multifida scattered through a grass community of Festuca altaica and Calamagrostis purpurascens. Although presently forested at the margins by Betula resinifera and Populus tremuloides, the rotting Picea glauca trunk in the foreground indicates a former coniferous cover that was destroyed by fire. June 14, 1960.

A. turgidum	+.2
Brachythecium salebrosum	1.4
Bryoerythrophyllum recurvirostre	+.3
Bryum sp. indet. (sterile)	+.3
Cephaloziella rubella	+.2
Ceratodon purpureus	1.2
Dicranum Bergeri	+.3
D. Muhlenbeckii	+.3
D. undulatum	r.3
Eurhynchium pulchellum	+.2
Hedwigia ciliata	+.2
Plectocolea rubra	+.2
Polytrichum juniperinum	2.4
P. piliferum	1.3
Rhytidium rugosum	1.4
Schistidium strictum	+.4
Splachnum sp. indet. (sterile)	r.1
Weissia viridula	+.2

Pteridophytes:

Dryopteris fragrans	+.1
D. Linnaeana	r.1
Equisetum arvense	+.2
Polypodium vulgare ssp. occidentale	r.2
Selaginella sibirica	3.4

Gymnosperms:

Juniperus communis var. montana	+.3
Picea glauca	1.1

Angiosperm woody plants:

Arctostaphylos uva-ursi	+.3
Betula resinifera	3.4
Ledum palustre ssp. decumbens	1.3
L. palustre ssp. groenlandicum	+.2
Populus tremuloides	1.3
Rosa acicularis	+.1
Salix Bebbiana	2.2
Shepherdia canadensis	r.1
Viburnum edule	r.1
Vaccinium uliginosum	1.3
V. Vitis-idaea subsp. minus	+.3

Angiosperm herbs:

Aconitum delphinifolium ssp. Chamissonianum	+.2
Anemone patens ssp. multifida	+.1
Arctagrostis latifolia var. arundinaceae	r.1
Arenaria laricifolia	1.3
Bupleurum americanum	+.2
Calamagrostis purpurascens	3.4
Conioselinum cnidifolium	+.1
Festuca altaica	2.3
Geocaulon lividum	1.2

Linnaea borealis ssp. *americana*	+.2
Melandrium Taylorae	+.2
Mertensia paniculata	+.1
Minuartia rubella	+.3
Pyrola secunda	r.1
Rumex Acetosa ssp. *alpestris*	2.1
Saxifraga tricuspidata	1.3
Silene Williamsii	1.2
Solidago multiradiata	+.2
S. sp. indet. (anomalous form)	r.2
Stellaria longifolia	r.1
Zygadenus elegans	+.1

These species are all found on slopes of other rock types in this area, with the exception of the anomalous form of *Solidago*. This list of species would also describe quite accurately the flora of similar but non-serpentine slopes in the region (calcicolous bryophytes and several probable calcicolous vascular plants excepted), exclusive of those species dependent on more dense forest shade than obtained at the West Fork site.

The pertinent conclusion of this comparison of vegetation and rock type is this: These boreal plant species may be considered oligotropic in respect to minimum requirements of the essential rock-derived elements, following the belief that it is the other environmental factors that are limiting. However, no proof is offered that the addition of phosphorus to the substrates would not increase the rate of growth. This procedure has been suggested for promoting wild berry production in this region of Alaska (Krause, Rieger, and Wilde, 1959, p. 495) and for increased timber production in British Columbia on nutrient-deficient substrates (Warren and Matheson, 1949, p. 54). Experimental evidences of the effects of this practice are highly desirable, but presently lacking.

A second compensating factor in the supply of phosphorus (also other nutrient elements) is the low rate of removal of these elements by leaching and runoff as they become soluble by weathering of parent material. This is effected by the prevalence of permafrost, by surface freezing of the substrate for eight months or more per year, and by the low rate of precipitation generally characteristic of arctic and boreal environments. Thus a relatively low available supply of these elements in the substrate suffices for "normal" plant growth when it is released by thawing at the time of year when plant growth is most active, then immobilized by freezing concurrent with the end of the growing season. The effects of this process are much less pronounced in temperate zones, and the process is absent in the tropics--therefore an additional requirement is imposed on the source of supply of these elements in the latter environments.

A third compensating factor in the phosphorus supply of these regions under consideration relates to the supply of phosphorus in a form most readily available to plants as a function of substrate pH, or more precisely, available calcium. Burd (1948, p. 240-241) states, "The fact is that H^+, Ca^{++} and PO_4^{---} comprise a mutually interdependent system in soils. The release of H^+ at soil-plant interphase has but little effect in lowering the pH of the system, but a great effect in terms of dissolved calcium, which in turn depresses phosphate solubility. Moreover, the fluctuations in the relative concentration of calcium and phosphate in such interphases and in the soil solution are greatly affected by the relative absorption of those ions by the plant. All of the available data indicate that the intake of calcium by plants growing in soils is quantitatively greater than their intake of phosphate . . . The plant is thus shifting the equilibrium in the direction favorable to the solution of phosphate." A process that removes the calcium ions from the soil solution, or immobilizes them in the solution by chemical combination or strong colloidal attraction thus favors phosphate solubility.

Soils that are distinctly alkaline have a predominance of the PO_4 ion, which is the form least readily used by plants. As the accumulation of humus (especially peat and muck) increases under the especially favorable environment furnished by arctic and boreal climates the soil solution becomes more acid due to added organic acids and to the great interfacial area presented by the organic colloidal particles which enables it to hold otherwise exchangeable bases (calcium, among others). Thus acidity is maintained in spite of large quantities of basic cations that may be present. With this increased soil solution acidity the HPO_4 and H_2PO_4 ions predominate; at still greater acidity the available phosphorus exists mostly as H_2PO_4 ions, which are the most readily absorbed by plants of all the inorganic forms of phosphorus in the soil solution (Lyon and Buckman, 1937, p. 237). Thus the biotic adjustment of soil solution pH controls the supply of usable phosphorus by its depressing effect on soluble calcium in these northern climatic regions, and is an additional factor in obscuring plant community-geologic formation relationships. In more temperate to tropical regions it is suggested that reduced organic accumulations due to rapid oxidation favored by higher temperatures render this biotic control of the phosphorus supply much less effective.

2. Potassium. The basic sources of potassium in the substrate are the original minerals such as feldspar and mica and complex secondary aluminum silicates, which may yield the simpler and more available forms, as follows: KNO_3, K_3PO_4, KCl, K_2SO_4, and K_2CO_3. Typical parent material of soil is abundantly supplied with potassium--the critical factor in plant nutrition is the often low supply of available potassium because the parent material does not readily yield this element in a soluble form. The supply of available potassium is usually low in sandy soils and very low in peat soils as compared to the amount in typical arable soils (Lyon and Buckman, 1937, p. 225). The availibility is increased by the action of organisms as the soil develops, due to the solvent effect of carbon dioxide on the element as it exists in parent material, and possibly other effects of vegetation. The developmental youthfulness of most soils in arctic and boreal regions indicates that a low level of available potassium is widespread.

The importance of this deficiency in determining plant succession and community development at high latitudes is suggested by Keller (1955, p. 24, 25) as follows: "Geologists observe that originally bare rock surfaces and undecomposed rock fragments are covered and invaded by the more primitive types of plants and by symbionts like the lichens. Botanists have shown that plants which are low in the scale of evolution can mobilize more potassium, for example, from relatively insoluble sources than do plants in the higher stages of development . . . The mechanisms by which primitive plants draw their nutrients . . . may be either, or all, of at least three possibilities: 1) That the roots of primitive plants generate an extra high concentration of H ions which are adequate to bring about weathering of even the feldspars in fresh rocks. The work of Lewis and Eisenminger supports this explanation. 2) That certain organic fluids secreted by plant rootlets may be strong chelating agents which can pull into solution nutrient ions from minerals . . . 3) That in the metabolic process of certain plants, diatoms for example, the relatively strong alumina-silica bond of silicates is broken, i.e., the silicate weathered, in order to furnish silica to the plant for its nutrition or growth. Clay minerals are decomposed by diatoms which leave an alumina-rich residue (a process for extracting alumina). The metabolic energy shown to break this bond is surprisingly large."

Lewis and Eisenmenger (1948, p. 498) present data, based on greenhouse experiments, demonstrating the relative extractive power of various angiosperm plants in obtaining potassium from feldspar, and state, "It seems rational to inquire why the low order plants have so much greater capacity to extract the K ion from minerals classified as relatively insoluble. It is entirely plausible to assume that the soil in the early periods of the earth's history was not like the weathered soil of today. The lower non-seed plants of the early geological periods had then and now a greater capacity to use the so-called unavailable ions. The fact that the older seed plants are more efficient than the newer ones in obtaining their ions from what might be called unavailable sources, indicates that their direct ancestors lived in an environment where frugality and slow growth were a necessity." To the list of extractive powers of primitive plants may be added the demonstrated ability of bacteria to dissolve "insoluble" phosphate compounds in apatite (Webley, 1960).

If the statements of these reports represent general principles, they furnish a basis for explaining many aspects of plant species distribution and community composition in arctic and boreal regions, where "frugality" and slow growth are still a necessity. Much of the regolith in the extreme north is affected neither by abundant plant growth nor weathering in the direction of soil development. This principle would explain, at least in part, the predominance of lichens and mosses in the most rigorous environments, and would also suggest a reason for the prominence of gymnosperms as pioneer tree species on certain sites. It would, in addition, give support to the concept of plant succession which presumes that invading pioneer species prepare the environment for those species which follow. If, for example, available potassium at a site is a limiting factor in higher plant community development, the extractive power of the cryptogams would enable them to invade the area first, and by their decomposition and soil formation, furnish available potassium to the higher plants, enabling them to become established. If this principle is literally true, oligotropic environments of this sort should show a precise successional pattern of species ranked according to their primitiveness. Field observations show this tendency appearing, but not unfailingly. This attractive viewpoint of "phylogenetically controlled" oligotropic succession needs further study in the field.

3. Other major elements. The elements of this group that are derived from rock are sulfur and calcium. They are used by plants in large amounts, but are generally available in sufficient quantity for metabolic requirements. Their other effects on plant communities are discussed in Chapter III, paragraph A.

4. Minor elements. These studies in Alaska have not shown evidence that a deficiency of any minor nutritive elements has had an effect on a plant species or on plant community composition; however they are admittedly inadequate for appraising this relationship. It is believed that the availability of these elements, and the requirements for them, are in part governed by the same principles discussed above for the major elements.

b. The kind and concentration of non-nutritive elements. This category of elements is a rather vague one, because the nutritive role of many elements has not been extensively studied. Further, some elements, although not considered to be nutritive in the usual metabolic sense, still are essential for certain plants, as for example, silicon in grasses and horsetails. According to Hawkes (1957, p. 292), "Some workers have even postulated that plants require a certain small amount of every element in the periodic table, but perhaps in quantities so small that the need could never be demonstrated in greenhouse experiments." Spectrographic analyses made during the course of these studies indicate the presence of at least thirty-one different elements in plant tissues; in addition, the gaseous elements and some other elements not capable of spectrographic determination from plant ash are known to be present. Although possible nutrient effects of most of these have not been demonstrated, it is known that certain of these elements have a toxic effect on plants. The most prominent of these toxic elements are probably copper, mercury, zinc, lead, aluminum, and the radioactive elements. Even nutritive elements, present in excess amounts, may be toxic (for example, iron and sulfur), but here the definition of "toxic" is involved. With some elements the range between a nutritive level is very small; for boron, this difference is only a few parts per million (Robinson, 1951). Plant communities were found in Alaska where species composition was determined by excesses of certain non-nutritive elements. These communities of very limited extent are discussed in Chapter IV.

c. The effect of the chemical nature of the rock on the pH of the water and soil in close contact with it. The direct influences of rock type on the reaction of soil water lie principally in the following three categories: (1) The amount of calcium and magnesium present for base exchange, (2) the capability of the rock to produce inorganic colloidal complexes (principally clays) with their accompanying buffering action, and (3) the presence of sulfur or sulfur compounds which may, by oxidation or hydrolysis, form sulfuric acid, and orthophosphates which may form phosphoric acid. An indirect effect of the rock type on the soil solution is the supply of nutrient minerals present, as discussed above, and their relation to the growth of vegetation, which in turn may largely control the pH of the soil water. Biotic activity in any substrate tends to increase the acidity of the substrate solutions, unless prevented by exchanges of bases. Thus a soil can remain neutral, or become alkaline, only through the presence of exchangeable bases provided by the rocks of the parent material of soil--not by the activity of organisms. The alkalinization of the upper soil horizons by decomposition of base-rich leaves mentioned by Braun-Blanquet (1932, p. 245) is merely a process of concentration due to the recycling of bases.

Under natural conditions in arctic and boreal environments the pH of the soil water may be changed appreciably by the presence of limestone in the soil parent material, and this may have an effect on plant species and plant community occurrence. However, the overriding effect of acid-producing vegetation generally holds these soils to neutral or somewhat acid reactions, and in areas of deep organic deposits the solum may be quite acid although overlying a limestone formation, or having limestone cobbles actually mixed with the soil. On the other hand, areas are quite rare in which the chemical composition of the rocks actively augments the natural tendency toward acidity of the soil solution. These are the "mineralized" areas in which sulfates and sulfides are prominent. Specific examples of plant communities showing the effects of varying pH levels are given in Chapter IV, paragraph D.

d. Properties of rock that influence vegetation through other relationships.

1. Effect of rock type on gravitational stability of the substrate. The control of plant communities of scree or talus slopes is due principally to the physical properties of the rock of which these slopes are composed. The metamorphic series of rock consisting of slate, phyllite, and schist produce very unstable colluvial deposits as compared to those ordinarily derived from other rock types. The natural cleavage planes of metamorphics often cause fragmentation into thin plates that easily slide over each other, this action often being assisted by the abundance of mica flakes. The dark colors, which may be greenish, reddish, gray, or almost black, make the rocks unstable to the thermal changes of insolation, so that outcrops of these rocks commonly produce a very unstable colluvial slope having a low angle of repose (Figure 5).

These slopes are often almost barren of vegetation—even bryophytes may obtain only a very precarious lodgement. However, if other environmental factors are generally favorable characteristic plant communities may develop marked by small number of species, low abundance-cover values, and medium sociabilities. These qualities of the community vary on an individual slope in response to the degree of stability of a particular portion of the slope, with higher abundance-cover values ordinarily at the base of the slope. Some characteristic plant communities of unstable colluvial slopes are given below.

Community A — "Metamorphosed" slate (approaching gray phyllite) slide. Near Mile 6, shore road, Douglas Island, near Juneau, Alaska. Altitude ca. 200 feet. Observed July 2, 1957.

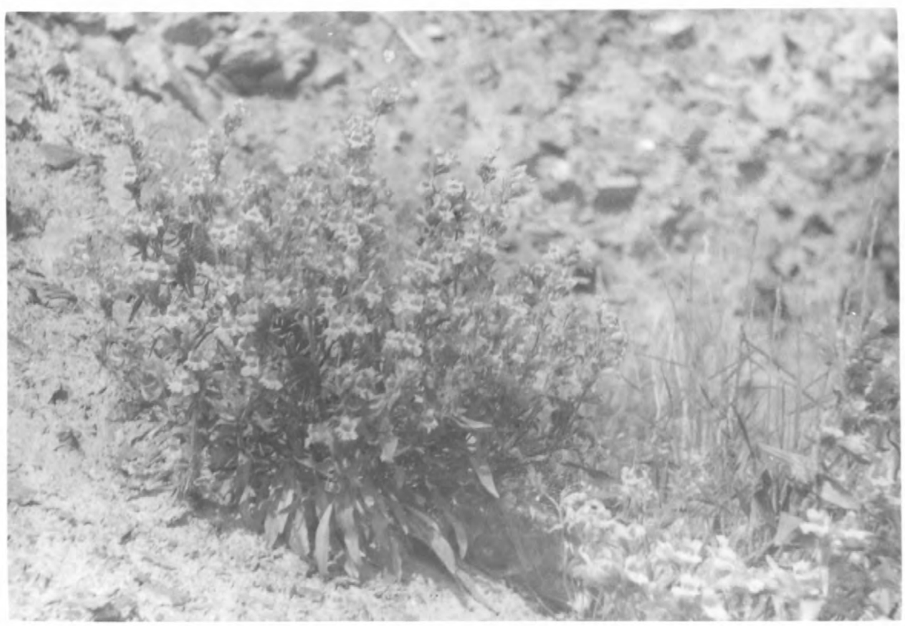


Figure 5. Schist colluvial slope, south-facing bank of the Fortymile River, Taylor Highway, Alaska. Pentstemon Gormanii was one of the few plants that could become established on this very unstable slope. June 25, 1960.

Bryum affine, Dicranum fuscescens, Oligotrichum aligerum, Pohlia cruda, P. proligera. These are all acrocarpous mosses; pleurocarpous mosses do not usually occupy unstable mineral substrates. The substrate was stabilized most effectively by the Bryum and Oligotrichum species. The location of this site in a shaded ravine probably contributed to the colonization by the Dicranum species. No vascular plants were invading the slide.

Community B -- Gray slate shingle of creek bank. Montana Creek, about 12 miles north of Juneau. Altitude ca. 50 feet. Observed July 2, 1957.

Pohlia gracilis, the only species present, was growing in full sun exposure, and had an abundance-cover value of about 3.

Community C -- Steep talus slope of muscovite schist. Southwest slope of Quigley Ridge, Kantishna, Alaska Range. Altitude ca. 2,000 feet. Observed July 27 and 28, 1958. (Figure 6).

Bryophytes: Ditrichum flexicaule, Encalypta brevicolla, Grimmia ovalis, Pohlia cruda, Rhacomitrium lanuginosum, Pylaisia polyantha, Rhytidium rugosum, Schistidium strictum, and Tortula ruralis.

Pteridophytes: Lycopodium complanatum, L. sabinaefolium var. sitchensis, and Woodsia ilvensis.

Angiosperms: Arnica louiseana var. frigida, Artemisia arctica, Luzula confusa, Minuartia obtusiloba, Salix torulosa, Saussurea angustifolia, Saxifraga tricuspidata, and Vaccinium Vitis-Idaea.

Figure 6. Schist talus slope on Quigley Ridge, Kantishna, Alaska Range. This lower portion of the slope supports a dense, but discontinuous, mat of Vaccinium Vitis-idaea subsp. minus. The small fern in the left foreground (Woodsia ilvensis) is more characteristic of the less-stable upper portions of the slope. July 28, 1958.

Of the rock types discussed here, schist talus forms the most stable slopes, and this is reflected in the large number of species found at this site. The rather large talus blocks provide niches for sciophytes (Pylaisia polyantha, Encalypta brevicolla, Pohlia cruda, and Schistidium strictum) and the chasmophyte Woodsia ilvensis, and in addition, stabilize the slope thus providing a more favorable environment for the other species.

Community D — Green and red phyllite of steep road cut. Livengood road near Globe Creek. Altitude ca. 1,000 feet. Observed September 6, 1957.

Ceratodon purpureus. This is a common pioneer species of bare mineral soil and other disturbed sites. This steep cut was very unstable, and had been available for plant occupancy five years.

Community E — Active schist slide, kept wet by a small rivulet. North bank of Eldorado Creek, about 2 miles west of Kantishna, Alaska Range. Altitude ca. 1,800 feet. Observed August 8, 1958.

Bryum cirratum, Leptobryum pyriforme, and Marchantia alpestris.

Community F — Long, steep, gray-slate slide. In cirque of unnamed creek north of Two Plate Creek, Maclaren Glacier, Alaska Range. Altitude 4,000 feet. Observed August 14, 1958.

Dry portion: Rhacomitrium canescens var. ericoides.

Moist portion: Gentiana glauca, Lupinus nootkatensis, Saxifraga tricuspidata, and Zygadenus elegans.

Wet portion: Asterella Lindenbergiana, Bryoerythrophyllum recurvirostre, Brachythecium Nelsoni, Bryum crassirameum, Cratoneuron falcatum, Jungermannia cordifolia, Pohlia albicans, and Tortula norvegica.

It is of interest to note that in this high altitude arctic-alpine environment the driest and wettest sites were occupied exclusively by bryophytes, and the mesic portion by vascular plants.

Community G -- Schist tailings pile, very steep. On Sourdough Creek, Steese Highway, Central Yukon district. Altitude ca. 1,850 feet. Observed July 5, 1960.

Bryophyte: Rhacomitrium canescens.

Angiosperms: Artemisia Tilesii ssp. elatior, Campanula lasiocarpa, Cardamine microphylla, Cerastium Beeringeana, Crepis elegans, Epilobium latifolium, and Erigeron purpuratus. Vascular plants directly invaded this man-made "colluvial slope" without being preceded by bryophytes. These were all growing as chasmophytes, the unsorted tailings rock providing many crevices for their lodgement. The only bryophyte present, Rhacomitrium, is a moss characteristic of dry, bare rock surfaces.

2. Effect on soil formation. In discussing the origin of soil materials Lyon and Buckman (1937, p. 175) write, "Where the original rock has been a limestone, shale, gabbro, diabase, or a granite low in quartz, the soil material resulting is likely to be clayey. Cherty limestone, quartzite, dolomite and slate often yield stony

residues, while sandstones and granites high in quartz give rise to sandy materials." The degree of resemblance of a soil to its parent material is determined by (1) the rate at which the weathering processes occur, (2) the chemical and physical nature of the parent material, (3) the influence of organisms, and (4) the length of time that these processes have operated. Thus an immature soil, particularly the azonal, may resemble parent material very closely, and the designations "soil" or "parent material" can only be rather arbitrarily applied. The intrazonal soils, because of the predominant effect of one environmental factor, resemble parent material to a lesser degree. The zonal, or mature, soil may show little resemblance, either physical or chemical, to its parent material because its characteristics are determined by the climate and the length of time it has had to form, according to the classical concept of soil genesis. It is then approximately accurate to state that the degree of resemblance of a soil to its parent material is a measure of its developmental age (not necessarily its chronological age) unless strong intrazonal processes are active. Applying these concepts to high latitude soils, it can be deduced that all are of a young developmental age as compared to temperate and tropical soils of equal chronological age. Because chronological age of a soil must be reckoned from the time of the most recent major deposit of parent material, most soils of the northern regions are also chronologically young, although existing on an area of land surface that has been continuously above sea level for many thousands of years. Major surficial deposits, such as alluvium, colluvium, loess, and volcanic ash are continually being laid down, or have been formed within recent times. It is from these deposits that the present surface soil (buried soils are excluded from this discussion) must develop. Therefore we find in many soils of Alaska the potential for a close correspondence between the properties of parent materials and the resulting soils. If the parent material is bedrock, there may be a high degree of similarity between the soil and the geologic formations as mapped.

However, two forces operate to obliterate this relationship. One, the development of well-marked zonality, is in itself a process which reduces this correspondence as the soil reaches maturity by means of the pedological processes operating in a favorable environment which includes moderate relief, moderate water content, and a favorable temperature level. The other, the development of intrazonal soils, likewise reduces the similarity of the soil to its parent material, but in a different manner. Here the orderly development of zonality is prevented by the predominant effect of one factor of pedogenesis--excess moisture, excess relief, or excessively low temperature. These same processes occur in temperate and, in part, in tropical zones. The distinctiveness of high latitude soils in this respect is that with the processes leading to zonality operating at a level so near the lower boundaries of possibility, even under the most favorable environments to be found here, the slightest decrease in efficacy of any one factor turns the whole process to one of intrazonality. Thus the development of zonality is very "sensitive" to minor variations of environment, which results in countless intergrade subtypes of soil. These intergrades may exert subtle influences on plant individuals themselves, and on the plant communities. From this viewpoint, the resulting mosaic of vegetation so characteristic of much of arctic and boreal regions is seen as one expression of the complexity of soil-forming processes and their relationship to plant communities.

Bedrock only, not surficial deposits, is ordinarily shown on geologic maps. The Alaskan geologic map of Dutro and Payne (1957) and the Alaskan surficial deposits map of Karlstrom (1960) show that there is seldom a land surface of materials that correspond to the bedrock--that the parent material for soil formation is most frequently transported rather than autochthonous materials. If, as is explained above, the soils of Alaska commonly show but little relationship to the parent material, they will show still less relationship to the geologic formations. In fact the only soils showing close relationship to bedrock in most of this region are the residual regosols and lithosols that are azonal or intrazonal. These occur most often in areas of strong relief that have not accumulated a covering of transported materials. In such sites direct weathering of bedrock to soil may be observed, but the other processes of soil formation are very weakly developed.

The Tundra and Arctic Brown soils of the Arctic Slope of Alaska are underlain with permafrost, which in areas of low relief effectively isolates the present soils from bedrock. Tundra soils are highly organic with some admixture of mineral particles; however, the origin of these mineral particles is obscure. They may have come mostly from bedrock deposits, having been elevated to the surficial zones by congeliturbation in the recent or distant past, or they may have been transported as aeolian and alluvial material. Present topography of this region, with its many meandering streams, drainage ways, and lakes suggests the latter origin of this material in much of the region.

In high latitudes, where rock weathering is more mechanical than chemical, the difference in rate of weathering of silicious and calcareous rocks is less pronounced than in temperate and tropical regions. Both rock types weather slowly, the rate being more dependent on their physical characteristics than on their chemical composition.

3. Effect on water relationships. Qualities of rock that influence vegetation through their effects on water relationships have been discussed in preceding paragraphs, principally in the effects on the chemical and physical reactions involved in soil formation. A more direct effect of rock type on water relationships lies in the varying permeability of the rocks to water, in their influence on ground water level by their function as aquifers or impervious types. Rock type influence on geologic structure, as distinct from the qualities of the rock itself, is important as a factor in the occurrence of springs. Properties of the rock, such as susceptibility to rapid weathering, which relate to the process of peneplanation and base levelling exert, over a long period of time, a great influence on drainage. However, throughout much of the arctic and boreal regions these direct effects of rock type on the water supply of vegetation are greatly reduced, or completely cancelled, by the occurrence of near-surface permafrost. This perpetually frozen zone of the substrate exerts by far the greatest

influence on surface water in regions of low relief, and promotes the excessive wetness of the substrate surface and near-surface portions that is so widespread in arctic regions, although precipitation may be quite low. Douglas and Tedrow, after having made extensive observations of arctic soils, state (1960, p. 300), "Water cannot penetrate the tjaele." Thus we have in arctic and boreal regions a distinctive factor that negates one of the more conspicuous rock-type influences of temperate and tropical regions. The presence of bodies of water in high latitudes often provides no information as to underlying geologic formations or structure, but indicates only that permafrost is present. Further, in these regions the existence of phreatophytes as indicators of ground water related to rock type or geologic structure is precluded by the permafrost, which also isolates other plants from effective contact with bedrock (Figure 7).

4. Effect of rock type on thermal relationships to vegetation. Although the color of soils has a great effect on these relationships, their color is in general largely independent of the color of the rock from which they were derived. As rocks disintegrate in soil-forming processes, the color of the resulting material is changed by mechanical comminution, chemical combination, leaching of iron and manganese, and incorporation of organic matter. Thus the dark color of soil is rarely due to its derivation from a dark colored rock, but is caused by the presence of organic matter. A reddish colored soil is not necessarily derived from a red colored rock, but most often indicates the degree of oxidation of the iron compounds of the parent material. Limestone does not ordinarily yield a light colored soil.

Figure 7. Ground ice covered with a thin vegetation mat supporting a sedge-willow plant community, near Livengood, Alaska. Road construction immediately adjacent had altered thermal relationships and started the melting of the clear ice. The melt water formed this pool which contains fragments of the former plant community. In such situations of thick ground ice the vegetation is effectively isolated from the chemical influences of the underlying rock formation. June 21, 1960.

However, the chemical nature of the rock through its influence on soil formation may indirectly contribute to the color of soils. It is mostly the young soils (regosols, lithosols, azonal sandy and gravelly soils) that show the direct effect of parent rock color. It is well known that a light colored object because of its high light reflectance absorbs much less heat from insolation than does a dark colored one. In the high latitude environments where the low temperature is the most important factor limiting all biotic activity, this property of the substrate to reflect or absorb heat is generally more significant than in low latitude environments. Slight differences in color of the substrate in the landscape produce a multitude of microenvironments in respect to meeting critical thermal requirements of plant species, giving rise to a complex vegetational pattern often composed of small micro-communities. This effect is particularly noticeable in bryophyte societies, which in general contribute more to the total aspect of vegetation in arctic than in more temperate regions.

The accentuated thermal extremes of dark-colored rocks such as basalt and hornfels accelerate disintegration by spalling and exfoliation, thus providing niches for chasmophytes. Without this process these rocks would weather very slowly. In cold climates the weathering of rocks is effected mostly by mechanical action; in temperate climates both chemical and mechanical action are important, and in tropical climates weathering is principally by chemical action. Since the color of rocks is most directly related to mechanical rather than chemical weathering, this feature is much more important in high than in low latitudes.

5. Features of the rock surface that influence vegetation. The exact properties of a rock surface that contribute to or make possible the occupation by lichens and bryophytes are difficult to separate in degree of importance on the basis of field observations alone. However, there are some generalizations that can be made. Under optimum climate the nature of the rock surface (both physical and chemical) is usually of little importance in its total colonization by these plants. In the humid coastal regions of southeastern Alaska the vigorous bryophytes, including Hylocomium splendens "var. giganteum," Rhytidiadelphus loreus, R. triquetrus, and Polytrichum formosum, may grow indiscriminately over various kinds of rocks as well as over logs and peat deposits. As environmental conditions become less favorable for most bryophytes, principally under water shortage, the surface nature of the rocks becomes a more critical factor, and the bryophyte communities occupying them are highly selective (Figure 8). Under these conditions the factors of color, texture, rate of weathering, and chemical composition may attain critical status. It is of course obvious that the rate of surface exfoliation or fragmentation of the rocks must be less than the rate of bryophyte growth if a community is to be established. Since both of these rates are greatly influenced by microclimatic conditions, there seems to be no constant association of bryophyte species and the dark-colored rocks (shales, slates, basalt). The bryophytes growing on limestone surfaces are, for the most part, decidedly calcicolous species, as are discussed in Chapter III, paragraph B. They may be

Figure 8. Mat of Rhacomitrium lanuginosum extending over serpentine talus, near Eagle, Alaska. A few small plants of Selaginella sibirica were becoming established in the moss mat; otherwise no vascular plants were present. The moss plants had no rhizoidal attachment to the rocks or to the 1.5 inches of reddish-brown highly organic "soil" on the surface of the underlying rocks; the upper part of the moss "stems" was living, and the lower part decomposing to form the "soil" of pH 6.0 beneath. The apparent growth rate of the moss plants was .25 inch per year; individual "stems" were about 9.5 inches long, and had a calculated age of ± 38 years. The time necessary to produce the underlying "soil" could not be calculated. The invasion of Selaginella was estimated to have occurred within the last ten years. This plant community had full sun exposure. June 28, 1960.

favored by the susceptibility of this rock type to chemical etching by the plant rhizoids and the relative stability of the rock surface, in addition to the direct effect of the calcium in the rock, or the effect of this element on pH and base exchange.

There is apparently no rock surface that is too smooth or chemically resistant to be occupied by some species of lichen or bryophyte (Figure 9). Vertical surfaces of massive crystalline quartz were found to support a growth of Dicranum fuscescens, Polytrichum piliferum, and Cephaloziella byssacea at Kantishna in the Alaska Range. The writer found glass bottles around old mine workings in the Rocky Mountains of Colorado to be supporting colonies of crustose lichens an inch or more in diameter which had etched the glass under them. Highly mineralized rocks may inhibit or prevent certain bryophyte species from colonizing their surface, whereas other species can resist this toxic effect of the minerals (Figure 19). Ore-inhabiting species were observed on Latouche Island (Shacklette, 1961a), Revillagigedo Island, and at other places in Alaska. High latitude environments, with their extreme physical conditions, because of their selective effect on species, offer very favorable areas for the study of ecological amplitudes of bryophyte species in the occupation of varying rock surfaces.

B. Acidity or Alkalinity of the Substrate.

Although this property of the substrate as it affects vegetation has been discussed briefly in other parts of this paper, the differences of opinion of botanists who have studied the arctic and boreal floras of North America are such that this subject merits more careful examination.

Figure 9. Colonization of shaded serpentine bedrock by Schistidium strictum, Selaginella sibirica, and crustose lichens at West Fork, near Livengood, Alaska. Primary succession on this shaded, stable surface of bedrock differs from that of the serpentine talus in full sun exposure of Figure 8, primarily because of the less xeric nature of this site. Amount of light has influenced this community mostly through its indirect effect on the water relationships--both the Schistidium and the Selaginella grow equally well in full sunlight if their small water requirement is met. June 21, 1960.

The most complete accounts of the floras of arctic and boreal western North America (those of Hultén, 1941-1950, and Anderson, 1959) give no information about the substrates of the species listed, in most instances. Scoggan's (1957) "Flora of Manitoba" and Spetzman's (1959) "Vegetation of the Arctic Slope of Alaska" are neither consistent nor complete in giving information on substrate pH. In marked contrast, the habitat descriptions and edaphic requirements of each species are given in the two major publications on the vascular flora of the eastern North American arctic. Polunin (1940) in his "Botany of the Canadian Eastern Arctic, Part I." very systematically gives careful observations on the "occurrence" or habitats of each of the 297 species included in the work. Particular attention is given to factors of ecological significance, including the nature of the substrate, exposure, and the role of the species in the community. Porsild's (1957) "Illustrated Flora of the Canadian Arctic Archipelago" also gives an account of habitats of each of the 340 species and major geographical races that are listed.

The fact has been mentioned previously that the effective substrate of a plant community may be quite different in chemical nature from the underlying rock formation. However, a distinction should be made in the evaluation of calcicolous and oxylophylic habitats in relation to the predominant rock types of the area. There is no natural method by which a substrate can become or remain alkaline except by the influence of basic (generally calcareous) deposits. This influence may be from associated geologic formations, or from the introduction of basic particles or solutions by wind or water. On the other hand, the substrate of a plant community will by biotic processes become more acid in itself unless buffered by basic ions, regardless of the presence or absence of "acidic" rocks. Therefore the occurrence of an obligate calcicolous species is an indication of a closely associated basic rock. The occurrence of an obligate oxylophylic species does not necessarily have a parallel interpretation. Because of this difference in plant-substrate relationship, the greatest attention will be given to the species of plants reported to be calcicolous.

Polunin's report (1940) was examined for references to plant species "preference" in pH values of the substrate, and the species were arranged by the present writer according to the outline which follows. A discussion of the validity of this classification of each species is also given, with significant reports of others.

a. Species definitely (perhaps obligate) calcicolous.

1. Saxifraga aizoides. Polunin (ibid, p. 262) says, " . . . everywhere limited to soils containing an appreciable amount of $CaCO_3$, although a few transported scraps of limestone will suffice. . . It seems as strongly calciphilous as any species; indeed, having now for several years past made a point of testing the soil around the roots of specimens met in ordinary acidic country in the north, and having never yet failed to find at least some scraps that would effervesce strongly with HCl, I am inclined to look upon it not merely as an obligate calcicole but as the one species that alone is a sure sign of the presence of

$CaCO_3$ in appreciable quantity, at least in the Arctic." This species is reported by Scoggan (1957, p. 333) as growing on peaty soil in Manitoba, which indicates but does not prove an acid substrate. It was collected by the writer at Sawmill Bay, Great Bear Lake, Northwest Territories in an area exclusively of sandstone formations, and was certainly not in a calcicolous environment.

2. Saxifraga Aizoon. Polunin (ibid, p. 267) comments, "Apparently limited to calcareous areas and always producing the characteristic concretions of $CaCO_3$ around the margin of the leaves." Raymond (1950, pp. 27, 31, 54, 64) lists the variety neogaea several times, but in various category classifications, so it is not possible to relate the plant to a definite substrate; as examples, it is listed under "D'especes arctique-alpines ou tourbicoles qui s'éntendent au sud" and under "l'enclave calcaire du lac Mistassini," "La Côte-Nord," and "plantes arctiques alpines." Most probably the Lake Mistassini plants were on a calcareous substrate. This species apparently does not occur in northwestern North America.

3. Lesquerella arctica. Polunin (ibid, p. 232) says of this species, "It appears to be a marked and perhaps obligate calciphile, whose peculiarly disrupted distribution is probably bound up with this property . . . very widespread on calcareous substrata almost throughout, but apparently absent from 'acidic' areas . . . never noted as really

abundant or important." Spetzman(ibid, p. 47) reports this species growing on "limestone pebble alluvial fan" on the Arctic Slope. On the other hand, a specimen collected by Louis H. Jordal (No. 2098, University of Michigan Herbarium) bears the legend, "Scattered tufts in slate rubble on steep exposed scree slope, altitude ca. 2,000 ft., 3 mi. n. of Wiseman, Brooks Range." This species was collected by the writer from crevices in granite at Port Radium, Great Bear Lake, Northwest Territories.

4. Braya purpurascens. Polunin (ibid, p. 249) says of this species, " . . . preferring open plains or solifluction slopes of stiff clay or gravel that are rich in lime . . . indeed in the south it appears to be entirely limited to limestone areas or dumps of transferred material containing limestone fragments." It is listed from northernmost Norway by Lid (1944, p. 279) as "På kalk." Spetzman (ibid, p. 46) gives as its habitat on the Arctic Slope "Sandy flood plains at Alaktak; limestone talus, Katakturuk River." This species is so infrequently found that it is not possible at present to evaluate its pH requirement, except to say that it appears to be associated usually with limestone.

b. Species said to have varying degrees of "preference" for basic rock formations, but not considered "obligate" calciphiles.

1. Agropyron violaceum var. hyperarcticum (A. latiglume (Scribn. & Sm.) Rydb.). Reported by Polunin (ibid, p. 96) as occurring on a highly calcareous substrate. Porsild

(1957, p. 40) says, "Common on well-drained, alluvial, calcareous, sandy or clay soils of the Palaeozoic series." Gjaerevoll (1958, p. 37) reports, "In Scandinavia Agropyron latiglume is generally found on calcareous substratum. All localities referred to above were gravelly places. It is strange, however, to notice that Agropyron latiglume did not grow in the limestone area of White Mountain. This may indicate an ecological difference between the races of Alaska and Scandinavia." This species was collected by the writer in soil derived from schist at Kantishna, Alaska Range; no limestone occurred at this site.

2. Carex nardina. Polunin (ibid, p. 108) says, "The species throughout most of our area, although it may occur on almost any type of soil, shows some preference for, and grows better on, substrata rich in calcium." Hultén (1941-1950, p. 299) cites some locations for this species that could hardly be calcareous. Spetzman (ibid, p. 43) gives for its habitat "Dry slopes and meadows: limestone slopes." Gjaerevoll (ibid, p. 42) reports it to be abundant on dry limestone peaks and scree slopes.

3. Carex rupestris. Polunin (ibid, p. 119) says that it is probably common everywhere except toward the highest latitudes, often showing some preference for calcareous substrates. Spetzman (ibid, p. 43) gives its habitat as "Dry alpine meadows; rubble slopes of limestone and sandstone." Hultén's distribution records cannot be interpreted with respect to

substrate. Porsild (ibid, p. 49) says, "A pronounced calcicole." Gjaerevoll (ibid, p. 44) reports it from limestone in the White Mountains, also from serpentine of the Alaska Range.

4. Carex glacialis. Polunin (ibid, p. 121) records its occurrence as follows, "Grows chiefly but not exclusively on calcareous material." Hultén (ibid, p. 366) shows at least two locations in its Alaskan distribution where calcareous rocks probably do not occur. Gjaerevoll (ibid, p. 54) reports it as a calcicolous species. Porsild (ibid, p. 56) says, "Calcareous sandy and gravelly places." The writer has collected it only once in Alaska--on a cherty talus slope, Livengood area, Central Yukon district.

5. Arenaria humifusa. Polunin (ibid, p. 198) writes, "Like some other 'relict' species, it appears to be somewhat calciphilous." Porsild (ibid, p. 79) reports it from "moist calcareous gravels, or in moist rock crevices." This species was collected by the writer at Great Bear Lake, Northwest Territories from crevices of granite rock, and among granitic glacial pebbles.

6. Arenaria Rossii. Polunin (ibid, p. 201) considers this plant to be "apparently calciphilous." Hultén (ibid, p. 681) hesitatingly considers the Alaskan Minuartia elegans (Cham. & Schlecht.) Schischkin to be a separate species from the above, and reports it from areas that are apparently non-calcic. Spetzman (ibid, p. 45) reports M. elegans from

"sandy flood plains." Porsild (ibid, p. 80) says, "Common in not too dry, turfy, gravelly or sandy calcareous gravels." The writer has collected a plant which he considers to be A. Rossii growing on schist talus at Eagle Summit, Central Yukon district.

7. Eutrema Edwardsii. Polunin (ibid, p. 228) says, "Apparently somewhat calciphilous, but of no real ecological significance either as an indicator or as a component of vegetation." Spetzman (ibid, p. 46) lists its habitat only as "arctic and alpine meadows." Hultén (ibid, p. 820) cites localities that are most certainly non-calcic. Porsild (ibid, p. 93) reports, "The species is strongly nitrophilous and mostly restricted to calcareous soils."

8. Draba subcapitata. Polunin (ibid, p. 236) remarks, "Never found by me on any surface that was not composed mainly of limestone or dolomite; hence apparently calcicolous." Porsild (ibid, p. 98) reports, "A pronounced calcicole not uncommon in dry tundra or in gravelly places." This species is not reported from the Alaska-Yukon area.

9. Draba cinerea. Polunin (ibid, p. 345) records that it appears to be markedly calcicolous, at least in the south. Spetzman (ibid, p. 46) gives the habitat only as "dry slopes and hilltops." Porsild (ibid, p. 99) lists "calcareous rocky barrens and sunny cliffs" as its habitat. This species was collected by the writer from crevices of bare granite rocks near Port Radium, Great Bear Lake, Northwest Territories.

10. Arabis arenicola. Polunin (ibid, p. 246) says " . . . showing some preference for those (areas) that are highly calcareous." Porsild (ibid, p. 100) gives its habitat as "calcareous sand and gravel." The species apparently is not found in the Alaska-Yukon area.

11. Parrya arctica. Polunin (ibid, p. 250) finds this species "chiefly on open areas of calcareous earth." Porsild (ibid, p. 103) reports it from "wet calcareous clay and gravel barrens." This species, according to Hultén (ibid, p. 892) does not occur in Alaska, but a closely-related species, P. nudicaulis ssp. interior including its two varieties, is of widespread distribution in this state. The writer has collected one of these, var. grandiflora Hult., at Twelve Mile Summit, Central Yukon district, in an alpine meadow turf over schist.

12. Astragalus alpinus. Polunin (ibid, p. 289) states that on calcareous areas it grows taller than it does when on other substrates. Porsild (ibid, p. 119) gives its habitat as "In well-watered calcareous sandy or gravelly places." The writer collected this species on the beach ridges of Cape Krusenstern, Arctic Ocean, growing vigorously on soil varying from pH 5.2 at the surface to 4.8 in the C horizon. He also collected it from talus below granite cliffs near Port Radium, Great Bear Lake, Northwest Territories.

13. _Epilobium_ _davuricum_ var. _arcticum_ (_E_. _arcticum_ Samuelss.). This variety is listed by Polunin (ibid, p. 302) as "apparently calciphilous." Hultén (ibid, p. 1,147) shows the typical species occurring at some locations which are most probably not calcareous. Scoggan (ibid, p. 406) lists it as occurring in muskegs. Porsild (ibid, p. 127) cites it as "Rare, in wet clay in tundra barrens."

14. _Androsace_ _septentrionalis_. Polunin (ibid, p. 320) says it " . . . grows chiefly in open areas of (probably calcareous) clay or gravel." Spetzman (ibid, p. 49) lists it as occupying "dry cutbanks and shale outcrops." Porsild (ibid, p. 134) lists it as "A polymorphous species growing in not too dry, calcareous, sandy or gravelly places." The writer found it on highly acid soil at Cape Krusenstern on the Arctic Ocean, on serpentine soil and talus at Mission Bluff by Eagle on the Yukon River, and on sandy banks derived chiefly from schist at Livengood.

15. _Chrysanthemum_ _integrifolium_. Polunin (ibid, p. 361) observes that it "seems to be somewhat calcicolous." Spetzman (ibid, p. 50) gives its habitat as "coastal dry ridges and dry alpine meadows." Porsild (ibid, p. 149) lists it from "Stony, calcareous barrens."

16. _Crepis_ _nana_. Polunin (ibid, p. 374) comments that it is "said to grow in dry calcareous areas." Spetzman (ibid, p. 50) lists its habitat as "shale outcrops and dry sandy flood plains." Many of Hultén's citations (ibid, p. 1,664) appear not to be

from calcareous areas. Porsild (ibid, p. 155) gives its habitat as "Dry, calcareous screes or gravel." The writer has collected this species from scree and talus of several different rock types, none of which are calcareous.

17. Deschampsia brevifolia. Polunin (ibid, p. 54) says of this species, "Fairly frequent in the north on open gravelly or muddy areas, showing a marked preference for those that are highly calcareous and lastingly damp in summer, and hence characteristic of solifluction slopes and polygon 'rutmarks'." This species is apparently included in the D. caespitosa (L.) Beauv. complex by Hultén (ibid, p. 173-175). He records species of this group from places where there are almost certainly no limestone or other non-acid rocks. Porsild (ibid) does not mention calcareous habitats for this species.

18. Salix calcicola. Of this species Polunin (ibid, p. 170) remarks, "Fairly common in its area, and sometimes abundant to dominant on open calcareous soils even in rather dry and exposed plateau land such as that of Akpatok Island." Scoggan (ibid, p. 235) reports it from "York Factory, gravel beach and floodplain of Hay Island." This species is not found in the Alaska-Yukon region, but a related species, S. Richardsonii Barratt is cited by Hultén (ibid, p. 538-539) from many localities in Alaska that are probably non-calcic. Porsild (ibid, p. 66) gives the habitat of S. calcicola as "Calcareous rocky and gravelly places." The writer has

collected S. Richardsonii from quartz sand at Sawmill Bay, Great Bear Lake, Northwest Territories.

C. Species believed to be definitely oxylophilic.

1. Lycopodium Selago. Polunin (ibid, p. 37) says that it grows from dry heaths to wet marshes, however seeming to avoid pure limestone. Porsild (ibid, p. 20) states that it occurs "chiefly on Precambrian rocks." Gjaerevoll (ibid, p. 17) says that it grows "on calcareous as well as on acid rocks." Spetzman (ibid, p. 41) lists the habitat of the var. adpressum Desv. as "Moist crevices in outcrops of limestone, shale, conglomerate, schist, and basalt; mossy slopes." The writer has observed the species growing on rather barren limestone slopes in Interior Alaska.

2. Luzula confusa. Polunin (ibid, p. 142) says, "The species is generally absent from limestone or exclusively dolomite areas." Spetzman (ibid, p. 43) makes no comment as to its pH requirements but shows it to occur in all ten of his distribution areas, and at all altitudes. This strongly indicates that on the Arctic Slope it is not exclusively oxylophilic. Porsild (ibid) does not mention its pH relationships. Gjaerevoll (ibid, p. 65) reports it from limestone sites in Interior Alaska. The author has collected it in Alaska from schist in the Alaska Range, highly acidic beach ridges at Cape Krusenstern, Arctic Ocean, and in chert rubble at Livengood, Interior Alaska. Throughout its range the species seems to be largely indifferent to soil acidity or alkalinity.

3. Saxifraga rivularis. Polunin (ibid, p. 253) says it is "markedly calcifugous." Spetzman (ibid, p. 47) lists it as in "coastal sandy beaches, late-snow areas in small alpine valleys." Porsild (ibid, p. 109) lists it only as "A pronounced nitrophile." The writer has collected it only near the Maclaren Glacier in the Alaska Range at an altitude of 4,310 feet, from a snowbed that was well irrigated. The pH of the substrate did not appear to be the important factor in its occurrence, but more data is needed on this point.

4. Cassiope tetragona. Of this species Polunin (ibid, p. 311) says, " . . . it is liable to be found almost everywhere, although growing poorly on limestone that is not well covered with humus." The writer's observations are that it grows poorly on any kind of rock that is not well covered with humus. Porsild (ibid,p. 131) says it is "A dominant or even ubiquitous arctic species . . ."

5. Antennaria spp. Polunin (ibid, p. 348-349) in speaking of the species of this genus, says, "All seem to be calcifugous . . ." However, the suggested tendency of this genus in this respect needs more investigation. A specimen of A. alaskana Malte collected by Louis H. Jordal (No. 3636, University of Michigan Herbarium) in the Brooks Range was, according to the label, growing "in limestone rubble." Several other species found by this collector are suspected of having been growing in a calcareous substrate because of their geographical location, although the labels do not specifically state this.

Porsild (ibid, p. 147-148) comments on some arctic species as follows:

A. angustata Greene - "non-calcareous"

A. Ekmaniana Porsild - "non-calcareous"

A. subcanescens Ostenf. - "calcicolous"

A. compacta Malte - "calcareous"

A. canescens Porsild - "common on dry and non-calcareous slopes."

A. glabra Porsild - "on calcareous soil."

Dr. Porsild is the recognized authority on this taxonomically difficult genus, and has also done extensive field work in this area. His comments above are doubtless based on numerous observations, but he does not state specifically if these are obligate tendencies. At any rate, it is apparent that the genus as a whole has a wide tolerance for substrate pH values, and is not definitely calcifugous.

d. Summary. The following table summarizes the remarks of Polunin regarding the substrate chemical relationships of his 297 species of vascular plants:

Species definitely (perhaps obligate) calcicolous . .	4
Species with various calcicolous "preferences" . . .	19
Species with oxylophylic tendencies	5
Total indicated to have a pH "preference"	28 = 9.4%

By examining the known or reasonably inferred substrate relationships of these species designated by Polunin as having a pH requirement or "preference," as reported in the literature, shown in herbarium specimens, or observed by the writer, the following revision of the above table may be made:

Species definitely (perhaps obligate) calcicolous . . 2

Species probably having a calcicolous "preference" . 7

Species with definite oxylophilic tendencies 1

Total species probably having a pH requirement or "preference . . . . 10 = 3%

e. Classification of Porsild. Porsild's (1957) discussion of habitat requirements of arctic plants is such that these species can easily be divided into the following categories in respect to pH requirements (the asterisk indicates that the species occurs in Alaska):

Obligate calcicoles --

1. Juncus castaneus. * Spetzman (ibid, p. 43) says of this species, "Sandy margins of streams and lakes." The writer has collected this plant on non-calcareous soil in Alaska, on quartz sand at Sawmill Bay, Great Bear Lake, and on weathered granite at Port Radium, Great Bear Lake, Northwest Territories.

2. Festuca baffinensis. *

3. Braya humilis. *

4. Saxifraga caespitosa ssp. uniflora. * The subspecies sileneflora occurs in Alaska, of which Spetzman (ibid, p. 47) writes, "Coastal sandy beaches, sandbars, late-snow areas, and crevices in sandstone and limestone."

5. S. flagellaris. * Spetzman (ibid, p. 47) says, "Dry alpine meadows, mountain slopes of limestone, sandstone, shale, conglomerate, and basalt."

6. S. tenuis. *

"Decidedly" or "Pronounced" calcicoles --

1. Poa abbreviata. *

2. Eriophorum triste. *

3. Kobresia simpliciuscula. *

4. Carex rupestris. * Spetzman (ibid, p. 43) says, "Dry alpine meadows; rubble slopes of limestone and sandstone."

5. Cerastium arcticum.

6. Arenaria Rossii. * (discussed above in Polunin's list)

7. Eutrema Edwardsii. * (discussed above in Polunin's list)

8. Draba Bellii. *

9. D. cinerea. * (discussed above in Polunin's list)

10. D. groenlandica.

11. Parrya arctica. (discussed above in Polunin's list)

12. Arctostaphylos rubra. * Described by Spetzman (ibid, p. 49) as occurring on "Dry alpine slopes, dry bevel along river terraces, sandbars, and crevices in sandstone and limestone." Found in abundance by the writer around Great Bear Lake, Northwest Territories, not associated with limestone.

13. Primula stricta. *

14. Androsace Chamaejasme var. arctica. * The var. Andersonii Hult. was found by the writer in great abundance on acid beach terraces at Cape Krusenstern, Arctic Ocean.

15. A. septentrionalis. * (discussed above in Polunin's list)

16. Plantago septata. *

17. Erigeron compositus. * Found by the writer in non-calcareous soil at Great Bear Lake, Northwest Territories. The var. discoideus Gray was found on Mission Bluff at Eagle on the Yukon River by the writer.

18. Erigeron eriocephalus. * Reported by Spetzman (ibid, p. 50) on "Dry meadows, cutbanks and sandbars."

19. Crepis nana. * (discussed above in Polunin's list)

Recorded as occurring in calcicolous habitats --

1. Equisetum variegatum. * This species has been collected near Fairbanks, Alaska in schist-derived sand, and in quartz sand at Sawmill Bay, Great Bear Lake, both by the writer.

2. Carex scirpoidea. * Spetzman (ibid, p. 43) says of this species, "Dry meadows, alpine rubble slopes of limestone, sandstone, conglomerate, shale, and chert; also on river sands and gravel." It was collected by the writer on non-calcareous substrate at Port Radium, Great Bear Lake.

3. Juncus albescens. * This species was collected by the writer on non-calcareous substrate at Port Radium, Great Bear Lake.

4. Tofieldia coccinea. * The writer collected this species on quartz diorite talus on Yakobi Island, Alaska.

5. Anemone ludoviciana. *

6. Hedysarum Mackenzii. * Spetzman (ibid, p. 48) records this species from "Sandy flood plains." The writer collected it on non-calcareous substrate at Glacier Bay, Great Bear Lake.

7. Chrysanthemum integrifolium. * Collected by the writer on mossy humus overlying metamorphosed sandstone at Coppermine, Northwest Territories.

Obligate oxylophiles --

1. Empetrum nigrum. *

"Pronounced" oxylophiles --

1. Arctostaphylos alpina. *
2. Campanula uniflora. *

f. Summary. The following table summarizes the classification of Porsild regarding the substrate chemical relationships of his 340 species and major geographical races of vascular plants:

Species considered obligate calcicoles	6
Species considered "pronounced" calcicoles . .	19
Species noted in calcicolous habitats	7
Species considered obligate oxylophiles . . .	1
Species considered "pronounced" oxylophiles . .	2
Total indicated to have pH requirements or "preference"	35 = 10.2%

g. Conclusions. By comparing Porsild's list of plants considered to have certain pH relationships in his area with other records in the literature, herbarium specimens, and observations of the writer the following revision may be made:

Species definitely (perhaps obligate) calcicolous . . .	3
Species probably having a calcicolous "preference" . .	8
Species with definite oxylophilic tendencies	3
Total species probably having a pH requirement or "preference"	14 = 4.4%

It is interesting to note that both Polunin's and Porsild's lists of plants considered to have a pH requirement or "preference" comprise about 10 percent of the total species listed. It is also noteworthy that when these lists were revised by the writer, one was reduced to 3 percent and the other to 4.4 percent. Although the areas described by these authors are overlapping (Polunin's going farther south and east, Porsild's extending farther north and west) and the two lists have a large percentage of species in common, only eight species are stated by both writers to have pH preferences, as follows (Porsild's phytogeographic classification follows each species):

Androsace septentrionalis (Circumpolar arctic alpine)
Arenaria Rossii (North American radiant)
Carex rupestris (Circumpolar arctic alpine)
Chrysanthemum integrifolium (North American radiant)
Crepis nana (North American radiant)
Draba cinerea (Circumpolar, low arctic)
Eutrema Edwardsii (Circumpolar high arctic)
Parrya arctica (Arctic archipelago endemic).

Two species listed by Polunin have tendencies that are difficult to explain-- Draba cinerea (" . . . appears to be markedly calcicolous, at least in the south") and Puccinellia Vahliana ("Fairly common in the north but rare in the south, where it seems to be limited to calcareous areas . . ."). The opposite tendency is recorded by Renaud-Beauverie (1936, p. 162-163) who, in speaking of the indirect action of calcium on vegetation, says, "Les vegétaux qui aiment la sécheresse sont de plus en plus liés, au fur et a mesure qu'on monte vers le

Nord, aux sols calcaires, parce qu'eux seuls leur offrent les conditions physiques qui leur permettent de vivre (échauffement rapide, bonne conduction de l'eau, bonne aération). Il en résulte que de nombreuses plantes réputées comme calcicoles dans le centre et l'est de la France sont indifférentes dans le sud; par example: Melica ciliata, Carex Halleriana, Hippocrepis comosa, Coronilla minima, Prunus mahaleb, Vincetoxicum officinale, Euphorbia Sequieriana. La réciproque n'est pas vraie et il est des plantes pour lesquelles les propriétés physiques du sol ne peuvent compenser l'absence de Ca, qui exerce outre son action physique sur le sol, un action chimique directe sur les plantes mémes." Porsild (1955, p. 42) agrees with Renaud-Beauverie by saying, "In the Arctic, the problem of edaphic discontinuity is further complicated by the fact that warmth-loving plants near the northern limits of their range tend to become facultative calcicoles, often confined to stony, calcareous soils. The reason may be that these soils alone afford them optimum physical conditions of temperature, water supply, and aeration."

The apparent physiological response of plants to substrate pH is not easy to explain because of the complicated relationships of soil chemical reactions, some of which have been already discussed. Calcium has many effects on the soil solution, and its effect on pH is only one of these. Therefore plant species that are found to be definitely calciphiles may have unusually high requirements for calcium in their metabolism, may have a higher than normal nitrogen requirement which is more adequately supplied in an alkaline soil, or may be dependent on physical characteristics of the soil imparted by the presence of large amounts of calcium. Burd's (1949, p. 388) analyses of plant tissues and the soils supporting them showed the calcium content of tissues to be a function of inherent capacity, rather than related to the amount in the soil.

It should be emphasized that the mere presence of limestone in the soil does not necessarily indicate that the soil solution is basic. Further, the substrates of arctic and north boreal regions are generally high in peaty organic matter, but it does not necessarily follow that peat soils must be low in calcium because they are highly acidic, as a rule. Lyon and Buckman (1937, p. 225-226) make the following pertinent comments: "The high lime content of peat soils is easily explained. Much of the water entering swamps is from seepage and has had ample opportunity of dissolving lime in its passage through the subsoil and substratum. Moreover, many swamps contain a deposit of bog lime or other calcareous matter in their lower profile. Consequently the waters in which swamp and bog plants live and decay are often heavily charged with calcium acid carbonate. As a result the living plants probably absorb considerable quantities of calcium. And since decaying organic matter is highly adsorptive and the calcium ion exceedingly mobile, the resulting peat soil cannot avoid the presence of large amounts of exchangeable calcium ions. Nor is leaching, as with mineral soils, such an important factor in robbing the surface layers of lime. High lime is an outstanding characteristic of most peat soils.

"In spite of this high lime content, many peat soils are distinctly acid. For instance, the average pH of twelve woody peat soils from Oswego County, New York, was 5.3 in spite of an average CaO content of

3.74 per cent. Cases even more striking are available. At first glance such a condition seems rather anomalous especially when it is remembered that high acidity in a mineral soil is correlated with low calcium. This explanation is offered. The adsorptive capacity of peat for exchangeable cations is exceedingly high, so great in fact that such a soil may carry an exceptionally large amount of calcium and yet contain a preponderance of exchangeable hydrogen. Under such a condition the dominance of the H ions will by equilibrium adjustments maintain an acid soil solution in the presence of large quantities of calcium. It must not be forgotten that we are dealing here with the soil solution and not with the alkaline drainage water lower down in the profile."

In discussing the ecology of bryophytes Richards (1932, p. 382-383) says, "Amann has rightly pointed out that many authors decide the presence or absence of lime on quite insufficient evidence. A species is often labelled calcicole or calcifuge merely because it is found on certain geological formations, but calcifuge species are often found on limestone, either because of leaching or because there is a superficial layer of acid humus. Calcicole species may be found on rocks supposed to be non-calcareous, because of the presence of calcareous inclusions, flushes from neighbouring limestone, or the transport of calcareous dust by the wind. Often on rocks containing a small proportion of lime, though the vegetation is in general calcifuge, calcicole mosses are found near springs. . . . It is quite possible that some species are 'calcicole' for one reason and some for another, i.e., there is no need to assume that the 'calcicole' mosses form a homogeneous ecological group. The same is of course true for the 'calcifuge' species." These same comments apply with equal validity to vascular plants.

h. General summary. This discussion of the relationships between the occurrence of basic geologic formations and the occurrence of certain plant species or plant communities may be summarized as follows:

1. Surficial deposits (not the bedrock deposits) may constitute the parent material of the soil, thus the soil may not be related to bedrock.

2. Permafrost may permit plants to grow only in the upper layers of the substrate, which are often largely organic, and have only an indirect relationship to the mineral soil parent material.

3. There are very few species of vascular plants of these regions that may be considered calcicolous or oxylophilic. These species, no doubt, have certain extremes of pH tolerance, and there are likewise optimum pH values for the species, but the range appears to be rather wide, and the pH effect on vegetation as a whole is masked by other predominant aspects of the northern environment. Polunin (1948, p. 140) describes the relationships of an apparent calcicolous plant community as follows: "Several of the above-mentioned phanerogams, such as Saxifraga aizoides, Carex glacialis, and Chrysanthemum integrifolium, as well as some others (e.g., Saxifraga aizoon and Salix calcicola) which did not occur in the quadrat listed, appear to be confined to these calcareous areas. Nevertheless, the more luxuriant heath developed under more favorable conditions of shelter and snow-covering is much the same whether basic or acid-weathering rocks form

the substratum; even the cryptogams, which include many mosses and fruticose lichens of good growth, tend ultimately to be similar. This is especially the case where humus has accumulated and so raised the surface that the reaction is neutral or slightly acid (in spite of the limestone)."

4. The nature of the underlying rock formations in boreal and arctic regions is not clearly and regularly indicated by the species of plants or plant communities growing above them. This is in contrast to these relationships as they so often obtain in more temperate regions.

5. It is interesting to note that no arctic or boreal species of the Family Ericaceae are considered by any of the authors quoted above to have oxylophilic tendencies, and this is also the observation of the writer. This is in marked contrast to the oxylophilic nature of many species of this family which occur in temperate zones. It is likewise noteworthy that the species of the Family Leguminosae are not considered to have calcicolous tendencies in the northern regions. Further, the Genus Primula has only one species that is reported to be calciphilic in high latitudes; this contrasts strongly with the well-known alkaline requirements of the cultivated greenhouse species (Primula obconica, P. sinensis, and P. malacoides, all from China). The seeds of these latter species germinate poorly and few seedlings survive on an acid substrate, such as sphagnum or peat, which must be employed as the common seed-germinating medium by most arctic and boreal species.

i. Conclusions. We may characterize the flora of the arctic and boreal regions of North America as being generally indifferent to pH of the substrate as a controlling factor in their distribution, since about 96 percent of the species occur in the presence of both "acidic" and basic rock formations somewhere in their total range. The one factor which cannot be evaluated in this study is the possible occurrence of biotypes of the various species, which would make comparisons of ecological amplitudes of so-called "species" invalid in this respect. It is thus quite possible that Polunin's observations are entirely valid for a "species" in his region, and that conflicting observations of the writer and others on the same "species" as it occurs in other arctic regions are equally valid. The results of this study, from whatever viewpoint they are examined, point to the general wide ecological amplitude of arctic and boreal "species," <u>sensu lat.</u> Whether this amplitude consists in adaptability of "species" that are genetically constant in their reaction to a wide variation in physiological requirements, or whether it is because of the existence of many physiological biotypes of a species each having a genetically-controlled adaptation to a narrow or wide range of environmental factors cannot be determined at this point. It is suspected that both conditions exist, but extensive studies would be necessary to determine which is the controlling condition in any certain species. The cytological studies of arctic plants by Löve and Löve (1957) represent an approach to this problem.

C. Nitrogen Relationships.

In contrast to the other essential elements for plant growth which may be limiting factors, nitrogen is not originally supplied to the substrate by the disintegration of rocks (certain rare cases excepted), but by complex, mostly biochemical, processes that utilize the atmosphere as the reservoir from which nitrogen is withdrawn and to which it may eventually return. The supply of nitrogen in the substrate is, therefore, only indirectly related to rock type in that the disintegration products of the rock chemically or physically promote or inhibit the biological processes that determine the amount of nitrogen. In nature, nitrogen in a chemical combination that is usable by higher plants is added to the ecosystem only by the activity of nitrogen-fixing organisms and by precipitation. Within the ecosystem the processes relating to nitrogen are those of chemical transformation of the nitrogen compounds and their recycling through the organisms of the ecosystem. The extremely mobile nature of this element makes these changes possible, and at the same time, contributes to the ease with which it is lost from the ecosystem by volatilization of certain of its compounds, and the solubility of others which makes them susceptible to ready removal by drainage. Its effectiveness in plant metabolism is in relation to this mobility; any factor that permanently reduces nitrogen mobility reduces the influence of nitrogen on the ecosystem. It is in this context that nitrogen relationships in the arctic and boreal regions often show a great difference from those characteristic of more temperate zones. In a well-developed plant community ("climax" in Clementsian terminology) of temperate or tropical zones, the nitrogen economy of the ecosystem comes into dynamic balance, with the input equalling the loss, with as high a nitrogen level held in the ecosystem as the other environmental factors permit. This nitrogen is all presently or potentially mobile; the temporarily immobile forms constitute a short-term reserve, in comparison to the life span of the community. Thus a high efficiency of nitrogen utilization, and a corresponding highly productive plant community, may result. In many arctic and boreal plant communities the nitrogen economy never comes into a dynamic balance; the substrate continues to gain nitrogen indefinitely in excess of loss, but this gain represents immobilized nitrogen withdrawn from recycling by organisms. The result is a low level of nitrogen utilization in the ecosystem and a corresponding plant community of low productivity.

Successional phases of vegetation in temperate zones progress on a nitrogen "impetus" of the substrate as a result of nitrogen compounds produced by prior vegetation and temporarily held in the substrate. In many arctic and boreal regions this successional "impetus" is greatly reduced--much of the nitrogen produced by prior vegetation is permanently immobilized in the highly organic substrate. Senstius (1925) states that mean soil temperatures of about 20 degrees C favor the accumulation of organic matter in soils, mean soil temperatures of about 30 degrees C favor its decomposition and consequent decrease, and at temperatures of about 25 degrees C the two phenomena are in equilibrium.

These concepts may be clarified by the example of a plant community observed on Yakobi Island, Alaska. The lower part of Bohemia

Basin on this island contains a soligenous bog of approximately ten acres in extent (Figure 10). Prospectors on the island reported that drilling had shown the bog to be as much as 120 feet in depth to bedrock. If we could calculate the amount of total nitrogen held in this deposit, based on a conservative figure of two percent nitrogen in peat, we would then visualize this bog as holding an enormous tonnage of nitrogen. Yet most of the bog surface is populated with a small leafy liverwort (Anthelia julacea) and occasional clumps of Sphagnum balticum through which twine depauperate specimens of Andromeda polifolia and Oxycoccus microcarpus (other species present, of low abundance-cover value, are presented in Chapter IV, paragraph C.). This is a community of extremely low productivity, yet it exists on a rich accumulation of perhaps its most important limiting mineral element--nitrogen. Here each year's supply of nitrogen is received largely from precipitation and the limited nitrogen-fixation that can occur under these conditions, the nitrogen is combined to form proteins, and the plant tissues that die annually carry most of this nitrogen into perpetual immobilization as the tissues are buried in the highly acid water and peat. Decomposition of these tissues, which alone can return the nitrogen into organic recycling, occurs at a decreasingly low rate, and finally ceases entirely at some (presumably shallow) depth beneath the surface. Thus the peat deposit slowly increases in thickness as the oligotropic vegetation continues at its low rate of productivity.

For a contrast between arctic climates and temperate and tropical climates in the production and decomposition of organic matter the

Figure 10. Soligenous bog in Bohemia Basin, Yakobi Island, Alaska. The dominant ground cover is a small leafy liverwort, Anthelia julacea. The elevated ridge in the foreground is vegetated with Phyllodoce glanduliflora, Vaccinium uliginosum, Luetkea pectinata, and Cassiope Stelleriana. Pinus contorta is the only tree growing in the flat portions (extreme left center), and Tsuga heterophylla is the most common tree on the ridges and bog margins. June 25, 1957.

following statement by Baldanzi (1960, p. 527) is given: "In an ambient lacking in climatic phenomena which limit the vegetation of the plants, it is not only the great mass of organic materials produced that must be considered, but also the continuousness of its production. While in temperate climates there is disposability of vegetal residue only in the autumnal season, in tropical regions the production and accumulation of residue is continuous." It should be noted that here the decomposition of residue is also continuous.

The essential processes of the nitrogen economy of plant communities, with special consideration of modifications and compensations imposed by a cold climate, are discussed in more detail in the paragraphs that follow.

a. Non-symbiotic nitrogen fixation. This process is sometimes termed "azofication" because of the prominence of the Azotobacter group of organisms in the process, but other organisms, including some of the fungi and blue-green algae, have the same ability. Micro-organisms of this type are generally distributed in soils, and the optimum temperature environment for most of them roughly coincides with that of the growing season of ordinary temperate zone plants. Meyer, Anderson and Böhning (1960, p. 344) state, "It is conservatively estimated that the saprophytic nitrogen-fixing bacteria add, on the average, about 6 pounds of combined nitrogen to each acre of soil each year." This reference is to the agricultural lands of the United States. Lyon and Buckman (1937, p. 298) give a higher figure for this accumulation, and write, "Considering the data quoted, meager as they are, it is perhaps fair to assume that azofication fixes in the representative arable soil as much as 25 pounds of nitrogen an acre a year. This is of the same order of magnitude as the removal by volatilization. For purposes of rough calculation it is perhaps not far wrong to consider that volatilization and azofication approximately balance each other." It is suggested that this same balance may be generally attained in far northern environments, for although azofication is presumed to occur at a greatly reduced rate, the prevailing low temperature also reduces the amount lost by volatilization, and is thus a compensating factor in maintaining a nitrogen supply in the substrate.

Organisms of the Azotobacter group are particularly sensitive to calcium deficiency in the substrate. They are not sensitive to acidity *per se*, but because the "available" calcium and the hydrogen ion concentration are usually inversely related, when the pH is lower than 5.5 azofication is greatly reduced. It is apparent that many northern plant communities can obtain but little nitrogen by azofication, because of the presence of a highly acid active soil layer, and because of the short growing season when temperatures are high enough to permit the process to occur. Skinner and Nygard (1930, p. 560) report on Azotobacter in peat soils as follows: "Fifty-five peat soils were examined for the presence of Azotobacter species. Peat soils, like mineral soils, supported Azotobacter only when at a pH of about 5.9 or above, although some of the soils are anomalous as regards the tolerance of acidity on the part of so-called 'calciphilic' crop plants. *A. chroococcum* was found in the more basic soils, and *A. beijerinckii* in the soils near the critical reaction (pH 5.9). One of the soils which had been previously fertilized with flowers of sulphur was the only one found to contain Thiobacillus thiooxidans."

It has been amply demonstrated that an undisturbed grass sod is especially favorable to azofication in temperate regions of low summer rainfall (Lyon and Buckman, 1937, p. 297-298). This is explained by these authors as a result of the incorporation into the soil of vegetation with a wide nitrogen-carbon ratio (i.e., total soil nitrogen is much less than total carbon in the organic matter) which provides abundant food for these microorganisms. An additional cause of increased azofication may be the pronounced calcium cycling ability of grasses, by which this element is concentrated in the upper, more biologically-active soil horizons (Byers and others, 1938, p. 970). A unique plant community dominated by grasses was found on Calico Bluff, Yukon River in eastern Alaska in which this process of calcium cycling and even calcification was very pronounced. The vigor of the plants, which grew below a steep slate slide that supported little vegetation, suggested that the increased calcium content of the upper soil horizons resulted in increased azofication. This community, and the soil profile developed with it, are considered in Chapter IV, paragraph C, but it should be mentioned here that adequate soil aeration, and high temperature because of its southern exposure, were the principal causal agents in this community development--both features being conducive to azofication.

b. Symbiotic nitrogen fixation. Organisms responsible for this process, which are mostly bacteria of the genus Rhizobium, are widely distributed in soils, and it is thought that while living saprophytically, may fix some atmospheric nitrogen. However, their importance in the nitrogen cycle is not fully expressed until they enter into symbiotic relationship with vascular plants. These plants are mostly of the Family Leguminosae, although a few species of other families may serve as hosts, including species of the genus Alnus (Goldman, 1961, p. 282-288). This bacterial relationship of these plants enables them to grow well in a soil very low in available nitrogen, if the soil is adequately aerated and if other environmental requirements are met.

The effect of this process in increasing the available nitrogen supply of the soil is believed to be of less importance in many arctic and boreal plant communities than it is in typical temperate zone communities. The nitrogen, produced in the root nodule, is mostly assimilated by the host plant, but, according to Meyer, Anderson and Böhning (1960, p. 342-343), "Under certain conditions some of the nitrogen-containing compounds in the nodules may move out into the surrounding soil where they can be absorbed by other species of plants. The quantity of nitrogenous compounds lost by nodules into the soil ordinarily is small and appears to be determined by the relative rates of photosynthesis and nitrogen fixation. Loss of such compounds from the nodules into the soil apparently occurs only when photosynthesis in the legume is sufficient to induce a favorable rate of nitrogen fixation but insufficient to build up an excess of carbohydrate. When carbohydrates are present in amounts greater than necessary to insure favorable rates of nitrogen fixation, they combine with the nitrogen compounds released by the bacteria, thus largely preventing loss of such compounds to the soil. Sloughing off and decay of root tissues of legumes is undoubtedly a more important source of nitrogen compounds in the soil than outward diffusion of soluble nitrogen compounds from their living roots."

The principal addition of nitrogenous compounds to the substrate is obviously that amount returned by the dead plant itself, because that is where most of these compounds are held. In a more temperate climate, where the decomposition of vegetation is more nearly complete and rapid, this protein nitrogen in plant tissue is quickly returned to the substrate as ammonia, nitrites, and nitrates, which are then available to succeeding generations of all plants in the community--both legumes and non-legumes alike. In the far northern regions, however, decay of the leguminous plant (as well as all other plants) may be slow and incomplete, resulting eventually in a deep organic accumulation on the soil still containing much of its original nitrogen content in a form not available for subsequent plant growth. Symbiotic nitrogen-fixation benefits the individual leguminous plant involved, but not much additional nitrogen is made available to the plant community. Thus it is believed that leguminous plants as members of a plant community do not have as much significance in these northern regions as they do in temperate climates, and that this represents another distinctive feature of cold climate regions.

c. Nitrogen compounds added to the soil by precipitation. Lightning discharges cause gaseous nitrogen and water vapor to unite, forming nitrous and nitric acid. Ammoniacal nitrogen occurs in the atmosphere, having been formed by the decomposition of organic materials. These compounds of nitrogen, which are readily assimilated by vascular plants, are washed out of the atmosphere by rain and snow, and are deposited in the soil. Schreiner and Brown (1938, p. 364) state that at Ottawa, Canada 4.42 pounds of ammoniacal nitrogen and 2.16 pounds of nitrate nitrogen are brought down in rain per acre per year, a calculation based on 10 years of record. It is assumed that perhaps less is provided by this source in more northern regions, because of less frequent lightning and less organic decomposition occurring there, but this effect may be modified by massive air movements carrying in gaseous nitrogen compounds from more southern regions. Whatever the amount added to the soil by these processes, its relative importance in the northern regions is much greater than it is in more temperate zones, because of the relatively small amounts added to far northern soils by soil organisms. Furthermore, much of the amount that is deposited in a soluble form is either used immediately by the plants, or held in the snow and ice until the beginning of the growing season. As has been mentioned earlier in regard to phosphorus, the arctic and north boreal climate does not favor loss of soluble elements by surface runoff and percolation, and thus compensates, in part, for the small amounts of nitrogen added annually to the soil.

d. The release of nitrogen by organic decomposition. The immobilization of nitrogen in the form of protein compounds has been previously discussed. If this nitrogen is to be changed into compounds that can be used by the vascular plants at least some of the following microbial processes must occur: decay, ammonification, and nitrification. Burning is excluded from consideration at present. Decay is accomplished by a variety of soil organisms; as a chemical process, it is the enzymatic hydrolysis of proteins to form complex amino-compounds and liberate carbon dioxide. The amount of these amino-compounds that is not used by the decay organisms themselves constitutes a surplus that may be (1) absorbed by mycorrhizal fungi and some of it passed directly to the host plant, or (2) transformed to the ammonium form by ammonification organisms. Chemically this process is enzymatic oxidation and hydrolysis of the amino-compounds to form ammonium compounds (usually ammonium carbonate, $(NH_4)_2CO_3$).

The function of ammonium carbonate in plant nutrition of arctic and boreal plant communities is believed to be of greater relative importance here than it is in more temperate climates, because of environmental conditions in the north (low temperature, high acidity, and low lime content of the substrate) which prevent or reduce nitrification, the next step in simplification. The ammonium carbonate may be (1) used by the producing organisms themselves, (2) absorbed by mycorrhizal fungi and some of it passed to the host plant, (3) used directly by many species of vascular plants, and (4) used by nitrite bacteria in the nitrification process. Some nitrogen may be lost into the atmosphere in the form of ammonia in the process of ammonification before the ammonia is joined to the carbonate radical, but the usual abundance of carbon dioxide released by decay ordinarily reduces this loss to a minimum.

It should be mentioned at this point that ammonium carbonate is derived not only by direct decomposition of plant remains, but is also produced by the decomposition of urine and excreta of animals by the action of urine-fermenting bacteria (Escherichia coli, Proteus *vulgaris*, *Pseudomonas fluorescens* and some other microorganisms (Braun-Blanquet, 1932, p. 237). The importance of this process in northern ecosystems is discussed in sub-paragraph g, which follows.

Although a high pH of the soil solution favors the intake of NH_4 ions by vascular plants (probably because under such conditions the absorbing surface of the rootlets carry a negative charge, and there is more chance of the acid radical accompanying the NH_4 ion being neutralized), the absorption of these ions does occur in an acid solution and many plants apparently are "forced" to use this form of nitrogen because of deficient nitrification in their environment. This is believed to be particularly important with plants growing in a high acid, low available lime substrate, such as bogs and tundras. It is then apparent that the relative ability of plant species to use this form of nitrogen becomes an important factor in determining species composition of plant communities under these conditions of low nitrification.

The rate of ammonification is favored by a circumneutral pH, abundant aeration, and medium moisture content of the substrate. Antagonistic to this process in much of the far north is the accumulation of undecayed plant remains mentioned above, which increases the acidity, thereby favoring the still-greater accumulation of undecayed organic matter. In much of this region a moderate soil water content is not maintained during the growing season (which is concurrent with the period of greatest microbial activity)--the Bog, Half-Bog, and Tundra soils are too wet, and the Lithosols and Regosols are frequently too dry.

We may summarize by saying that the environment here is often unfavorable for ammonification, that these detrimental conditions are ordinarily not ameliorated by continued vegetational development but may be intensified; however, such ammonification as does occur is relatively more significant in plant community development here than it is in more temperate zones because of the environmental suppresion of the other microbial nitrogen-releasing processes.

Nitrogen in the form of nitrates (HNO_3) is by far the most important in the metabolism of the majority of plant species and is the form most used by plant communities in general. The two-step oxidation process by which ammonium compounds (principally ammonium carbonate) are transformed is termed nitrification. The first step of this process produces nitrite (HNO_2) by the action of nitrobacteria of the genera Nitrosomonas and Nitrosococcus and is favored by the presence of calcium and magnesium. Nitrite nitrogen cannot be used in the metabolism of vascular plants, and is, in addition, highly toxic to them in any concentration. However, it does not accumulate in the soil, but is immediately absorbed by the nitrate bacteria of the genus Nitrobacter. These bacteria oxidize the nitrite one step farther to form nitrate (HNO_3). The nitrate so formed may be (1) used by the microorganisms themselves, (2) used by vascular plants, (3) lost to the soil in drainage water, and (4) volatilized and thus returned to the atmosphere.

The conditions favoring the process of nitrification are: adequate light, soil moisture content up to the capillary saturation of the soil, adequate aeration, circumneutral to alkaline soil solution, and warm temperatures. These requirements are met in varying degrees by the many micro-environments of arctic and boreal plant communities. In these regions it is apparent that the soil moisture content is often unfavorable, and often the soil solution pH as well. Although nitrification decreases with increased acidity, it still occurs but at a low rate even in peat soils at a pH as low as 3.6 (Braun-Blanquet, 1932, p. 237). The effect of light on the process is not well understood, but may become evident when more light is admitted to the substrate, as by removing trees from a forest. However, other factors are also affected by this operation, therefore the increased nitrification due to increased light itself is difficult to ascertain. If light does actually have an important effect on the rate of this process, it may be significant that in arctic and boreal regions the season when nitrification is permitted to occur (by favorable temperature) is also characterized by very long to total daylight, although the total season is short as compared to more temperate zones. If this supposition is correct, it constitutes another compensating factor in the generally low nitrogen-cycle activity in this region. The temperature relationships of nitrification are as follows: optimum temperature range, 80° to 90°F.; minimum temperature, 40°F.; maximum temperature, 130°F (Lyon and Buckman, 1937, p. 283). In Alaska soils rarely attain the optimum temperature range even during the growing season, and many soils fail to reach the minimum temperature except in the uppermost layer on the warmest days of the season.

Throughout the northern regions the process is completely suspended for three-fourths or more of the year.

The process of volatilization is accomplished by the same micro-organisms that accomplish decay and ammonification, in response to a requirement for oxygen that is not met by the amount in the substrate at the time. Thus their principal metabolic activities can shift from decay and ammonification when the soil is well aerated, to reduction of nitrates when the soil is poorly aerated (i.e., excessively wet or compact). Under these conditions poor aeration of the substrate not only inhibits the increase of nitrogen compounds usable by vascular plants, but actively reduces the supply that is already present. Chemically, volatilization is a reduction process, beginning with nitrate and going successively to nitrites, hyponitrites, and gaseous nitrogen, with the release of oxygen at each step. Although the excessively wet substrate that is so widespread in arctic and north boreal regions tends to favor volatilization, the prevailing cool temperature is a compensating factor in reducing the amount of nitrogen lost in this fashion by reducing microbial activity. However, as shown above, under these wet conditions there may be not much nitrate formed that could be lost by volatilization.

e. The release of substrate nitrogen by burning. A second method by which the nitrogen stored in organic surficial deposits may be recycled by becoming available to growing plants is by means of burning the organic matter. It is suggested that the proteins in the upper humus layer are oxidized to form nitrites and nitrates, whereas those in the reducing environment of the lower layers may form ammonia.

This ammonia probably reacts quickly with the abundant carbon dioxide produced by combustion to form ammonium carbonate. The volatile nitrogen compounds that escape into the atmosphere may to some extent be returned to the soil by precipitation, as explained earlier.

On examination of the literature on the effects of forest fires in increasing the available nitrogen in the soil following the fire, no reference was found to the direct formation of nitrates by the high-temperature oxidation of plant proteins. On the contrary, Lutz (1956, p. 77) says, "Nitrogen contained in organic matter that is consumed by fire is, of course, volatilized and lost to the site." In order to clarify this matter, high-protein plant tissue was ashed in platinum crucibles by heating to 500°F. for 16 hours in an electric oven, the ash mixed with distilled water to extract soluble compounds, and the mixture filtered. The filtrate was analyzed by the diphenylamine method, which gave a strong positive reaction for nitrates. Aqueous suspensions of the ash also gave a positive reaction. Quantitative analyses of total nitrogen in the ash were not made, so it is not known how much nitrogen escaped as volatile compounds, but the resulting ash could be characterized as rich in nitrates.

In a tropical climate, where complete nitrogen release takes place by microbial decomposition of the organic matter, the effects of burning this organic soil covering has been investigated by Greenland and Nye (1960). In Accra, Ghana a mulch of rice straw (nitrogen content, .60% and maize stover (nitrogen content, .63-.67%) was spread on the soil and plots established that were (1) burned, and (2) not burned. Decomposition of the unburned litter was complete and rapid. Fortnightly nitrogen determinations were made for six months, and the means show (1) burned plot, 10.1 NO_3-N and 25.3 nitrifiable nitrogen, and (2) unburned plot, 10.0 NO_3-N and 22.1 nitrifiable nitrogen, all amounts expressed as parts per million of oven dry soil. Thus there was shown to be no significance difference in nitrogen content of the soil where the organic matter was burned, or left to completely decompose. The implications of these results as applied to arctic and boreal regions, where decomposition is very incomplete, is that burning releases available nitrogen compounds to the soil that otherwise remain unavailable in the organic matter.

This increase in available nitrogen in the soil is an important factor in revegetation following forest fires. The burning of an area is often followed by an increase of nitrophilous plant species of which the fireweed (Epilobium angustifolium) is the most widespread and conspicuous (Lutz, 1956, p. 66). Certain bryophyte species are just as characteristic of burned areas (Ahlgren and Ahlgren, 1960, p. 502), but are not so conspicuous. The following comparison of two burn-area plant communities (in both locations, on the site where a small wooden building had burned) illustrate this tendency in climatic extremes of Alaska:

Community A -- Burn area approximately 10 by 20 feet, near cabin in Bohemia Basin, Yakobi Island, southeastern Alaska. Altitude ca. 800 feet. Observed June 27, 1957.

Epilobium Hornemanni -- Abundance-cover and sociability, 5.5. The plants were very slender and closely spaced, and did not occur outside the burn area. The only vascular plant on the burn.

Marchantia polymorpha -- +.2. This plant was apparently disappearing from the community because of competition with Epilobium. The burn probably occurred 10 or more years prior to this observation, and Marchantia was undoubtedly more prominent in the early successional stages than it was when observed.

Ceratodon purpureus -- 1.3. This is an ubiquitous species on disturbed areas throughout Alaska, and probably should be classified as having nitrophilous tendencies, although it also grows abundantly on areas of apparently low nitrogen supply.

Bryum affine -- +.1. This is a common moss species of wet sites and its occurrence here is not believed to be especially related to soil nitrogen content.

Community B -- Burn area approximately 6 by 8 feet. In wet tundra 3 miles northeast of Barrow village, near Point Barrow, Arctic Alaska. Altitude near sea level. Observed August 31, 1958.

Epilobium angustifolium -- +.1. This plant was seen elsewhere in the vicinity only on bird-roost mounds.

Marchantia polymorpha -- 4.4. The burn had probably occurred not more than 5 years prior to this observation, and this liverwort formed a very vigorous colony that was fruiting abundantly. It did not occur outside the burn area.

Ceratodon purpureus -- +.2.

Bryum pseudotriquetrum -- +.2. This species is not believed to be nitrophilous because it is common throughout central and northern Alaska on wet soil and in bogs that are usually low in available nitrogen. At this site it was not restricted to the area of burn, but was found throughout the wet tundra.

Bryum tortifolium -- r.2. This is a rare, but widely distributed, species; other than its association with wet sites, its ecological relationships are unknown.

A comparison of these two burn areas which are in greatly differing climates show a remarkable similarity for such a specialized habitat. In the more southern location Epilobium Hornemanni clearly filled the role of primary vascular plant invader, which in the northern location was assumed by E. angustifolium. Marchantia was the dominant bryophyte in both locations, and Ceratodon took advantage of a "pyrosere" to establish itself. The appearance of the other moss species appears to be merely incidental.

In addition to the above-mentioned effects of fires on the soil, there is generally an increase in soil alkalinity, as reported by Marshall and Averill (1928), Lutz (1956, p. 77), and others. If excessive acidity has been an inhibiting factor in the nitrogen-cycle organisms in a soil, burning may result in greater microbial action and a consequent increase in available nitrogen; if the soil is already at optimum alkalinity, burning obviously would not have this effect. This difference in soils under varying types of forest cover explains, at least in part, contradictory reports on soil nitrogen gain by burning. Ahlgren and Ahlgren (1960, p. 517) say, "The acidity of the soil is usually lower after fire. Generally there is also increased soil calcium, phosphorus, and potassium, but reports regarding increase and decrease of nitrogen are contradictory. Burning usually stimulates biotic nitrogen fixing activity in the soil." If the soils are actively recycling nitrogen, burning will obviously reduce the effective nitrogen supply (due to some loss by volatilization), for the total supply was already effective. However, many high latitude forest and bog soils have been shown not to have a high rate of nitrogen recycling, thus burning may increase the available supply in the soil. Lutz (1956, p. 77) reports an increase in available nitrogen following forest fires in Alaska, and it is probable that this is true over most of the arctic and boreal regions.

f. The effect of soil disturbance on the available nitrogen supply. In soils that are excessively wet, cultivation or any mechanical moving often promotes better drainage, thus aeration is improved. Likewise, soils that are excessively compacted have their aeration improved by cultivation or other displacement. These mechanical displacements may also elevate some of the very wet soils above the water level and thus contribute toward increased dryness and aeration. Increased dryness of the soils also makes them warmer. These changes combine to make a more favorable environment for soil microorganisms than existed previously, and result in increased amounts of available nitrogen. Other soil fertility factors also are promoted at the same time. This soil displacement may be effected by (1) activities of man, (2) activities of other animals, and (3) any of several types of frost action. Of these methods of disturbance the first is often the most noticeable because of its suddenness and the abrupt boundaries of the disturbance.

One of the features of Alaska that makes a vivid impression on even the casual observer is the almost continuous occurrence of fireweed (Epilobium angustifolium) on many highway shoulders, which is very spectacular when this plant is in bloom. The undisturbed areas beyond the highway shoulders often do not bear a single plant of this species. This rapidly-invading nitrophilous plant is responding to the increased fertility of the shoulders due to their having been formed by pushing soil in from the areas that are to become the drains along the highway. These shoulders may be called areas of "disclimax", and not only fireweed, but other species also have had time to become established in an "open" community. These communities are quite new, for the habitat has been available only recently; their eventual vegetation type will not be predicted here, except to state that fireweed will probably decrease in importance.

In the arctic tundra soil displacement by man's activities has a marked and probably lasting effect on the vegetation. Tracks of vehicles that crossed the tundra near Point Barrow are still very distinct after ten years or more, although the vehicle used that route only once. The very wet, highly organic soil is compacted and depressed in the tracks and elevated slightly at the edge of the tracks, which has changed the soil-water relationships and caused a distinguishable flora to develop at these two new soil levels. Different nitrogen relationships of these two levels may be a factor in this difference of vegetation, or it may be other effects of soil water content. The bryophyte flora in particular sharply delimits these contrasting levels.

Soil displacement by other animals often causes a change in the vegetation on the disturbed soil. Even old mounds of earth produced by burrowing mammals, including mice, ground squirrels, woodchucks, foxes, and bears, often can be recognized from a distance by their distinctive vegetation, although the disturbed soil itself is no longer visible. The vegetation of old beaver dams and huts ordinarily is quite distinct from that of the surrounding (usually very wet) areas (Figure 11). In addition to the cause of enrichment already described, fecal material and uneaten food deposits may be a source of nitrogen on these burrows. The effects of frost displacement of soil are discussed in Chapter III, paragraph F.

g. The importance of animal feces as a nitrogen source. The hypothesis is offered that animals may play a much more important role in soil fertility with respect to nitrogen in the arctic and boreal regions than they do in more southern latitudes. The luxuriance of musk ox meadows has been noted by several arctic travelers. Polunin (1948, p. 38) in his discussion of eastern Devon Island, writes, "The ground consists of raised beaches and low, rolling plains of solid rock, with depressions that tend to be boggy and carry a rich vegetation. A contributory factor toward the richness of the vegetation just here is the presence of quite numerous musk-oxen." In more southern latitudes the nitrogen combined in plant proteins may be all reduced in the soil to ammonia, or oxidized to nitrates as described earlier in this report, due to the higher temperature which permits

Figure 11. Effects of a beaver dam on vegetation, near Fairbanks Creek north of Fairbanks, Alaska. Impounding of the water has contributed to the development of the Salix-Picea Mariana community in the background, whereas on the dam itself (foreground) a "weedy" community composed principally of Epilobium angustifolium has developed. June 11, 1960.

the processes to occur at a high rate for much of the year. In these northern regions the temperature of the soil is too low for this important microbial activity to occur readily, and the nitrogen of the plant proteins largely remains in the plant tissues that comprise the often thick undecomposed organic deposits. In the more temperate regions there will be rather complete release of the nitrogen of organic compounds whether the plants are eaten and digested by animals and some nitrogen returned to the soil in dung and urine, or whether the plants merely fall to the ground and are decomposed by soil microorganisms. Therefore the animals actually contribute nothing to the available supply of soil nitrogen that would not have been returned to the soil without the animal action. In the far north, on the other hand, if this vegetation is eaten by animals much of the nitrogen content is returned to the soil in an available form in the dung and urine, and finally in the dead body of the animal. This represents a real gain in available nitrogen by the soils. The metabolic processes of the animal convert most of the insoluble nitrogenous (proteinaceous) compounds into simpler, soluble nitrogen compounds, part of which are used by the animal. Furthermore, ruminants have a very active bacterial flora in the rumen which also assists in decomposition of the organic matter. The intestines provide a warm environment for bacteria (*Escherichia coli* and others, as mentioned earlier) to produce ammonium carbonate by the decomposition of the intestinal contents. Thus the bodies of the animals act as "bacterial incubators," functioning throughout the year. When the dung is excreted during the winter months it is quickly frozen and the soluble nitrogen compounds are retained in this state until summer thawing releases them. Plants may then quickly absorb them with a minimum loss by leaching and volatilization. The urea of urine, which can also be converted to ammonium carbonate by E. coli and other bacteria , is quickly frozen when excreted and likewise preserved until the beginning of the vascular plant growing season. This same process also occurs in temperate zones, but intermittent or premature spring thawing usually releases these soluble compounds when plant growth is inactive and much of the total amount is lost by leaching.

In describing these high latitude nitrogen relationships in ecosystem terms, the vegetation may be designated the "producer" component. Microorganisms, the ordinary "decomposers," are largely inactive except when in symbiotic relationship with warm-blooded animal "consumers." This relationship in the far north is unique in that warm-blooded consumers are believed to be essential for most effective nitrogen recycling--in temperate zones, animal consumers carry on the same processes, but are not essential for nitrogen recycling. To be effective the decomposers are not required by a low temperature environment to live in a symbiotic relationship with animals. A temperate zone plant community can thrive and increase in extent without the animal consumers, and in fact may grow even better without animals in the ecosystem than with them. Reference here is, of course, to the larger animals--the protozoan and related faunas are often important as organic decomposers. Expressed in pedological terms, the animals in the northern environment may compensate for the low amount, or absence, of the process of azofication in the soil.

It is therefore suggested that warm-blooded animals, preferably ruminants, are essential for maximum vegetation growth in the arctic regions. As the animal population increases, the amount of available nitrogen supplied to the plants tends to increase, causing the plants to grow more luxuriantly and thus be capable of supporting more animals. This cycle can continue until the nitrogen supply is no longer the limiting factor in plant growth, then the carbohydrate supply for the animals becomes limiting for their increase. An absolute limiting factor may be finally approached--the amount of photosynthesis that can occur in this physical environment due to the greatly reduced growing season, light intensity, and temperature. This level of ecosystem development represents the highest possible utilization of the environment by organisms. Reports from observers suggest that musk ox meadow communities may represent a close approach to this theoretical maximum, and the communities in this state certainly typify the highest attainable goal in wildlife management and conservation throughout the entire high arctic zone.

However, it is not only the musk oxen, moose, and caribou that can play this part in the nitrogen economy of the northern regions. Porsild (1957, p. 13), in discussing the formation of Dryas-Kobresia hummocks by congeliturbation, says, "During the final stages of the process, the furrows between the hummocks provide a habitat for other plants besides those that formed the tussocks. Draba Bellii, D. lactea, Parrya arctica, and Salix arctica are among the first to arrive. Lemmings use the furrows between the hummocks as runways and undoubtedly distribute seeds and other organic matter. In peak years of lemming cycles, the dung of these animals probably contributes an appreciable amount of fertilizer."

A net gain in nitrogen supply by a land flora is also provided by sea birds which inhabit rock cliffs or other land surfaces for nesting and roosting. The high nitrogen content of plant communities associated with bird rocks in the northern regions and also at high altitudes of temperate regions is well known. Polunin (1948, p. 234-235), in describing the vegetation of Cape Wolstenholme on Hudson Strait, Ungava where there are extensive cliffs occupied by sea birds with the attendant guano deposits, writes, "Bearing in mind the desert barrenness not far away of the typical area of plateau . . . we may be rightly amazed to compare . . . cliff top areas, which being more exposed, would doubtless be still more 'sterile'--were it not for the birds. These cliff tops are covered with a continuous dense sward of thickly matted 'peat' and vegetation, which brings home most forcibly the fact that a general deficiency in food-salts is one of the chief factors inhibiting plant growth over most areas of arctic terrain."

On the flat tundra in the vicinity of Point Barrow there are many low mounds (up to two or three feet high) that probably originated as frost mounds. Jaegers were observed by the writer to be using these mounds as perches while eating the rodents and birds that they had captured. Judging from the feathers and pellets on the mounds, owls also used these elevated places as perches. Both the dung of the birds and the uneaten or regurgitated pellets consisting mostly of hair and bones added to the fertility of the mound, and the vegetation was more luxuriant here than on the adjacent flat tundra. This rank vegetation added its remains to the height of the mound, therefore the mounds in use were continually becoming taller. The mound flora did not appear to be composed of particularly nitrophilous species, with the exception of bryophytes of the Splachnaceae family, and occasional Epilobium angustifolium plants.

h. Nitrophilous species. This term has been used rather loosely in ecological literature to include not only the few species whose occurrence is absolutely predicated by an unusually high nitrogen concentration in the soil, but also those species which merely thrive better and are therefore more conspicuous in an area of nitrogen enrichment. In fact, the usage of this term is difficult to limit; almost all species of terrestrial plants on almost all sites will grow more luxuriantly if a nitrogen fertilizer is applied. This, however, does not necessarily indicate that they will reproduce more effectively, for rank vegetative growth is often antithetical to reproduction.

The common fireweed (Epilobium angustifolium) is often asserted to be nitrophilous, most probably because of its frequent occurrence in areas of presumed soil nitrogen enrichment. This species and the grass Calamagrostis purpurascens are commonly the first species in much of Alaska to dominate an area following destruction of the vegetation, or extensive soil disturbance. This strongly suggests that they are nitrophilous in the sense that an increase in available soil nitrogen gives them a competetive advantage in initial invasion over other plant species that are present. This hypothesis may be related to the studies of Sweetman and Brundage (1960, p. 4) on the protein content of Alaskan forage plants. They found fireweed and Calamagrostis sp. to contain 19.4 and 17.5 percent crude protein respectively (based on total dry matter) when growing wild on unfertilized soil. In contrast, forage plants grown on soil "fertilized according to current recommendations" (the application of 30 pounds of nitrogen, 60 pounds of phosphate, and 30 pounds of potash per acre is recommended) contain the following percentages of crude protein: Sedge, 10.3; Equisetum, 9.2; bluegrass, 8.2; timothy, 9.2; bromegrass, 12.2; oats and peas mixed, 12.1. It is believed to be significant that fireweed and Calamagrostis contained much more protein, even on unfertilized soil, than did any of the cultivated plants that were fertilized. It follows that if the former plants normally have a high protein content, a high nitrogen level in the soil probably is required. Thus the chemical analyses quoted above support the opinion that these two species should be considered to be definitely nitrophilous.

If we limit our category to include only obligate nitrophiles we find one group of plants that is conspicuous in this respect--the members of the bryophyte family Splachnaceae, or the "dung mosses." Species of this group are almost always found growing only on dung of mammals or on the remains of dead animals. A most impressive demonstration of this fact was observed on Yakobi Island, where a deer had died and decomposed in place. The skeleton was intact, and the complete and detailed silhouette of the whole animal was formed on the ground by a dense, solid carpet of the dung moss Tetraplodon mnioides, indicating the exact area where the flesh had decomposed on the soil. Other habitats of the dung mosses include hair, bones, regurgitated owl pellets, horns, antlers, and hides. The following species of this group were collected by the writer in Alaska: Splachnum luteum, S. melanocaulon, S. ovatum, S. rubrum, Tetraplodon angustatus, T. mnioides, T. paradoxus, T. urceolatus, and Tayloria serrata (Figure 12).

i. Summary and conclusions. There are numerous reports in the literature of nitrogen being a limiting factor in arctic and boreal plant community development. A general principle is stated by Braun-Blanquet (1932, p. 239) as follows, " . . . All plant communities which form raw humus are poor in nitrates. This has some connection with lack of bases. Even though nitrate bacteria can endure strongly acid reactions, their activity is, nevertheless, greatly decreased in acid media. Soils of forests and heaths rich in Calluna, Vaccinium, and Empetrum all have a low nitrifying power." Laughlin (1958, p. 24) summarizes the situation in Alaska in this respect as follows: "The work carried out at the Alaska Agricultural Experiment Station shows that: (1) Practically all Alaskan soils are extremely low in nitrogen and phosphorus." Dr. R. E. Shanks (oral communication, 1948) reported that preliminary testing at Barrow showed tundra plants to have a marked response in increased growth rate to the application of a "complete" commercial fertilizer. The rapid response noted was most probably the effect of the nitrates in the fertilizer, although phosphates may have been quite important.

The effect of the low soil nitrogen level at Point Barrow as stated by Scarseth (1960, p. 8) may be quoted as follows: "The cold 6 to 10 inches of thawed soil over the permafrost of the subsoil is too

Figure 12. Nitrophilous bryophyte community on dung deposit, northwest slope of Money Knob near Livengood, Alaska. The conspicuous moss with the large expanded hypophysis is Splachnum luteum. The species with shorter setae and only a swollen hypophysis is S. ovatum, and the low-growing species with a slightly enlarged hypophysis is S. melanocaulon (a very rare species). June 18, 1960.

refrigerated for any extensive microbial decomposition to release nitrogen locked in the organic matter. The result is that all the tundra vegetation shows marked nitrogen starvation in the growing temperatures of the long days, but short summers. This observation was made in the tundra plains in the vicinity of Point Barrow, Alaska in 1956. Plant tissue tests confirm this observation."

If it is true that in arctic and boreal environments the available nitrogen usually occurs in amounts far below the optimum level for greatest plant growth, it follows that the plant communities here are generally composed of inherently facultative oligotropic species in respect to nitrogen. In spite of the generally unfavorable conditions for nitrogen recycling which prevail in the far north, there are certain compensating factors either restricted to a cold climate, or of more significance here than in the temperate zone. Although nitrogen fixation, ammonification, and nitrification are greatly reduced because of low temperatures and excessive wetness or dryness, the leaching of the soluble nitrogen compounds is also reduced due to the underlying impervious permafrost, or to their immobilization in ice. Volatilization of nitrates is also reduced because of reduced microbial activity.

The general process of decomposition is very slow and incomplete, but most of what does occur is during the growing season when the soluble nitrogen compounds released thereby can be immediately absorbed by growing plants and their loss by runoff and percolation thus prevented. In more temperate regions, these soluble compounds may be lost during the period when there is no active plant growth. Warm-blooded animals are believed to be of greater importance in northern than in temperate regions in their effect on protein decomposition by their own digestion and by harboring an intestinal and rumen microflora that is very effective in the high temperature of the animal bodies. They may thus be considered cold environment substitutes for soil-promoted azofication of temperate zones. The dung of other animals, including birds, is of more relative importance in the north than in more temperate regions where the nitrogen supply is not so critical in regard to its effect on plant communities. As a consequence of the generally low nitrogen supply of these northern regions, nitrophilous species are not common, but at the same time are more conspicuous than they are in regions of more plentiful nitrogen supply.

The dispersal of obligate nitrophilous species of plants throughout a vast area that is generally very deficient in available substrate nitrogen requires an explanation. Because sites of nitrogen enrichment here are very small and discontinuous in distribution, it is clear that nitrophilous species are at a great disadvantage in step-by-step migration. It is suggested that obligate nitrophiles of high latitudes must (a) have wind-borne propagula by means of which great distances between suitable habitats can be covered, and (b) produce very numerous propagula to compensate for the small chance of their finding a high-nitrogen habitat, or (c) be transported by animals and thus increase their chances of becoming associated with sites of nitrogen enrichment. The nitrophilous species discussed in this report meet the first two requirements listed above. In more southern latitudes, where moderate to high available soil nitrogen levels are often maintained over large, continuous areas, no special adaptive features are required by this type of plant to become associated throughout the area with its nitrogen requirement. The hypothesis is therefore advanced that arctic and boreal plants are generally species having a low nitrogen requirement, for otherwise these species could not exist as extensive populations in these regions.

D. Soil Type.

The expression "soil type" as used here is a non-technical term that is intended to include any convenient grouping of soil characteristics, chemical or physical, that are to be discussed at the time. Its use thus purposely avoids the restrictions that are inherent in the genetic classification system of soils in expressing relationships of vegetation and soils. It permits the incorporation of soil studies in autecology, as expressed by chemical and physical properties of the soil, which are not necessarily implied in their genetic classification.

Many chemical and physical attributes of soils have already been stated or implied in the discussion of the effect of rock type on vegetation, and they will not be repeated here. Nor will all effects of soils on vegetation be outlined, as these can be found in general ecology references; rather certain properties of soils will be considered that are thought to have a unique relationship to plant communities in high latitude regions. In this discussion it does not seem necessary to adhere to a restrictive definition of soil, but rather to use the word in its ordinary English indefiniteness and appropriateness to refer to the supporting medium of plants. At the same time, the fact that a plant (Crepis elegans) was occupying a fresh coal pile at a power station in Fairbanks and a moss (Kiaeria Starkei) had colonized a rotting cotton mattress on Latouche Island does not require us to define the coal and cotton fibers as "soil" just because they supported plants. By this concept of usage one avoids the contradictions of some classifiers who name a soil type which is, by their own definition, not soil. "Substrate" becomes a convenient generic word to use when the particular substance in question does not conform to the general meaning of the word "soil." It is pedantic to try to distinguish the point at which, for example, regolith or organic debris becomes soil, in a discussion that is primarily ecological rather than pedological.

The nature of the colloidal particles of a soil determines to a great extent its degree of chemical activity, principally as a result of the great surface areas of the external and internal interfaces of these particles. These colloids may be divided into two categories, the organic and the inorganic. In typical arable soils of temperate zones both types play important roles, and the percentage importance of each is often closely related to soil horizons. The soils of Alaska that have potential agricultural use (principally the Subarctic Brown Forest and Podzol groups) are described by Kellogg and Nygard (1951, p. 125) as " . . . exceeding low in total clay relative to silt and very fine sand." However, other soils in the high latitudes often have a significant, and occasionally preponderant, amount of clay, and their areal extent is probably greater than the soils characterized above. Many soils throughout the boreal and arctic regions have been described as "clay" or "clayey" by botanists and other observers.

The activity of organic colloids is mostly on the exterior surface, whereas inorganic colloids present two areas of active surface, the exterior and the interior interfaces. This latter phenomenon is due to the laminar structure of the inorganic colloids (principally silicate clays except in tropical regions) forming the nucleus or micelle of the colloid particle. The laminae are crystalline plates of silica ($2\ SiO_2 \cdot H_2O$) and alumina ($Al_2O_3 \cdot 3\ H_2O$). Two groups of clays are recognized, the kaolin and the montmorillonite, being differentiated by the arrangement of these laminae--the former is composed of one silica and one alumina plate, the latter has one alumina plate between two silicate plates. Due to the greater interface area of the montmorillonite clay particles, their smaller size, and the greater space between laminae, this group is much more active in promoting chemical reaction and in forming a plastic, cohesive soil. If not counteracted by other factors, a wet substrate favors the predominance of clays of the montmorillonite group, whereas a dryer substrate favors the formation of the kaolin group.

Although the wetness or dryness of parent material as related to clay type genesis is usually considered as a function of regional climate, this differentiation can be made in the formation of clays of two contiguous small areas having different water content of the same parent material. Dr. W. R. Griffitts (oral communication, 1961) reported an area he had studied in Chaffee County, near Salida, Colorado where the surface was rhyolite tuff composed of glass and orthoclase feldspar. Weathering of this rock had formed kaolinite on a dry, exposed surface, whereas a few feet away in a depression that was wet, montmorillonite had formed. These clay types were determined by mineralogical studies.

Rock type has an influence on clay formation in that there must of necessity be silicon and aluminum in the weathered material if clay is to develop. However, most parent material has enough of these two elements to provide for clay formation, and the degree of wetness and other environmental conditions may be the determining factor in the type of clay produced. Granite and pegmatite tend to favor kaolin formation, and gabbro, diorite, and muscovite tend to favor montmorillonite development. Shale often contains both kaolinite and montmorillonite in the rock, and by weathering may contribute to a deposit of either type of clay.

In respect to the effect of organic material on clay development, Ross and Hendricks (1946, p. 60) state, "Organic material in association with certain bacteria results in reducing conditions in the clay-forming system. This would favor montmorillonite formation . . ." The deeper layers of a bog, particularly if it is umbroginous, maintain a definite reducing environment. Soligenous bogs, with a pronounced movement of water through them as evidenced by drainage from the bogs, are much weaker in reducing quality and probably can be somewhat oxidizing. In the latter bogs there may be less clay formation <u>in situ</u>, but incoming water may import clays and silts to be incorporated into the organic matter. Research on a soligenous bog on Yakobi Island, Alaska showed the prominence of imported mineral particles by the bog's high copper content at certain sample sites which is thought to relate to former channel deposits in the muck, the copper having come from ore outcrops in the watershed. Ionic migration from possible underlying ore veins was almost certainly insufficient to penetrate upward through the deep (perhaps more than 100 feet) organic deposit.

The reducing nature of the lower material in wet arctic tundra was indicated by samples of clay obtained from a depth of ten feet at a site two miles west of Nome, Alaska. The material was a fine clay strongly colored a bluish-gray by ferrous iron, which is formed only in an environment of low oxygen supply. The nature of the clay has not yet been determined by X-ray diffraction, but its physical properties strongly suggest that it is montmorillonite. On the other hand, shallow, finely comminuted mineral matter obtained at a depth of two feet from wet arctic tundra overlying beach gravel at Cape Krusenstern on the Arctic Sea was non-clayey and was colored an intense orange-red by ferric iron, which is evidence of a strongly oxidizing environment. This was attributed to the adequate subsurface drainage provided by the beach gravel deposit. Regarding the clay types found in the arctic tundra Brown and Tedrow (1958) describe two tundra soils from the Arctic Slope of Alaska as follows: "X-ray analysis of the clay fraction indicate that the 2 : 1 -layer silicate and kaolinite predominate, with traces of clay-size quartz."

The distinctiveness of soligenous and umbroginous mires, as discussed by Drury (1956, p. 27-28) may in part be due to the difference in proportion of organic and inorganic colloids of the two, rather than in the proportion of silts as such. This is suggested in the account of the ombrotropic and minerotropic peatlands of the Hudson Bay lowlands as discussed by Sjörs (1959, p. 3). Silt is not colloidal, but by weathering may develop clay colloids. The properties of bogs, mucks, and muskegs of the northern regions need to be studied with these factors in mind.

The high plasticity and cohesion of the montmorillonite clays may contribute to the maintenance of the wet substrate by the formation of a layer impervious to percolation, which in turn favors their continued production in the weathering processes. The conversion of montmorillonite to kaolin is prevented by the reducing environment maintained by the impervious nature of layers of montmorillonite, which reduce its further weathering (Ross and Hendricks, 1946, p. 60). This clay layer has been discussed as it relates to the formation of sedge meadow pools on Latouche Island, Alaska (Shacklette, 1961b, p. 197) which are outside the permafrost region. The lack of vegetational indicators that distinguish permafrost areas from those of no permafrost has been mentioned by Sigafoos (1958, p. 165) and by Steere (1961, p. 265). The suggestion is made, based on field observations, that this distinction is obscured or prevented by the nature of clay formation in these regions. This may be because the impervious clay substrate (which in itself relates in part to plant growth) causes excessive soil wetness in the same manner as does permafrost, and the vegetation reacts to this wetness, not to permafrost _per se_.

The hypothesis is proposed that the development of a bog community (particularly of the ombroginous type) in areas of discontinuous permafrost may originally start due to wetness related to a permafrost area and by its development of increased wetness contribute to increased formation of montmorillonite clays which seal the lower layers of the permeable unfrozen perimeter, thus allowing the bog to increase in diameter. The permafrost area may then increase in size to include the previously unfrozen lower substrates. This could be effected as a result of two factors, (1) the comparative low specific heat of the newly-developed organic covering, and (2) the high specific heat of lower horizon clay particles (due to their high water-holding capacity) as contrasted to the lower specific heat of the larger particles (silt and sand, which hold less water) that occupied this zone before clay formation.

In arctic and boreal environments the other moisture extreme exists in much of the regolith areas, particularly in lithosols of colluvial slopes. This low moisture content favors the formation of kaolin clays, instead of montmorillonite clays, which have low colloidal properties in promoting chemical activity in the soil. Ross and Hendricks (1946, p. 60) state, "Oxidizing conditions or a parent rock whose iron is in the ferric state seem to form kaolinite rather than montmorillonite. Climate and biotic ecology seem to be of secondary importance." Although the prominence they impute to parent rock type is not questioned, the great influence of climate and vegetation on altering oxidizing conditions (which they list as the first requirement) probably is not of secondary importance in high latitude soils.

Kaolin formation contributes to the development of an infertile soil for vegetation, somewhat independent of rock type of the parent material, and the resulting poor development of vegetation in turn reduces the amount of organic colloids produced. In addition, the low plasticity and low cohesion of kaolin clays do not greatly reduce percolation. Consequently the excessive dryness of the soil is very slowly corrected, and the alteration of the xerophytic habitat by vegetation and soil-forming processes occurs at a very slow rate. The low average temperatures that obtain in arctic and boreal regions reduce chemical weathering and soil reactions to a low level, which makes these soils and plant communities all the more vulnerable to the disruptive forces of frost action and gravitational displacement--that is, their return to the previous state of stability is very slow. These soils and plant communities do not ordinarily reach a condition that may be considered "climax" by means of a long sequence of successional phases, and such locations have an unalterably low biotic productivity, which, with increased environmental extremes, is reduced to that of the "polar desert" with an almost zero plant productivity.

In summary, it can be said that in high latitude environments the natural processes of soil and plant community development tend to cause a wet soil to become wetter and to correct very slowly, if at all, excessively dry sites. This trend of processes is in strong contrast to the generalizations of Clementsian concepts of succession in a temperate climate, in which extremes of wetness and dryness are presumed to advance toward a mesic habitat developed by the successional processes themselves.

E. Water.

The effects of water on vegetation in the high latitudes cannot be separated from the effects of other substrate factors that already have been discussed. The supply of water to the plant at the proper time and in proper amounts is probably the most important variable in community development of a particular region, and plays a larger part in determining species composition than does the nature of the substrate parent material, in the majority of cases. Water is a controlling factor not only as a physiological essential, but in its indirect effect on all the other chemical and physical properties that relate a plant to its substrate.

The water relationships of the arctic and boreal environments are unique in that there is a low to very low annual precipitation rate in most regions, which sets a basic xerophytic pattern for plant communities, but superimposed on this pattern are features of the northern environment that can turn the habitat to aquatic or any degree of wetness leading thereto. The degree of actual wetness of a site can be controlled by physical or biological variables. If there were a high precipitation rate in these regions at present and other physical factors were relatively constant there could be no mesophytic or xerophytic habitats--all would be very wet to aquatic until finally glaciation eliminated all plant communities. Therefore arctic and boreal plant communities may range from xerophytic to aquatic within the same precipitation regimen. In a temperate habitat of equally low precipitation physiographic and biologic factors cannot be so effective in the transformation of a xeric site to one of moderate or extreme wetness. The difference in these contrasting water relationships lies basically in the low temperature of these northern regions.

The cold climate has the effect of increasing the supply of water to plants by several methods. It reduces substrate evaporation and plant transpiration, and also immobilizes winter precipitation by freezing. Therefore much of the entire year's precipitation is potentially available for plant use during the short growing season. In temperate regions much of the precipitation of winter months is lost by runoff and percolation and the supply stored in the soil is usually depleted during the long growing season unless supplemented by summer rainfall. The past and present cold climate has caused the development and preservation of permafrost. The water in the solum freezes and thaws annually, but the permafrost zone is an effective impediment to percolation, thus the melt water can be lost in summer only by surface runoff and evaporation. If the terrain is of low relief, runoff is greatly reduced and evaporation is inadequate to remove the surplus water, thus a pool or bog results. Even on areas of great relief the insulating organic surface layer and the shading vegetation may delay summer melting of the frozen solum (particularly on north-facing slopes) until there is insufficient time during the growing season for drainage to develop a somewhat mesic condition. This causes the development of "mountain muskegs" that are abundant in interior Alaska, or in more extreme cases, "hanging bogs." The water-absorbing ability of the dense moss mat that is characteristic of these sites also in itself greatly reduces drainage. In fact, on sites without permafrost hanging bogs may develop if summer precipitation is adequate. Thus in Eastern Coastal Alaska, where there is heavy rainfall and no permafrost, the steep slopes are ordinarily blanketed with hanging bogs (Figure 13). Zach (1950a) has shown that in the waterlogged watersheds of this region the substrate is usually almost completely saturated, and that total rainfall therefore drains out in a few hours. The organic surface mat does not have here the stabilizing effect on stream flow that is one of its most significant features in regions of less constant substrate saturation. This ability of the mosses to impede runoff until saturation is reached and then to remain saturated to the detriment of forest development has been discussed for Southeastern Coastal Alaska by Zach (1950b, p. 304-306), and for interior Alaska by Krause, Rieger, and Wilde (1959, p. 495). In the former district the mosses are said to cause a forest of Sitka spruce (Picea sitchensis) to disappear and to be replaced with a bog having Pinus contorta and Tsuga Mertensiana as the principal trees. In interior Alaska the effect is mostly that of permitting black spruce (Picea Mariana) to grow, and preventing or limiting the growth of white spruce (P. glauca).

The development of hanging bogs appears to be initiated by species of the moss genus Sphagnum, whether the bogs are related to permafrost effects or are outside the permafrost area and are caused by the high precipitation rate. The succession of other mosses finally reduces the dominance of sphagnum, which in older bogs is ordinarily restricted to very wet sites such as slight ravines or pockets of the slope. Profiles made through these mats often showed a lower organic layer derived almost entirely from sphagnum, with other mosses increasing in the

Figure 13. Hanging bogs, upper Bohemia Basin, Yakobi Island, Alaska. The steep slopes between the snow beds in the upper center are blanketed with a mat of mosses in which grows herbs and shrubs, and an occasional tree. The ridge at the left supports a narrow line of <u>Tsuga Mertensiana</u>. In this region of heavy rainfall the more even slopes are often too wet for this species. This is in contrast to the xeric mountain slopes of interior Alaska, where the trees are limited to the ravines. June 14, 1957.

upper portions. This succession of other mosses and vascular plants is thought to be an essential factor in the maintenance of hanging bogs on very steep slopes. Sphagnum is an acrocarpous moss, essentially unbranched (the short side branches are determinate), of very low tensile strength, and without rhizoids, therefore it develops a mat of very low "textile" strength. The development of an almost pure sphagnum mat that absorbs and impounds an increasing large amount of water may finally cause the entire mat to slide down the slope as an "avalanche." A recent slide of this sort was observed to have occurred on Yakobi Island involving a sphagnum mat of several hundred square yards, leaving the essentially bare bedrock exposed. The succession of pleurocarpous mosses, which are branched and become interwoven and which also have more tensile strength than does sphagnum, acts to reinforce the mats and increase their textile strength.

The pleurocarpous mosses are of a more mesophytic nature than is sphagnum and they grow over the sphagnum mat, which is relatively dry on the very surface. This suppresses the sphagnum by reducing the available light until finally the surface of the mat is almost entirely composed of pleurocarpous mosses. The continued development of these latter mosses does not increase the volume of water held by an amount corresponding to their thickness as compared to sphagnum, for they lack the special water-absorbing anatomical features of sphagnum. The increased shift toward a mesophytic habitat favors the invasion of certain herbs and woody plants which by their strong roots and stems permanently secure the mat essentially in place. There is often some slumping of the mat causing a terraced effect, or in more northern regions solifluction features may form, but no well-developed hanging bogs were observed to have completely pulled loose from the substrate and slid down the slope.

The development of large polsters by species of the moss genus Polytrichum often follows the primary pleurocarpous mosses, which seems to be related to the acidification of the substrate by conifer needles. These species were observed to follow black spruce colonization of hanging bogs in permafrost regions and to accompany Sitka spruce and other conifers on the high-precipitation type of hanging bogs. Although it is an acrocarpous moss, its very tough "stems" and abundant and strong rhizoids develop dense polsters that are very difficult to pull apart. When well developed they contribute a considerable increase in strength to the mat.

These two types of hanging bogs have almost parallel development in spite of their very different environment, and each has distinctive species fulfilling the several functions in community development. These types will be described by giving the following examples:

Community A. Relevé of a high-precipitation hanging bog in Bohemia Basin, Yakobi Island, Southeastern Alaska.

The bog occupies a steep southwest-facing slope at an altitude of ca. 800 feet. Observed June 30, 1957 (Figure 13).

Species	Abundance-Cover and Sociability Values
Bryophytes:	
Sphagnum species -	
Sphagnum balticum	r.2
S. papillosum	+.1

S. Warnstorfii	1.3
S. squarrosum	1.3
Pleurocarpous species -	
Hylocomium splendens	+.2
Mnium glabrescens	r.2
Pleurozium Schreberi	1.4
Ptilium crista-castrensis	+.2
Rhytidiadelphus loreus	2.4
Later acrocarpous species -	
Paraleucobryum enerve	r.2
Polytrichum formosum	+.4
Gymnosperms:	
Picea sitchensis	r.1
Tsuga heterophylla	+.1
T. Mertensiana	+.1
Angiosperm woody plants:	
Alnus crispa ssp. sinuata	1.3
Cladothamnus pyroliflorus	3.4
Menziesia ferruginea	+.1
Oplopanax horridus	r.1
Ribes bracteosum	r.1
Sorbus sitchensis	r.1
Vaccinium ovalifolium	+.2
V. uliginosum	+.2

Herbaceous plants:

Carex macrochaeta	+.2
Eriophorum gracile	+.2
Fauria crista-galli	2.4
Geum calthifolium	r.2
Listera cordata var. nephrophylla	r.2
Majanthemum dilatatum	+.2
Pinguicula vulgaris	r.2
Plantanthera stricta	r.1
Streptopus amplexifolius	+.1
S. streptioides var. brevipes	+.2
Veratrum eschscholtzii	1.2

A miniature hanging bog was observed in the upper part of Bohemia Basin that is thought to be of a unique origin heretofore undescribed. A small cold stream, fed by snow melt from the adjacent peak of about 2,000 feet altitude, coursed rapidly down a steep ravine of amphibole epidote schist talus. At points along the stream two leafy liverworts, Nardia compressa and Scapania paludosa, had extended over the stream and formed a tight, closed mat which impounded the water in a series of terraces (Figure 14). The water pressure had caused occasional "blowouts" in the mat which were conical and crateriform (Figure 15). Herbaceous plants and shrubs were colonizing the mat, and in the better-developed portions the water was flowing under this stabilized hanging bog. The ability of these liverworts to impound this swift stream lies in their adaptation to a very wet to aquatic habitat, and their intricately interwoven growth which gives considerable textile

Figure 14. Pool formed by the liverworts *Nardia compressa* and *Scapania paludosa* damming a small mountain stream, Bohemia Basin, Yakobi Island, Alaska. The intertwined stems of these plants are able to withstand the force and pressure of the water; *Sphagnum* species, which are equally well adapted to the aquatic habitat, do not form a mat sufficiently strong to grow here. June 23, 1957.

Figure 15. Portion of the stream shown in Figure 14 which has been completely closed over by leafy liverworts. The mounds of liverworts with the "blowout" holes in the center are believed to have formed by the closing of pools like the one shown in the preceding figure. The holes are probably caused by rupture of the mounds by water pressure at times of heavy runoff. The stream here flows completely under the vegetation mat, which is being invaded by Cassiope Stelleriana, Fauria crista-galli, and finally by Cladothamnus pyroliflorus shrubs. June 23, 1957.

strength to the mat. Sphagnum shares their hydrophytic adaptability, but does not produce a mat of sufficient strength to impound a rapid stream on a steep slope.

Community B. Relevé of a permafrost hanging bog on Money Knob overlooking Ruth Creek, near Livengood, Central Yukon River district, Alaska.

The bog occupies a steep north-facing slope at an altitude of ca. 1,600 feet. Observed June 17, 1960.

Species	Abundance-Cover and Sociability Values
Bryophytes:	
Sphagnum species -	
Sphagnum fuscus	+.2
S. Girgensohnii	1.3
Pleurocarpous species -	
Aulacomnium turgidum	+.2
Hylocomium proliferum	+.2
Pleurozium Schreberi	5.5
Rhytidium rugosum	1.2
Later acrocarpous species -	
Dicranella subulata	+.2
Polytrichum commune	+.3
P. juniperinum	+.3
Splachnum luteum	r.1
S. melanocaulon	r.1
S. ovatum	r.1
Tetraplodon mnioides	r.1

Gymnosperms:

Picea Mariana	1.1

Angiosperm woody plants:

Alnus crispa	r.1
Chamaedaphne calyculata	+.1
Betula resinifera	+.1
Ledum palustre ssp. decumbens	2.3
Salix Bebbiana	+.1
S. pulchra var. yukonensis	+.1
Vaccinium uliginosum	2.3
V. Vitis-idaea ssp. minus	+.3

Herbaceous plants:

Pedicularis labradorica	+.1
P. Oederi	r.1
Moehringia lateriflora	r.2

This bog consisted of an organic mat about 16 to 18 inches thick, with no preceptible mineral soil, overlying permafrost that was mostly clear ice with very little incorporated soil. The paucity of herbaceous plants is noteworthy. Mountain muskeg or "half-bog" communities were adjacent which had a deeper thawed solum of mineral soil under the mat and on which grew many more herbaceous species. This hanging bog is also distinguished from adjacent mountain muskeg communities by the absence of Betula nana ssp. exilis, which in the latter generally occurs in great abundance (Figure 16). The almost complete absence of Alnus crispa in the hanging bog is also noteworthy; on an adjacent slope having a mineral solum over permafrost this shrub forms a large, almost impenetrable thicket. The nitrophilous mosses Tetraplodon mnioides, Splachnum luteum, S. melanocaulon, and S. ovatum were growing on dung deposits, and perhaps were not related to this particular community; however it is of interest to note that S. luteum is ordinarily a species of very cold climates, and S. melanocaulon is extremely rare in North America (this may be the first record of its occurrence here) (Figure 12).

The effects of water relationships on clay formation and on the availability of essential minerals have been described earlier. The features of the common bog types have been discussed by many writers (e.g., see Dachnowski-Stokes, 1941a, 1941b; Drury, 1956; Sjörs, 1958). There is a voluminous literature on the formation, extent, and special features of permafrost, which will not be reviewed here. The water relationships of the named soil series of Kellogg and Nygard (1951) will be discussed in Chapter IV.

F. Unique Conditions of Intense Frost Climates.

The instability of the substrate is often an outstanding feature affecting plant growth in regions of intense frost action, even in areas of low relief. The plant communities are frequently prevented from reaching a condition of relative stability because of periodic disturbance of the soil by cryopedological processes. This effect on vegetation has been discussed by Benninghoff (1952) with reference to conditions obtaining in northwest North America. Hopkins and Sigafoos (1951, p. 51) summarize the effects of these unstable soils on vegetational development as follows: "The concept of 'climax' vegetation must be modified when applied to tundra vegetation. Disturbance of the substratum recurs repeatedly, and all stages in the plant succession exist on unstable surfaces. The vegetation in areas of frost scars, peat rings, tussock rings and groups, and vegetation polygons represents an equilibrium assemblage adjusted to the climate in which it exists, but differs from a 'climax' assemblage in that bare areas and areas covered by pioneer plants are intimately mixed among areas covered by assemblages representing the highest stage in the succession."

The amount of this disturbance, expressed in quantitative terms to define the separate and combined effects of gelifluction and frost creep on the downslope movement of the soil, has been given recently from measurements made in arctic regions of Greenland by Washburn (1961, p. 168A) who states in summary, "Preliminary analysis of several thousand observations shows that in stony loam at sites studied: (1) the component of downslope movement due to gelifluction (solufluction associated with frozen ground) can be distinguished quantitatively from that due to maximum possible frost creep (frost heaving and vertical settling); (2) frost creep can exceed the flowage component, and vice versa; (3) on a slope of 11° to 15½° the combined rate of movement by gelifluction and creep ranged from 0 cm/yr to 6 cm/yr; (4) on this slope moisture influences movement more than vegetation does; (5) a retrograde movement with respect to the vertical reference plane is common during summer and lessens downslope movement."

These conditions are not characteristic of all areas in arctic and boreal regions; many sites have a relatively stable surface. If a dense vegetational cover develops, especially if composed of a thick mat of mosses, lichens, and shrub stems and roots, the soil surface may merely raise and lower with freezing and thawing with but little lateral displacement occurring, even on moderate slopes. The control of soil instability exercised by vegetation is especially marked in some areas of intensely cold climate in interior Alaska. Here the plant communities may reach a stage of balance that may be fitted into polyclimax concepts, the development of which is predicated upon the presence of a relatively stable substrate. At other sites in the same region this degree of stability is never reached by the plant community, and cyclic disturbance of the substrate reduces the site to one that is barren of vegetation, or to one developing a sparse vegetation consonant with the cycle of surface disruption. These contrasting developments occur under the same climatic regime, which points up the observation that it may not be the direct effect of extremely low temperature on the plants themselves that determines their ability to grow on a particular site. It is probable that most species of this region can withstand extremely low temperatures, as is shown by their occurrence somewhere in their range, although the insulating effect of snow cover cannot be disregarded in making this appraisal.

The degree of adaptation of a species to the prevailing water relationships most commonly determines the plant's ability to become established in a community occurring in regions having very cold climate. The extent of desiccation of a site is affected by its exposure to insolation and wind (with their secondary effects on snow cover), the physical properties of its substrate, and its altitude. Air movement and insolation not only dry out the soil, but increase transpiration, which may be particularly critical when the soil water is frozen and thus unavailable to the plant. Excessive transpiration at this time may limit the altitudinal occurrence of evergreen trees (specifically, white spruce) in these regions--at least it is noted that tall deciduous shrubs and low evergreen shrubs attain higher altitudes and latitudes than do evergreen trees. The evergreen shrubs that have tolerances similar to those of deciduous shrubs for this factor are chasmophytes of low growth, therefore they are usually protected by a snow cover during this critical period. The adjustment of white spruce to the prevailing snow cover at or near "tree line" is shown by the striking "krummholz" form developed there, in which most of the densely-branched, shrubby form is protected by winter snow cover (Figure 16). Occasional vertical leaders may rise above the average snow depth, only to be killed during winters of extremely severe weather. It is difficult to assess the relative importance of the insulating and the reduced transpiration effects of the snow cover; both are undoubtedly important.

Hopkins (1959, p. 216) has pointed out that the climatic factors that seem to best differentiate tundra from forest, and interior forests from coastal forests, are the number of "degree-days" above 50°F. and the mean temperature of the coldest month. While this may be true in a regional characterization of vegetation types, at a particular location site occupancy often does not appear to relate to the direct effect of temperature; however, microclimatic data are not available to settle this question, therefore indirect evidence must be used. Field observations of adjacent contrasting sites in interior Alaska made by

Figure 16. "Krummholz" form of Picea glauca in mountain muskeg community at Eagle Summit, Steese Highway, Alaska. The dominant ground cover of this community is Betula nana subsp. exilis, which is covered by snow in winter. The horizontally-spread branches of this spruce tree indicate average snow depth; the leaders rising above this mat of branches are periodically killed by exposure. The one-foot ruler on the dead leader gives scale. June 5, 1960.

the writer suggest that maxima or minima of temperatures, or their extent in time during the year, do not necessarily differentiate these plant communities of unlike composition. There is a sufficiently long warm period during the summer at all these sites for the major community species to grow and reproduce. Two contrasting communities observed by the writer at Eagle, Alaska on the Yukon River near the Yukon Territory-Alaska boundary are discussed below. The weather bureau at Eagle is one of the oldest in Alaska, having been in operation more than 37 years, and it records an average temperature of the coldest month as -12.4°F., with an absolute minimum of -75°F. The Eagle area is thus one of the coldest parts of Alaska, and it is near Snag, Yukon Territory, the coldest place in North America (with the possible exception of the summit of Mt. McKinley and other very high Alaskan mountains).

Community A. Relevé of a south-facing slope, bluff above Mission Creek at Eagle, interior Alaska.

> The bedrock is composed of ultra-mafic and mafic intrusives of greenstone habit. The slope is less than 25% vegetated with small clumps of plants, or single individual plants. The effects of frost action are shown on the large area of exposed soil (Figure 17). Altitude, 1,550 feet. Area, 10 X 10 meters. Observed June 26, 1960.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes - none present	
Grasses -	
Calamagrostis purpurascens	1.2
Festuca altaica	1.2

Figure 17. Discontinuous ground cover on colluvial slope of Mission Bluff near Eagle, Alaska. The forbs in the foreground are *Zygadenus elegans*, *Senecio conterminus*, and *Artemisia frigida*. The small trees on the skyline are *Populus tacamahacca* and *P. tremuloides*, both growing in a slight ravine. June 26, 1960.

Forbs -

Anemone patens subsp. *multifida*	+.1
Artemisia frigida	+.1
Conioselinum cnidifolium	r.1
Minuartia laricifolia	1.2
Saxifraga reflexa	r.1
Senecio conterminus	+.1
Zygadenus elegans	1.1

Overstory stratum:

Trees -

Populus tacamahacca	+.2
P. tremuloides	r.1

Shrubs -

Rosa acicularis	+.1

The primary controlling factor in the formation of this community is believed by the writer to be the water supply--not the temperature. Desiccation of soil and plants by wind in both summer and winter and the intense insolation received during the growing season contribute to make the site too dry for optimum community development. The resulting sparse vegetation exercises but little control over intense frost action, which in itself inhibits plant colonization and community establishment.

The problem presented by a site of discontinuous ground cover is one of fundamental importance, and raises the question which can be only partly answered--if certain species can grow on the site as individuals, why is not the entire ground surface occupied by these species? Of course sufficient time must have elapsed to have made this possible, if not prevented by physical or biotic deterrents. It is well known that in many arid communities of the temperate zone a discontinuous ground cover is evidence that the water supply is critical, and that as many plants are growing here as the water supply will permit. In such areas the subsurface occupancy of the site by plant roots may be complete, although the above-ground parts may be rather widely spaced. At this Eagle site, although water supply may be the limiting factor, the subsurface soil was not completely occupied by roots--in fact, the few roots encountered in soil profile studies was a noteworthy feature. The answer to this problem at this site may be that the unstable soil, due to frost action and gravitational displacement on a moderate to steep slope, disrupted individual plants at sufficiently frequent intervals to prevent a closed cover developing.

In ground cover formation there is a relationship of the life span of an individual plant to the frequency of new plant establishment as controlled by the environment. If the average individual life spans of the perennial species of a site are longer than the period of time necessary for invasion and ecesis to replace these individuals with new plants, the site will tend to have a continuous ground cover and there will be competition between individual plants. On the other hand, if the average life span of these species is shorter than the period of time necessary to replace these individuals the site will have a discontinuous ground cover and little or no competition between individual plants. Thus the development of the plant community on these unstable sites is affected not only by the quantity of diaspores supplied to the site and the coincidence of their arrival with climatic conditions favorable to their growth, but also by the chance factor of which species, with their characteristic life spans, reach the site. The plant communities on adjacent unstable substrates may show little resemblance to each other--the vegetational pattern of the area as a whole is determined by a complex interaction of processes, some of which are strongly influenced by chance. These communities taken together may look as if they constitute randomized assemblages of the plant species that occur in the region.

The vegetation of arctic and boreal regions is unique in that there are very few annual plants present. Everywhere perennial plants predominate, often to the exclusion of annuals. However, the life span of a perennial plant is not indefinitely long, but is controlled by genetic and environmental factors. Whereas some specimens of a perennial species may attain a great age at a location, others in sites of more extreme environment will be found dead or dying at a relatively young age. The latter sites require a more rapid rate of invasion and ecesis of new individuals if a continuous cover is to be maintained, but it is precisely at such sites that the environmental extremes operate to diminish the rate of such colonization. The frequency of individual plant establishment is controlled by the abundance of diaspores supplied to the area and the fortuitous coordination of climatic and edaphic variables. The more nearly the limit of plant species tolerance at which these variables exist, the less frequently will new colonization succeed, and concomitantly, the fewer diaspores that are likely to reach the area. Frost action is but one of these variables, and at one site it may appear to dominate these relationships, whereas at another site the degree of wetness or gravitational stability may predominate. At sites of discontinuous cover individual plants are scarcely competing with each other for space, but are in effect "competing" with the climatic or edaphic factors that are most nearly limiting at the time of invasion. We may eliminate from consideration the factor of inhibitory root secretions by the individual plants, which has been found by some investigators to be a method by which individuals maintain their isolation, for at more favorable sites at these northern locations all the species may grow closely together to form a continuous ground cover.

The importance of chance as a determiner of present plant community composition is ordinarily inversely proportional to the length of time since primary invasion. In communities of an intense frost action environment the occurrence of predictable species composition is not to be expected, for chance is an important element in determining the composition at a particular time of observation--the passing of time does not exert its usual influence in eliminating the expression of the chance factor, because of the unstable condition of the soil. These species appear to be adapted to "primary" invasion, and are characterized by Drury (1956, p. 102) as follows: "All species must remain adapted to disturbed conditions and be capable of 'pioneering'."

The fact that some species of plants do colonize these generally unfavorable areas suggests that there must be certain compensating factors in operation in arctic and boreal environments which ameliorate the effects of this "hostile" environment. These are discussed as follows:

1. The physical disturbance of the soil by frost action promotes a relatively favorable soil structure for microbial action in the upper soil layers during the growing season. This subject has been discussed in prior paragraphs in relation to nitrogen and phosphorus utilization.

2. The bare mineral soil of frost scars thaws earlier and warms up earlier in the spring than does soil with an organic surface layer. It also freezes earlier in the autumn--however, days gained at the beginning of the growing season by the mineral soil sites are more important to plants than days gained at the end of the growing season by organic soils, insofar as the establishment of new seedlings is concerned, for the reason that seedlings depend on favorable soil temperature (not just favorable air temperature) to begin their development from seeds, and also that a well-established plant is less injured by the onset of frosts than an individual not so well established. For these reasons alone the use of organic mulches on agricultural lands in Alaska is not recommended, although other effects of mulches would be very beneficial (Kellogg and Nygard, 1951, p. 125). Many species of northern plants can complete seed maturation during periods of intermittent frosts, and the earlier freezing of the mineral soil is of no particular disadvantage to these plants.

3. The seeds of certain species may germinate better in a mineral soil than in a moss- or lichen-covered soil. This has been demonstrated by Godman (1953, p. 1), who writes, "Surface moss, characteristic of climax forests of Southeast Alaska presents a real danger to satisfactory

regeneration on cutover areas, if left undisturbed by logging. First year records from artificial seeding showed that only a fifth as many seeds germinated in the moss as on mineral soil and these had 28 percent lower survival." Similar effects of a moss mat on forest establishment in England is reported by Richards (1932, p. 303). Allen (1929) has studied the effect of a Cladonia ground cover on seedling establishment. She reports that seeds on the mat surface germinate poorly, and that shrinking and swelling of the lichens with changes in water content heave out seedlings whose cotyledons extend through the mat. It is not known if these data can be applied to plant species of the intense frost action regions, but this is a factor to consider in explaining community composition of mineral soil sites. It is certain that among species there are varying abilities in this respect, because some species are never found on mineral soil sites, whereas others are common on such sites.

4. The writer suggests that relative abilities of seedlings to use the various compounds of essential elements may be of importance in determining colonization and community species composition on these frost action sites. For example, it can be stated as a generalization that seedlings of a species are better able to use ammonium carbonate than are adults of the same species. If this ability is directly related to plant age, it would tend to favor seedling invasion of certain sites supplied with this compound (due to improved aeration by frost action) and would contribute to a shorter life of the adults with the consequent uncertainty of ecesis on the site. This difference in ability to use ammoniacal nitrogen also exists between adults of

different species (Allison, 1931). This known nutritional peculiarity suggests the possibility of others occurring, and that more research is needed in this matter.

5. The preponderance of perennial plants in these northern regions. Once the perennial plant is successful in becoming established as a result of the infrequent combination of favorable conditions it may, in the adult stage, survive many seasons having climatic and edaphic characteristics that prevent seedlings becoming established. In many arctic and boreal regions some plant species may not mature seeds every year--they are living at a point so near their tolerance limit that only in exceptionally favorable years is sexual reproduction possible. Annual plants cannot exist under these conditions unless provided with a delayed seed germination mechanism or other special adaptive features (i.e., ability to mature seeds under a snow cover).

6. Soil surface microorganisms whose presence is favored by exposed mineral soil, may be an important compensating factor on these sites. The direct effect of algae in plant succession on tundra soils of the U.S.S.R. is stated by Shtina (1960, p. 630-631) as follows: "In polygonal tundras, for example, on the bare vegetation-free patches thin crusts composed of various green, yellow-green and blue-green algae are found; the base of this layer is mostly compiled by Stratonostoc commune (Vauch.) Elenk. In connection with this the important role of algae in the overgrowth of bare patches and accumulation of organic substances in the primitive tundra soil was noted."

The plant community near Eagle that contrasts with Community A, although both have developed in the same climate, is presented below.

Community B. Relevé of a northwest-facing slope in the valley of American and Mission Creeks near Eagle, interior Alaska.

The bedrock is essentially the same as that at Community A, but it is much less weathered due to its exposure, and the soil under the dense vegetation mat is shallow and stony. This forested site, which is actually an old colluvial slope, is adjacent to talus "rivers" (Figure 18). Altitude, 1,500 feet. Area, 10 X 10 meters. Observed June 28, 1960.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
Pleurozium schreberi	1.3
Polytrichum commune	2.4
Rhacomitrium lanuginosum (limited to exposed colluvium)	+.3
Grasses - none present	
Forbs -	
Geocaulon lividum	1.3
Silene acaulis (limited to exposed colluvium)	+.3
Shrub stratum:	
Betula nana subsp. *exilis*	+.2
Rosa acicularis	+.1
Vaccinium uliginosum	2.2
V. vitis-idaea	+.3

Figure 18. Forest of Betula resinifera and Picea glauca near Eagle, Alaska. The closed cover prevailing in most of the forest reduces the number of herbs and shrubs, and contributes to the accumulation of deep litter. The nature of the underlying soil varies with the amount and acidity of this litter--often the presence or absence of Polytrichum species is the deciding factor of soil type formation in this mixed forest. June 29, 1960.

Overstory stratum:

Alnus crispa	r.1
Betula resinifera	4.4
Picea glauca	1.1
P. mariana	r.1

This birch forest community was scarcely affected by frost action--the only observed results of this effect were the stones which appeared to have been slowly worked upward through the vegetation mat by the heaving effect of freezing. The favorable exposure of this site had permitted sufficient moisture for the development of a forest with a dense moss mat under the trees. The winter minimum temperature here is undoubtedly very close to that of Community A, and this forested area most probably had fewer "degree days" above 50°F. because of the northwest exposure and the shade of the trees than did Community A, yet had a dense vegetation cover in contrast to the sparse community of intense frost action on the southern exposure. The weather bureau records at the Eagle station, about two miles distant from each site, would be of little value in predicting the difference in vegetation of the two sites.

The microclimatic difference at these two sites is principally in the lesser insolation received by Community B and the resulting lower soil temperature over intermittent permafrost. The reduction of soil temperature by permafrost may be more significant in diminishing soil microbial activity than in its direct effect on vascular plants. Insolation can compensate for the latter, but not to the same extent for the former. Baldanzi (1960, p. 527) states in this connection, "Insolation is important for the plants in vegetal matter production but not for microorganisms which decompose it, for which soil temperature is very important."

The comparison of these two communities shows again a general characteristic of boreal and arctic plant communities that has been discussed earlier. In a region of climatic extremes single variable non-climatic factors can only with difficulty be evaluated in their effects on community development because of the over-riding influence of microclimate.

SECOND HALF,

OPEN FILE REPORT

CHAPTER IV.

THE CONTROL OF PLANT COMMUNITY SPECIES COMPOSITION BY SOIL FACTORS

A. Information Derived from Botanical Prospecting.

The control that soil exercises over the plant community is ordinarily through its moisture content, texture and structure, temperature, and the supply of major and minor nutrient elements. These factors of soil influence on plants have been discussed already, and it has been shown that plants can cause certain changes in these factors by their growth and decomposition. There may be, however, certain properties of soils that are generally deleterious to plants that the vegetation can change but little, if at all. In this category are some of the metallic elements, if present in greater than "trace" amounts. The concentration of these metals in soils is ordinarily related to mineralization of the bedrock, particularly if they occur as ore. If the soil overlying this mineralization is residual, it is likely to contain those minerals that survive weathering during the disintegration of the soil parent material. If the soil is non-sedentary the mineral elements in the underlying bedrock may migrate upward into this soil in capillary water, by ionic movement, by the action of burrowing animals, and by upward transportation in plant roots. This property of soil to indicate underlying ore concentrations is the basis for geochemical prospecting by chemical analysis of the soil, Plants may indicate this anomalous concentration in the soil, or by means of their roots effectively sample the ore body itself. This method of locating mineral concentrations has been variously termed "biogeochemical," "geobotanical," or "botanical" prospecting, and the principles involved and methods of application have been summarized by Nasvetailova (1955), Hawkes (1957), Carlisle and Cleveland (1958), and others.

There are four types of plant reactions to abnormal concentrations of certain elements or compounds in the soil: (1) changes in morphology (size, shape or color of parts, or habit of growth), (2) certain species by their presence indicate requirements for, or tolerances of particular elements, or by their local absence, indicate intolerance (the so-called "indicator" plants), (3) the plant community may show variation in species composition over a particular kind of mineral concentration, and (4) the plant tissue may show variation from the normal range of element content. Botanical prospecting has come to mean the employment of only the first three principles listed above, and the discussion in this section will follow this usage.

1. Changes in morphology. Botanical prospecting is greatly simplified if the vegetation of the area gives morphological indication of anomalous mineralization in the bedrock. When the species of plant showing variation and the nature of the variation have been correlated with the occurrence of a specific element in anomalous amounts visual inspection of the region from the ground or from the air may clearly reveal mineralized areas. This method has been used with success in the Soviet Union (Victorov 1955, p. 82-172), also elsewhere by other investigators. In field studies by the writer at Great Bear Lake, Northwest Territories, Canada in 1948 conspicuous morphological variation was found in *Vaccinium uliginosum* and *Epilobium angustifolium* that were growing over pitchblende outcrops. The *Vaccinium* plants

bore fruits of abnormal shapes (cubical, elongate, pyriform, and depressed-spherical), and each shape of fruit was borne only by clonal descendants of one plant. Many specimens of this species were examined that were not growing near radiation sources, in both Canada and Alaska, and the fruits were found to be quite uniform in shape. The Epilobium growing over pitchblende bore flowers that formed a series of color variations from pure white through pink, normal magenta, to deep purplish-magenta suggestive of mutations, probably produced by radiation from the pitchblende. Color variations are known to occur in widely separated areas of the range of this plant (Fernald 1918, p. 4); however so much variation within one colony, as was found at Great Bear Lake, strongly suggests the causal influence of the underlying ore. The writer gave particular attention to the occurrence of flower color variation in Epilobium during three summer field seasons of wide travel in Alaska and only in the vicinity of Circle Hot Springs, central Yukon district were both white and pink color forms found. It so happens that this is one of the areas in interior Alaska having higher than background radiation (White and Tolbert, 1954), which is associated with the granitic intrusives that are the source of the hot springs. Since completing these field studies the writer has been informed of another occurrence of color variation in this plant (R. M. Chapman, personal communication, 1961) in interior Alaska, at a site where the geologic structure favors the occurrence of anomalous radiation, but this has not been proven.

On the serpentine outcrop at West Fork, near Livengood, central Yukon district, an anomalous form of Solidago was found in which ray flowers were lacking, and the tubular flowers were green. This plant, which appeared normal in other features, formed a colony of several dozen plants restricted to the thin lithosol just over the serpentine. Soil samples taken on a traverse over this outcrop contained the following metals: nickel, 300 to 3,000 ppm, chromium 400 to 800 ppm, and copper 25 to 80 ppm. These upper values are very high amounts of nickel and chromium for soils to contain. The maxima in plant ash from this site were: nickel, 1,100 ppm, copper 600 ppm, chromium not analyzed. There were no other examples of morphological variation found during these studies that could be attributed to anomalous metals in the substrate.

2. Indicator plants. These are described by Nasvetailova (1955) as belonging to two groups: (1) "Universal indicators," which includes those plants species that are found, throughout their total distribution, to be exclusively adapted to soils or rocks having a particular mineral content, and (2) "local indicators," which are common, widely-distributed plants that in some local situations may indicate certain properties of the soils and rocks. Several species of plants occur in Europe that have long been known to be restricted to substrates rich in certain elements, as for example Viola calaminaria and Thlaspi calaminare, which are found only on or near zinc deposits. In studies of the Colorado Plateau, Cannon (1957, p. 404) states, "Selenium-indicator plants are the only group definitely known to be completely dependent on the presence or absence of a single element. The selenium indicators . . .

include a tribe of Astragalus species, Stanleya, Aster venustus, Oryzopsis, and several other plants." She states further that selenium concentration in carnotite ore caused a marked tendency for the Astragalus group to grow more abundantly in the vicinity of these ore deposits. These plants which aided directly in the location of uranium ore were termed "primary indicators" by Cannon.

In these studies in Alaska no flowering plants were found that could be definitely classed as universal or primary indicators. However, several species of bryophytes that have been classified as universal indicators under the general term "copper mosses" were found associated with mineral deposits. Resistance of mosses to heavy metals is discussed by Url (1956), and the association of a moss species with recent syngenetic copper deposits is described by Fraser (1961). The moss Merceya latifolia was found only once (on copper-nickel ore deposits, Yakobi Island, Alaska) by the writer; this plant is known to occur only near copper deposits, and is one of the most widely-recognized "copper mosses " (Persson, 1956). Another moss, Oligotrichum hercynicum, was found at only seven sites in Alaska by the writer; at six of these sites it was closely associated with copper-bearing ore, sulfides with dispersed copper, or areas of presumed copper enrichment in the immediate vicinity of copper mines. To determine whether this moss is a "universal indicator" requires further study; at least it is definitely established to have a high tolerance to copper and certain associated minerals. In these studies the liverwort Gymnocolea acutiloba was found only on Latouche Island and only in close association with copper mineralization (Shacklette, 1961a). This species is known to be usually, but not exclusively, associated with copper deposits throughout its world-wide range, and its occurrence is an an indication of the likelihood of mineralized substrates.

Local indicator species are much more likely to be found than are universal indicators; however it is more difficult to relate them to a specific metal, and their usefulness varies from place to place. As a general principle it can be stated that any plant that has a high degree of tolerance for abnormal metallic concentrations is a potential local indicator. Very few vascular plants were found in these studies to have a high tolerance for lead, zinc, or copper. Where these metals were in high concentration, such as in finely pulverized ore around abandoned mills, or on old dumps of ore in the vicinity of mines, vascular plants were notably absent, although bryophytes often grew in profusion. Mineral-related bryophyte communities of Latouche Island, Alaska have been discussed in detail by the writer (1961). One species of vascular plant, Saxifraga ferruginea, was found on this island to have a high resistance to copper concentration and to form dense, pure stands in soil heavily salted with pulverized copper ore. A few other vascular species occurred on this salted ground, but were barely existing and most probably were not reproducing.

During the field work in Alaska 1,750 collections of bryophytes were made, and these were tabulated by species to indicate (a) those growing directly on mineralized substrates, and (b) those growing sufficiently near a mineral deposit to be presumed to receive anomalous amounts of the mineral from their substrates (Figure 19). These factors, as well as other factors of the environment, are

Figure 19. Bryophytes on and near a galena-sphalerite ore vein at Mahoney Creek, Revillagigedo Island, Alaska. The exposed vein at the ruler and in the foreground is precisely indicated by the dark-colored area of the liverwort *Cephalozia bicuspidata*. The surrounding black slate is vegetated with *Mnium glabrata*, *Scapania undulata* forma *pallida*, *Marsupella emarginata*, *Diplophyllum albicans*, and *Pohlia nutans*. June 15, 1958.

summarized in Table II. Analysis of the bryophytes themselves to determine mineral content is not practicable because they usually grow so near the substrate that they have heavy surface contamination which on analysis completely obscures the very small amounts that the tissues may contain. There were 32 species-occurrences of mosses and 20 species-occurrences of liverworts (the term "species-occurrence" is defined in Table II) associated with copper minerals, galena, sphalerite, and pyrite. These numbers do not represent different species--some species grew on more than one mineral. These individual species and their associated metals are given in Table I.

Both bryophytes and vascular plants showed a remarkable indifference to substrate mercury in view of its general toxicity to many commercial greenhouse plants, as well as to other plants. These studies included plants growing directly over cinnabar vein deposits, in drainage from a cinnabar mill in which metallic mercury could be found by visual inspection, and on a mountain tundra slope immediately adjacent to and on a level with the exhaust stacks from a mercury smelter. At these sites no changes of any sort in the vegetation were detected. However, some vascular species absorbed anomalous amounts of mercury, as shown by chemical analysis of their tissues.

Plant communities occurring on serpentine rocks or on soils derived principally from serpentine are of considerable interest in that the number of endemic species is often large in comparison with the total species present. This feature has been observed in many parts of the world, and the exact properties of serpentine which cause the development of these unique floras have not been specifically

Table I. Bryophytes Associated with Metallic Minerals

Species	copper minerals	galena	sphalerite	pyrite
Mosses:				
Barbula icmadophila	near	- - -	- - -	- - -
Brachythecium albicans	near	- - -	- - -	- - -
Desmatodon latifolius	near	- - -	- - -	- - -
Dichodontium pellucidum	- - -	- - -	- - -	near
Dicranum muhlenbeckii	near	- - -	- - -	- - -
Eurhynchium praelongum	- - -	on	on	- - -
Isopterygium elegans	- - -	on	on	- - -
Kiaeria blyttii	- - -	- - -	- - -	on
Lyellia lescurii	on	- - -	- - -	- - -
Merceya latifolia	on	- - -	- - -	- - -
Mnium glabrescens	- - -	near	near	- - -
Oligotrichum aligerum	- - -	- - -	- - -	on
O. hercynicum	on,near	- - -	- - -	on
O. paralellum	near	- - -	- - -	- - -
Pohlia nutans	- - -	on,near	on,near	- - -
P. rothii	near	- - -	- - -	- - -
Polytrichum piliferum	near	- - -	- - -	- - -
Rhacomitrium canescens	near	on	on	near
R. fasciculare	- - -	- - -	- - -	on
R. sudeticum	on	- - -	- - -	- - -
Sphagnum cuspidatum	- - -	- - -	- - -	near
Tortula norvegica	near	- - -	- - -	- - -

Table I. Bryophytes Associated with Metallic Minerals (continued)

Species	copper minerals	galena	sphalerite	pyrite
Liverworts:				
Calypogeia mulleriana	- - -	- - -	- - -	on
Cephalozia bicuspidata	- - -	on	on	on
C. media	on	- - -	- - -	- - -
Diplophyllum albicans	- - -	on,near	on,near	- - -
Frullania nisqualensis	- - -	on	on	- - -
Gymnocolea acutiloba	near	- - -	- - -	- - -
Marsupella emarginata	- - -	near	near	- - -
Nardia scalaris	- - -	- - -	- - -	on
Scapania undulata	on	near	near	on
Tritomaria quinquedentata	near	- - -	- - -	- - -

determined. Because serpentine is neither a specific mineral nor an exact technical term it obviously cannot be defined on the basis of its chemical content. It is in the class of mafic or ultramafic rocks, is ordinarily green to dark-colored, and is generally easily recognized in the field. Its low content of major essential elements (especially phosphorus) is given by some investigators as its most important characteristic related to plant growth, whereas others consider the usually excessive amounts of certain metallic elements to be the major influence. Walker (1954, p.266), who studied the factors affecting vegetation on serpentine soils of Washington, writes, "They differ from other soils in these principal characteristics: low contents of total and adsorbed calcium, high magnesium content, and high contents of chromium and nickel. . . . It is concluded that plants which grow well on serpentine areas must first be tolerant of low calcium levels, and, in addition, must be tolerant of one or more of the following in special situations: high concentration of nickel and chromium, high magnesium, low levels of major nutrients, low available molybdenum, and unfavorable physical aspects of shallow soils."

The flora of a serpentine outcrop has been given in Chapter III, and the conclusion drawn that no effects were observed of this substrate reducing the number of plant species by its limited supply of essential nutrient elements, or that its content of metallic elements differentiated the flora of this site from that of adjacent sites having different soil parent material (the anomalous Solidago form constituting a possible exception). This indifference to this substrate not only indicates the general oligotropic nature of these plant species of the region in regard to nutrient elements, but also shows that their tolerance for nickel and chromium is high. Judging from the contrary observations on temperate zone serpentine floras, these boreal and arctic floras are believed to be unique in their degree of indifference to the peculiar features of serpentine soils. This suggests a negligible usefulness of botanical prospecting for nickel and chromium in this region; however, if these elements occur in ore grade, it is possible that the tolerance limits of certain species might be exceeded.

Other serpentine outcrops in Alaska were studied, with the same general conclusions resulting as for the Livengood site mentioned above. Differences in the vegetation at the Eagle serpentine sites have been attributed to factors of soil stability and microclimate (Chapter III). The floras of adjacent, but non-serpentine, sites could not be differentiated from the former sites on the basis of the effects of soil parent material. However, it is interesting to note that four species of flowering plants not previously reported as occurring in Alaska, and other species that are rare in this state, were found in these studies only on the Eagle serpentine outcrop (Figure 20). Because of the small amount of plant collecting that was done on other substrates in this area the conclusion is not warranted that these species are limited in their occurrence to serpentine. However, it can be said that they have a high degree of tolerance to the peculiar conditions associated with serpentine.

Figure 20. Herbaceous community on the lower slope of Mission Bluff at Eagle, Alaska. The lithosol of this serpentine talus slope supports a discontinuous cover of very showy flowering plants, including a number of rare species and species not previously reported to occur in Alaska. June 26, 1960.

These species, with their Abundance-Cover and Sociability values, are listed as follows (size of area, 10 X 10 meters):

Campanula aurita	+.2
Cryptantha sobolifera (first report for Alaska)	+.2
Erigeron compositus var. discoideus (second report for Alaska)	r.3
Eriogonum flavum (first report for Alaska)	r.1
Erysimum angustatum (first report for Alaska)	1.1
Erysimum inconspicuum	+.2
Linum perenne subsp. lewisii	1.1
Oxytropis viscida forma albida (second report for Alaska)	1.1
Phacelia mollis	+.1
Phacelia sericea (first report for Alaska)	r.1
Senecio conterminus	1.1
Silene repens subsp. purpurata	+.1

Other species found at this site that are not rare in Alaska, but which were not listed as occurring at the Livengood serpentine area, are noteworthy in that they have a tolerance for such sites and are listed below:

Arabis lyrata subsp. kamchatica	1.1
Artemisia frigida	1.3
Hedysarum mackenzii	1.1
Populus tacamahacca	+.2
Rosa acicularis	+.1
Saxifraga reflexa	r.1

In conclusion, it can be stated that the influence of anomalous amounts of substrate metals is very marked in certain bryophyte communities, which is probably related to their degree of intimate association with the substrate as compared to that of vascular plants. Some species are very resistant to high metal concentrations, and no explanation is offered here for this resistance. It is suggested, however, that the apparent resistance may in fact often be illusory in respect to the actual situation that obtains. Bryophytes probably are largely ectohydric--their water supply does not necessarily come from the substrate, but may be absorbed from the air, or directly from precipitation. In an environment in which the humidity is high and the substrate is ordinarily saturated (as at the Latouche Island site) but little substrate water may ascend the plant by external capillarity. However, the protonemata essential for their initial establishment on isolated sites are in intimate contact with the water of the substrate and must possess a tolerance for the mineral content of this water if they are to survive. The absence of a species from mineralized sites constitutes negative evidence that, unless supported by numerous observations of its limited occurrence and sharp lines of demarcation in its growth on mineralized substrates, cannot be interpreted as caused by a lack of tolerance. Nevertheless, for whatever reason, the fact remains that some bryophyte species do indicate mineralized areas by their occurrence, whereas others have a high tolerance for heavy metals and their occurrence in dense stands on certain sites, to the exclusion of most other species, suggests substrate minerals in anomalous amounts.

The influence of excessive metal concentrations on plants is limited to relatively few sites in Alaska, inasmuch as ore outcrops are not common. Vascular plants were not found to be inhibited in their growth on or near outcrops, but at ore mills, dumps, and tailings (which are areas of artificial mineral concentration) the anomalous amounts of certain metals may prevent revegetation of the sites. Changes in morphology of two plant species were observed to occur only in areas of anomalous substrate radiation. This is a very special substrate effect, believed to alter the genetic structure of the plant cells which causes the unusual forms to develop.

The evidence of substrate influence on vegetation presented by botanical prospecting may be very definite and striking, but it occurs so rarely in the arctic and boreal regions as a whole that its usefulness is believed to be very limited. However, the indifference of most of the species of vascular plants to substrate metal concentration, insofar as growth and reproduction is concerned, is presented as a noteworthy feature of this flora.

B. Evidence of the Control of Vascular Plant Communities by Soil.

1. The genetic classification of soils. The objective of this discussion is to determine if the types of soils, as defined and named in the genetic system, exert a controlling effect on the currently-developing and subsequently-invading plant communities. The many effects of soil properties on plant community development and composition in arctic and boreal environments have been discussed in Chapter III. In these analyses the physical and chemical properties of soils were emphasized in their separate and combined effects on

the individual plant and on the plant community. In this study of many regions of Alaska examples of all the recognized Great Soil Groups (except Ground-Water Podzols) were observed and the plant communities on each were studied.

When types of soils are discussed by the pedologist the category-type name is ordinarily stated or implied--not some descriptive appellation emphasizing a physical or climatic property as "stony soils" or "cold soils." The formal categorization in common use is that currently followed by the soil scientists of the U. S. Department of Agriculture and affiliated agencies which was founded by Marbut, Baldwin, Jenny, Kellogg, and others largely on the basis of Russian, Western European, and American soil genesis concepts. It is not within the scope of this report to discuss this classification in detail; rather, the system will be used in application to these northern soils as presented by Kellogg and Nygard (1951), Tedrow and Cantlon (1959), Tedrow and Hill (1955) and others, with some modifications by the writer.

In order to achieve simplicity of presentation, the genetic classification of arctic and boreal soils will be outlined in a key, which enables one at a glance to grasp the essence of organization of the system, and at the same time gives a concise characterization of the properties or genetic factors of each category.

A Key to the Identification of the Great Soil Groups of Arctic and Boreal Regions

I. Soils having a well-developed profile, formed under conditions of good drainage -- Zonal Soils

II. Soils having some profile development, but formed under conditions of poor drainage or other profile-inhibiting factor -- Intrazonal Soils

III. Soils having no profile development (i.e., upper layers undifferentiated from the parent soil material) -- Azonal Soils

---

I. Zonal Soils

1a. With a distinct whitish to gray zone just above the B Horizon - Podzols

1b. Soils without above-mentioned Horizon - 2

- 2a. Having a compacted B Horizon, indicating illuviation; formed in forested subarctic regions - Subarctic Brown Forest Soils
- 2b. Lacking a distinct B Horizon, indicating lack of illuviation; found in arctic tundra regions - Arctic Brown Soils

II. Intrazonal Soils

1a. With hardpan in the B Horizon - Ground-Water Podzols

1b. Without hardpan - 2

- 2a. Soils of high elevations; not completely saturated; both gleization and calcification evident - Alpine Meadow Soils
- 2b. Soils of low elevations; completely saturated most of the year; gleization only may be present - 3

3a. With a tough, fibrous mat over the surface, above a 2 to 10 inch layer of dark humus soil, overlying a lighter gray or mottled gley zone - Tundra Soils

3b. With a surface layer of peaty or mucky material; with or without a gley zone - 4

4a. Soils containing appreciable amounts of both organic and inorganic material lying on a light gray gley zone - Half-Bog Soils

4b. Soils principally organic in all horizons, without a gley zone - Bog Soils

III. Azonal Soils

1a. Soils of fluvial origin (sand, silt, and gravel), without definite horizons but often stratified - Alluvial Soils

1b. Soils not of fluvial origin - 2

2a. Soils composed of partly weathered loose rock, usually on steep slopes, closely related to bedrock; or the nearly barren weathered bedrock - Lithosols

2b. Soils composed of unconsolidated rock of any size, including loess, volcanic ash, morainic debris, beach sands, exposed cuts of unconsolidated rock, and colluvium - Regosols

It can be seen that this classification system is based on properties that the soil now has, on the qualities of the physical environment of the soil, and also on genetic processes that are presumed to have made it what it now is. Although the general philosophy of the system is that of genetic determinism, the actual categorization is obviously a posteriori--the soils are taken for what they now are and fitted, with a certain degree of success, into postulated causal factors and the whole presented as a genetic system. There is much experimental and observational evidence that the soil-forming processes do operate as postulated. Agricultural soils literature is replete with reports of the effects of tillage and erosion on soil profile maintenance and alteration.

2. Soil Groups, soil profiles, and associated plant communities. The effect of soils, as considered in this discussion, in controlling plant communities becomes the question of whether the named Great Soil Groups (Podzol, Bog, Tundra, Alpine Meadow, etc.) can be related to their support of specific plant communities as presently existing in the regions under consideration. This can be best answered by giving some actual examples of plant communities and their underlying soils, some of which were found to form a series of transitions with definite spatial relationships to some factor or factors of microclimate or topography.

a. Half-Bog and Bog Soils on Yakobi Island, Alaska. The most common Soil Group in upper Bohemia Basin on this island is the Half-Bog (Figure 21). Soils of this Group are moist to very wet or saturated, depending on the degree of slope and drainage factors, because of the very heavy precipitation (about 85 inches annually) and the cool climate (January mean, 43.6°F; August mean, 55.9°F) (U. S. Weather Bureau, 1943). The soil A horizon (largely undifferentiated) ranges from 0.3 foot to 2.5 feet in thickness and commonly is at least 1 foot thick. The B and C horizons are not clearly distinct near their contact owing to frost action, solifluction, and the movement of abundant vadose water which causes them to be somewhat intermixed.

Figure 21. Profile of Half-Bog soil, Bohemia Basin, Yakobi Island, Alaska. The A horizon is characterized by its darker color owing to high organic content, and the abundance of roots. The B and C horizons are more yellowish and have a larger proportion of mineral fraction; however, disturbance of the soil due to frost action and soil creep downslope has prevented the formation of sharply delimited zonation. This hole was blasted with dynamite, which resulted in the fracturing of the bedrock shown in the center of the hole. June 18, 1957.

On many of the steeper slopes the soil is immediately underlain by talus rather than by undisturbed bedrock, and the soil has infiltrated between the blocks, essentially obliterating horizon zonation.

The postulated genesis of these soils shown in profile in Figure 22, involving the factors of parent material, slope, elevation, drainage, and vegetation, follows.

The better drained forested area of sample sites 4 through 7, with a varied understory vegetation, has the shallowest soil profile represented here, and is characterized by the relatively thin A horizon with a conversely corresponding increase in the B horizon, which indicates active percolation of water. This results in the maintenance of a shallow A horizon by eluviation of the decomposed organic matter. The process requires aeration of the top layers, which is provided here by the relief and the permeable substrate. The material that is removed from the A horizon is deposited in the B horizon (illuviation). The ground cover plant communities under the forest vary according to the edaphic factors and the biological control asserted by the tree species as they affect light penetration and the nature of the humus of the A_{oo} and A_o horizons. These sample sites are classified as Half-Bog Soils, and have a thick B horizon with varying degrees of greenish to bluish color indicating the extent of gleization.

Sample sites 8 and 9, on slopes at the sides of the more level area, have a deep A horizon that appears not to have entirely formed in place, but to have included additional soil provided by downslope movement. The soil formed here is an intergrade subtype of mixed Bog and Half-Bog composition. The slope at and above site 8 is a

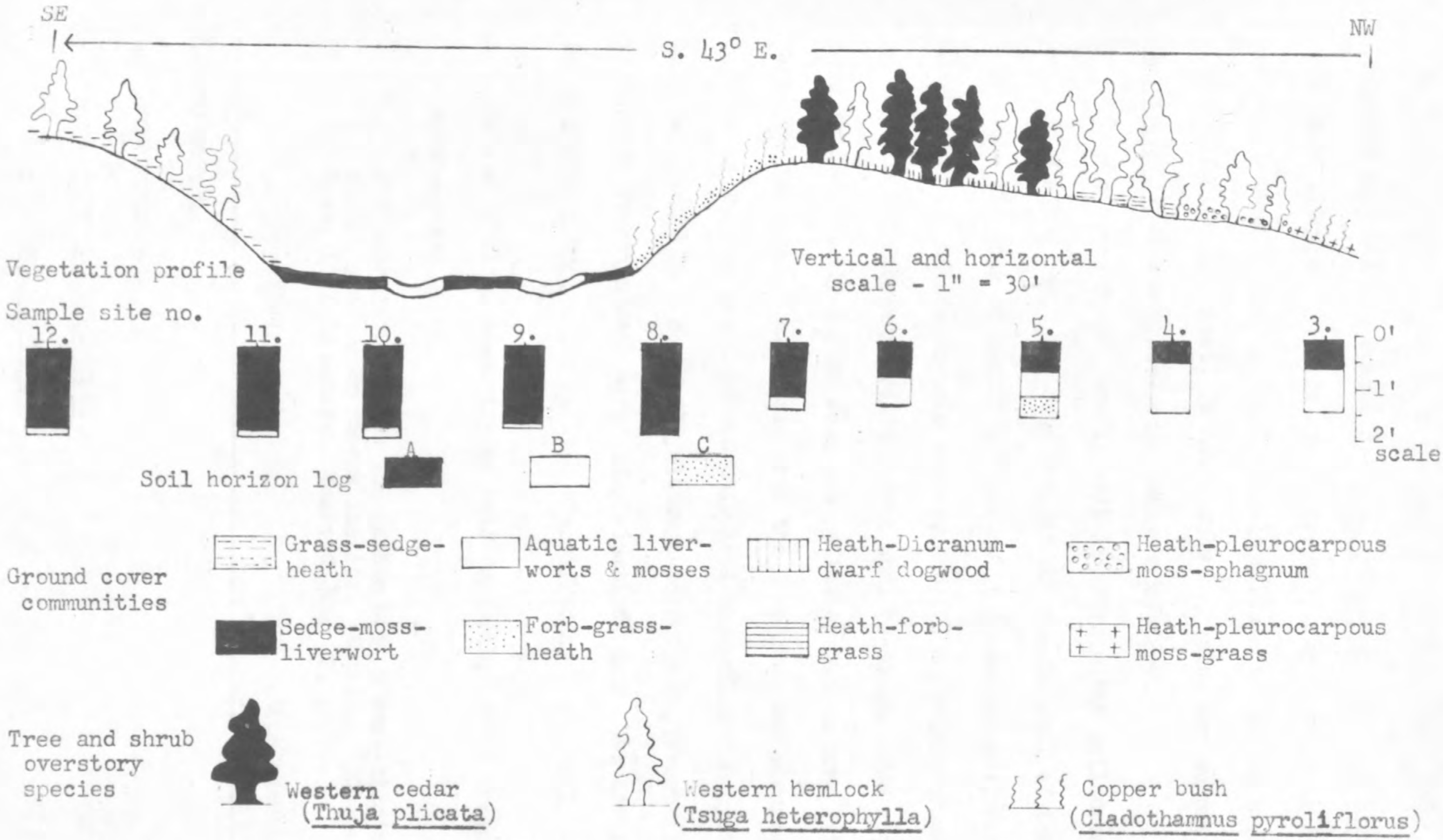


Figure 22. Cross-section diagram along traverse A, Bohemia Basin, Yakobi Island showing relationship of slope, elevation, drainage, and vegetation to soil profile development.

snow bed supporting a community of Cladothamnus pyroliflorus, grasses, and forbs (Figure 23). The slope across the drainage area from the latter, between sites 11 and 12, while similar in degree of slope to the one facing southeast, is not a snow bed, thus can support Tsuga heterophylla with a grass-sedge-heath understory.

Sample sites 9, 10, and 11 well illustrate the soil development of a soligenous bog. The deep deposit of organic soil of the A horizon indicates (1) lack of aeration (because it is saturated), resulting in slow oxidation of the organic matter, and (2) alluvial accumulation of organic and inorganic residue from upslope sites. The shallow B horizon is actually a gley zone and indicates that a very slight downward movement of materials from the A horizon has occurred. Because of lack of precision in this soil classification system, this must be classed as a Bog Soil, although somewhat different (in amount of mineral fraction and degree of gleization) from that developed in an ombroginous bug, which is also classified as a Bog Soil.

Relevé of plant community on Half-Bog Soil, Yakobi Island, southeastern Alaska.

The bedrock is norite and gabbro having some traces of nickel and copper mineralization. Altitude, 300 feet. Area, 10 X 30 meters. Observed June 12, 1957.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
Bazzania tricrenata	+.2
Dicranum fuscescens	1.3

Figure 23. Dense stand of copperbush (Cladothamnus pyroliflorus) on a snowbed slope, Bohemia Basin, Yakobi Island, Alaska. These slender shrubs are bent downslope by the heavy snow cover, and form an almost impenetrable thicket where very few other plants can grow. The shrubs had not yet begun to produce leaves when this picture was made. June 23, 1957.

Hylocomium splendens	1.2
Mnium glabrescens	r.2
Paraleucobryum enerve	+.2
Plagiothecium curvifolium	r.2
Pleurozium schreberi	3.4
Ptilidium crista-castrensis	+.2
Rhytidiadelphus loreus	2.3
Sphagnum warnstorfianum	2.4
Pteridophytes -	
Blechnum spicant	r.1
Lycopodium complanatum	+.2
Lycopodium selago	+.1
Grasses and Sedges - (grasses present, but immature)	
Carex macrochaeta	1.2
Carex pauciflora	r.1
Carex phyllomanica	+.2
Carex pleuriflora	+.2
Scirpus caespitosus subsp. *austriacus*	2.2
Forbs -	
Coptis asplenifolia	r.1
Coptis trifolia	r.2
Fauria crista-galli (Figure 24)	2.4
Gentiana douglasii	1.1
Lysichitum americanum	r.1
Veratrum eschscholtzii	+.1
Viola glabella	r.1

Figure 24. Deer cabbage (Fauria crista-galli) and copperbush (Cladothamnus pyroliflorus) community near Wilson Bay, Latouche Island, Alaska. These plants are characteristic of late snowbeds throughout southeastern Alaska. On more level sites of restricted drainage deer cabbage predominates, forming an almost pure stand. On slopes where subsurface drainage presumably is better, copperbush may reduce or eliminate the deer cabbage by shading. July 30, 1957.

Shrubs and Semi-shrubs -

Cassiope mertensiana	2.3
Cassiope stelleriana	1.3
Cornus suecica	1.4
Empetrum nigrum	+.4
Loiseleuria procumbens	+.3
Luetkea pectinata	+.4
Shrub stratum:	
Cladothamnus pyroliflorus	3.5
Menziesia ferruginea	+.1
Phyllodoce glanduliflora	1.3
Rubus spectabilis	+.2
Vaccinium alaskensis	1.2
Vaccinium ovalifolium	1.2
Vaccinium uliginosum	+.2
Tree stratum:	
Tsuga heterophylla	3.4
Thuja plicata	3.4

Relevé of plant community on Bog Soil, Yakobi Island, southeastern Alaska.(Figure 10).

The bog is developed over a valley filled with glacial debris probably consisting of igneous and metamorphic rocks. Altitude, 200 feet. Area, 10 X 10 meters. Observed June 13, 1957.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	

Anastrophyllum _donianum_ (first North American record)	r.2
Anthelia _julacea_	5.5
Kiaeria _blyttii_	r.3
Diplophyllum _albicans_	2.4
Drepanocladus _exannulatus_	+.2
Mnium _cinclidioides_	r.2
Paraleucobryum _enerve_	1.2
Philonotis _americana_	r.3
Pleuroclada _albescens_	+.2
Rhacomitrium _brevipes_	1.2
Sphagnum _balticum_	1.5
Pteridophytes -	
Equisetum _pratense_	+.2
Equisetum _variegatum_ subsp. _alaskanum_	r.2
Lycopodium _selago_	+.1
Grasses and Sedges - (grasses present, but immature)	
Carex _pleuriflora_	2.2
Eriophorum _gracile_	3.4
Forbs -	
Dodecatheon _viviparum_	+.2
Drosera _rotundifolia_	+.1
Epilobium _hornemanni_	+.3
Fauria _crista-galli_	2.4
Geum _calthifolium_	1.1
Lysichitum _americanum_	+.1

Pinguicula vulgaris	+.2
Tofieldia coccinea	1.2
Veratrum eschscholtzii	r.1
Viola langsdorfii	r.1
Shrubs -	
Andromeda polifolia	2.3
Cassiope mertensiana	+.3
Oxycoccus microcarpus	2.2
Shrub stratum:	
Kalmia polifolia	r.1
Phyllodoce glanduliflora	+.3
Ribes bracteosum	r.1
Sambucus racemosus subsp. *pubens*	+.1
Vaccinium uliginosum	+.2
Tree stratum:	
Chamaecyparis nootkatensis	+.1
Pinus contorta	r.1
Tsuga heterophylla	+.1

b. Half-Bog Soil at Mahoney Creek, Revillagigedo Island, Alaska. A grid of soil profile studies based on a traverse across a heavily-forested slope was made near the mouth of Mahoney Creek (Figure 25). The soils on the grid were all characteristic Half-Bog Soils with but little variation in profile, overlying a slate talus slope. This has been described and plotted by the writer (Shacklette, 1960) and its geochemical and biogeochemical properties analyzed. This region is far south of the permafrost zone.

Figure 25. Coastal coniferous forest at mouth of Mahoney Creek, Revillagigedo Island, Alaska. Picea sitchensis is the largest and most abundant tree in the alluvium near the shore, and a mixed forest of Tsuga heterophylla, Chamaecyparis nootkatensis, Thuja plicata, Malus fusca, Sorbus sitchensis, and Alnus crispa subsp. sinuata extends up the slope. At altitudes of 100 feet or more Tsuga mertensiana (upper left corner) becomes a prominent component of the forest, but seldom occurs at sea level. June 10, 1958.

A generalized profile of this soil is given in Figure 26. The soil varies considerably in thickness over the irregular C horizon of black slate and schist talus blocks. These blocks are loosely arranged thus have abundant spaces between them through which percolating water may pass into subsurface drainage. The area sampled is on a southerly-facing talus slope that extends downward at angles of 20 to 30 degrees from bedrock cliffs. There is very little surface runoff, in spite of the heavy precipitation (approximately 150 inches annually, U. S. Weather Bureau, 1943) because of the very absorbent organic surface layer (A_{oo} and A_o horizons) consisting of mosses and forest litter, and the usually deep, porous A horizon. This latter horizon is light brown to dark brown in color, is loose and friable, and somewhat resembles commercial "peat moss" with very little inorganic matter present. The cool temperature (mean August, 58.4°F; mean January, 33.3°F, U. S. Weather Bureau, 1943), abundant rainfall, and low evaporation rate promote the process of gleization in this peat soil. The gley (or B) horizon thus formed is brown to reddish-brown in color and of a gel-like nature, which on drying shrinks about 75 percent in volume. It forms at the contact of the A and C horizons, and ranges from 0.5 inch to 2 inches in thickness. Immediately below this horizon a deposit of inorganic soil is usually found which ranges from a surface film to a layer one inch in thickness. This deposit is gray, blue-gray, or almost black and has a very fine texture; it appears to have been derived directly from weathering of the talus blocks. It is found only on the blocks that have a relatively flat, level surface; on the more sloping surfaces it is probably removed by the abundant vadose water as fast as it is formed.

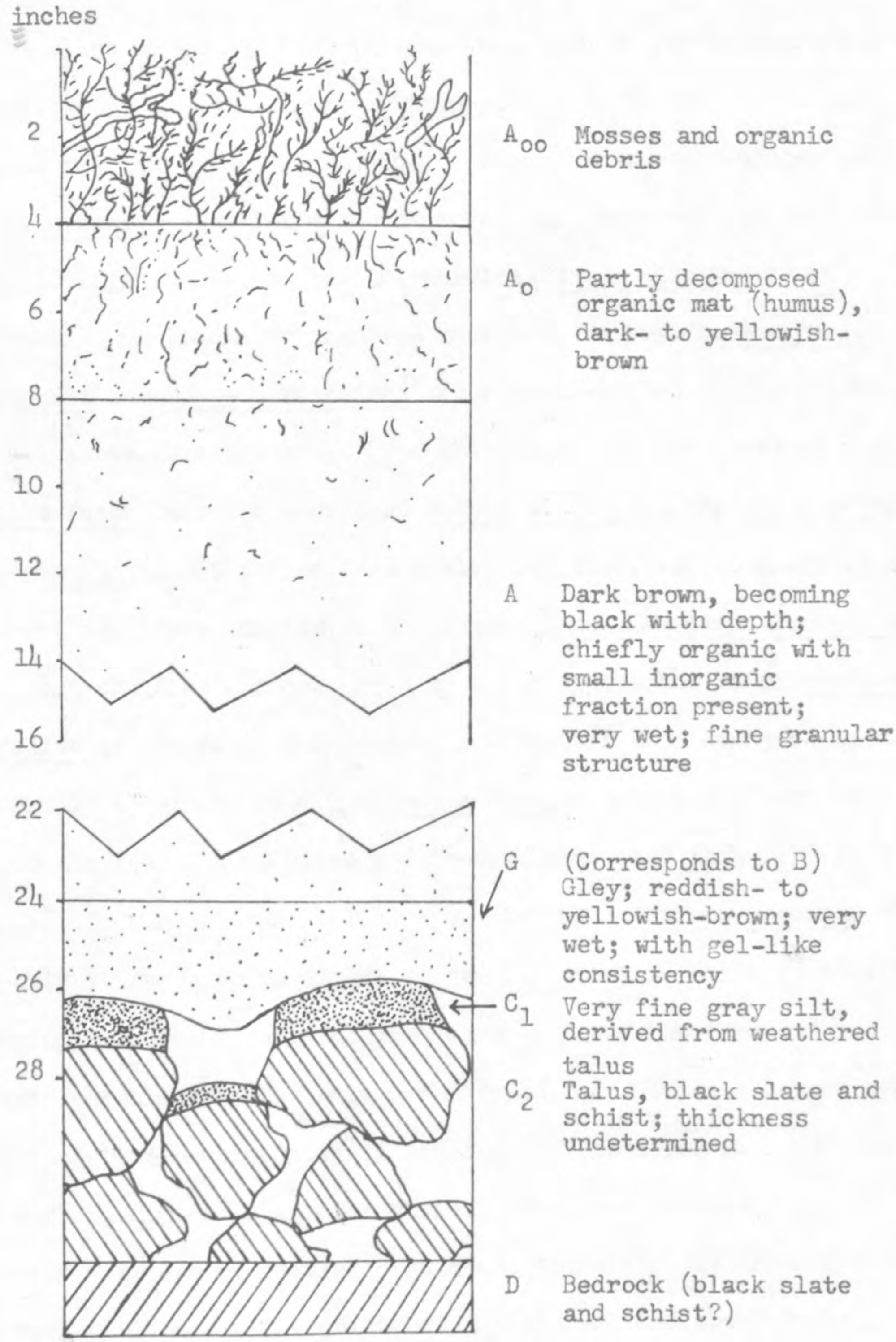


Figure 26. Soil profile diagram, Half-Bog Soil at Mahoney Creek, Revillagigedo Island, Alaska. Observed June 14, 1958.

The plant community at this site is a typical coastal spruce and hemlock forest, in which Tsuga heterophylla is ordinarily the most prominent species. This prominence is shared at certain places with Picea sitchensis, especially on the more open, disturbed areas. As competition with these two species permits, Thuja plicata occurs sporadically, particularly near the seashore. A few Chamaecyparis nootkatensis and Tsuga mertensiana occur at altitudes of about 150 feet just above this traverse. The only deciduous tree species present are Malus fusca near the shore and Sorbus sitchensis and Alnus crispa subsp. sinuata in wet drains of the slopes. The shrub communities of the forest are those adapted to the dense shade; Menziesia ferruginea is the most abundant species and occurs throughout the site. Vaccinium ovalifolium is common in the forest; however, it does not grow in the most densely shaded areas. Gaultheria shallon is a characteristic shrub of the less-shaded sites and is best developed above 150 feet altitude. The least shade tolerant semi-shrub is Cornus suecica, which grows only at the borders of the forest or in areas that were cleared for mining operations. In the most dense part of the forest three species of orchids are the only herbs found. The less dense hemlock and spruce groves, especially if composed of old trees with but few low branches, support a greater variety of herbaceous species.

Bryophytes are particularly abundant at this site, occurring in all forested areas and on the rocks of the shore and creek gorge. An epiphytic moss (Antitrichia curtipendula) and an epiphytic liverwort (Herberta sakurai subsp. sakurai) form long festoons and ball-shaped masses on the tree branches, which on some trees appear to be shading the leaves sufficiently to kill the branches. In the forested areas a deep cushion of mosses completely covers the ground, growing equally well on rock surfaces, humus soil, decaying tree trunks, and stumps. The dominant species is Hylocomium splendens, which comprises about 85 percent of the total ground cover. In the more mesic sites it is accompanied by Rhytidiadelphus loreus and R. triquetris, whereas in the more xeric sites it is associated with Pleurozium schreberi. The hydric environment of small drainage channels is dominated by Sphagnum nemoreum and S. girgensohnii. Sphagnum does not constitute a significant percent of the total moss vegetation and there is no evidence that it is increasing its extent in this forest. Many other species of bryophytes, as well as a few species of lichens, occur in this dense, humid forest, which, together with the heavy growth of shrubs and dense shade of the large trees, gives a "rain forest" aspect to the landscape. Vegetational succession occurs here in a greatly abbreviated cycle as compared to that of dryer regions. Disturbance of the area by mining operations has provided many areas where the process can be observed in operation. The vigorously growing moss mat rapidly extends over bare rocks or fallen trees, forming a dense humus layer in which Tsuga heterophylla (considered by some writers to be the "climax" species) becomes directly established, without prior herb or shrub succession. The tree seedlings germinate readily in the moss mat, which is usually moist but may at times be dry on the surface. Godman (1953) shows, as has been mentioned earlier, that these tree seeds germinate better in an inorganic soil; however, sufficient seedlings were becoming established at this site to allow a continuation of this forest type.

A list of plant species found along the traverse through this forest follows. This does not represent the total flora of even this small area of the forest, but to list all would necessitate including other soil types and other altitude ranges.

Relevé of plant community on Half-Bog Soil, Mahoney Creek, Revillagigedo Island, southeastern Alaska.

Heavily forested talus slope below slate outcrop. Galena and sphalerite mineralization in the slate bedrock, occurring as suboutcrops. Altitude, 50 to 110 feet. Area, 10 X 20 meters. Examined June 15-16, 1957.

Ground stratum:

Bryophytes -

Calypogeia mulleriana	r.2
Cephalozia bicuspidata	r.2
Dicranodontium uncinatum	r.3
Diplophyllum albicans	r.2
Drepanocladus fluitans	1.3
Eurhynchium oreganum	r.2
Hylocomium splendens	5.5
Hypnum circinale	2.2
Isothecium stoloniferum	+.2
Microdiplophyllum plicatum	r.1
Pellia neesiana	r.2
Plagiothecium undulatum	+.1
Polytrichum strictum	1.4
Rhytidiadelphus loreus	2.3
Rhytidiadelphus triquetrus	2.3

Scapania bolanderi	r.2
Scapania undulata	+.2
Sphagnum girgensohnii	1.4
Sphagnum nemoreum	1.4

Pteridophytes -

Lycopodium annotinum	+.2
Lycopodium obscurum var. dendroideum	r.1
Polypodium vulgare subsp. occidentale	r.2

Grasses and Sedges - (none found)

Forbs -

Clintonia uniflora	+.4
Coptis asplenifolia	r.2
Fauria crista-galli	r.2
Listera caurina	+.2
Listera cordata var. nephrophylla	+.2
Majanthemum dilatatum	1.3
Platanthera stricta	+.2
Streptopus amplexifolius	+.2
Tiarella trifoliata	+.2

Semi-shrub -

Cornus suecica	+.3

Shrub stratum:

Gaultheria shallon	+.2
Menziesia ferruginea	4.3
Oplopanax horridus	+.3
Rubus nutkanus	+.2

Vaccinium ovalifolium	2.2
Vaccinium parvifolium	2.2

Tree stratum:

Alnus crispa subsp. sinuata	+.1
Malus fusca	r.1
Picea sitchensis	3.1
Thuja plicata	+.1
Tsuga heterophylla	5.5

Epiphyte stratum:

Antitrichia curtipendula

Herberta sakurai subsp. sakurai

The study of the vegetation and soils of the Yakobi Island and the Revillagigedo Island sites, both having soils that must be classified as Half-Bog by the genetic system, shows that not only are the soils somewhat different, but the plant communities also are different, although having many species of plants in common. When these relationships are compared with those of the soils and plants of the Half- Bog Soil over permafrost the differences of the plant communities on this Soil Group are even more strikingly emphasized.

C. Half-Bog, Subarctic Brown Forest, and Podzol Soils of Calico Bluff, Yukon River, interior Alaska. Calico Bluff is a spectacular bluff rising almost vertically on its north face from the Yukon River about nine miles north of Eagle near the Canadian-Alaskan boundary. It is composed of thinly bedded limestone and shale of the Mississippian Calico Bluff formation (Mertie, 1930). The steep south-facing slope is a shale slide, with intermixed limestone, which at the summit meets a flat-topped ridge trending generally east and west. Whereas the active portion of the shale slide is totally bare of vegetation, there are slight ravines and benches where zonal soils have developed, favored by the good subsurface drainage and the intense insolation received.

The lowermost soil sample site was on a small terrace of the slope (Figure 27). At this site a unique soil horizon was found. The B horizon at 15 inches below the surface contained many irregular overlapping white to gray-mottled lenses 1 to 3 inches long and 1 to 2 inches thick that effervesced strongly with hydrochloric acid and had a pH of 8.0. This horizon is a zone of strong calcification that has resulted in a distinct carbonate layer. Although its color and the depth at which it occurred correspond to those of typical podzol horizons in the region, this horizon definitely is not a podzol.

The process of calcification is described by Byers, Kellogg, and others (1938, p. 970) as follows: "The calcification process results in the redistribution of calcium carbonate . . . in the soil profile without complete removal of it . . . The areas so affected are normally those of restricted rainfall . . . Since the rainfall is low, the percolation of water through the profile is not sufficient to remove wholly the calcium carbonate that existed in the parent material or was produced by reaction between carbonic acid and the calcium hydrolyzed from silicate minerals. The usual result is the development of an accumulation of calcium and magnesium carbonates at

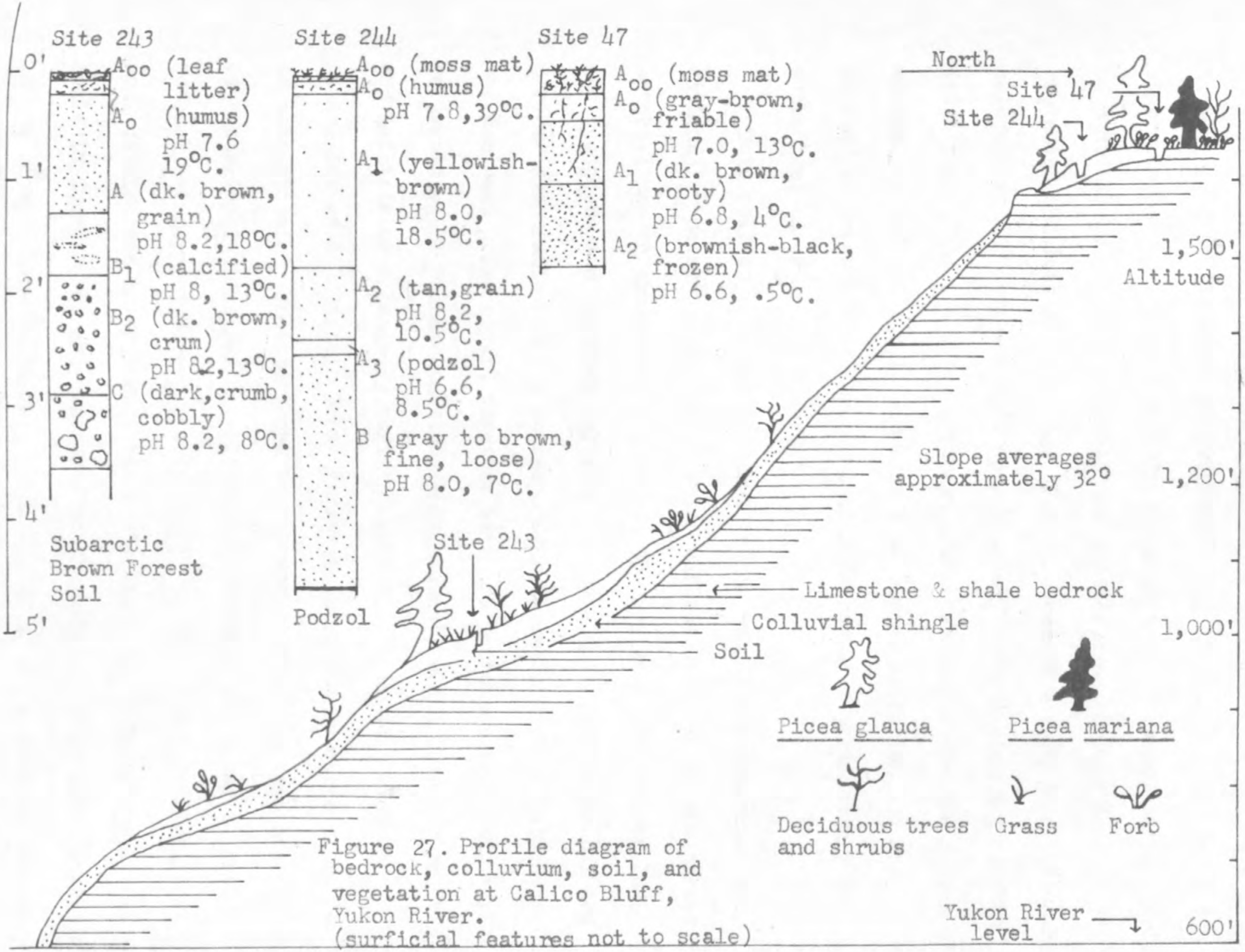


Figure 27. Profile diagram of bedrock, colluvium, soil, and vegetation at Calico Bluff, Yukon River. (surficial features not to scale)

some point in the profile below the surface, approximating the depths to which surface waters most frequently percolate . . . Grasses and other plants requiring relatively large amounts of bases, particularly of calcium, bring these bases to the surface, and through decay, replenish the loss of leaching. For this reason the surface soils are seldom strongly acid--usually approximately neutral--and may be even faintly alkaline . . . Brown Forest soils presumably owe their lack of eluviation and illuviation to this kind of calcification and are limited to areas with a forest vegetation having a particularly high content of bases in its leaves."

This soil is in an environment meeting the above-described conditions for development of a definite carbonate horizon. The parent material has an abundance of calcium, the regional rainfall is low, the steepness and southern exposure of the slope increase runoff and surface evaporation with a corresponding decrease of percolation, and the dominant grass cover, together with the deciduous trees and shrubs, recirculate the soluble calcium, thus preventing its complete removal and maintaining a basic A_0 horizon (pH 7.6). This soil must be classified as a Subarctic Brown Forest Soil having an extreme degree of calcification, because there is no more appropriate category recognized as occurring in this region, although it appears to belong to the Pedocal category of Marbut. Lutz (1956, p. 72) describes a similar soil development as follows: "An indication of the variation in Alaskan soils is found on an aspen-covered southerly slope near Sheep Mountain in the upper Matanuska Valley, where a gray or white zone of calcium carbonate accumulation may be plainly seen. The material effervesces vigorously when treated with dilute acid and has a pH of 8.32."

Relevé of plant community on Subarctic Brown Forest Soil, Calico Bluff, Yukon River, interior Alaska.

Shale and limestone talus slope, on bench where soil had accumulated to 5 feet in depth due in part to slump. Altitude ca. 1,350 feet. Area, 10 X 10 meters. Observed June 27, 1960.

Species	Abundance-Cover and Sociability values
Ground stratum:	
Bryophytes -	
Ceratodon purpureus	1.3
Hypnum cupressiforme	+.2
Tortula norvegica	+.3
Weisia viridula	1.3
Grasses -	
Calamagrostis purpurascens	4.4
Forbs -	
Anemone patens subsp. *multifida*	r.1
Hedysarum mackenzii	+.1
Galium boreale	+.2
Shrub stratum:	
Cornus stolonifera	+.2
Rosa acicularis	1.2
Shepherdia canadensis	+.1
Viburnum edule	+.1
Tree stratum:	
Picea glauca	r.1
Populus tremuloides	+.2

The second soil profile study here was at a site almost at the summit of the slope in which the soil surface was covered with a thin, interrupted mat of *Pleurozium schreberi*, with *Picea glauca* forming a discontinuous overstory. The site was just 17 feet downslope from the edge of the dense coniferous forest on the summit, and was apparently receiving additional spruce needles from this forest. The insolation was extremely intense at this site--air temperature in the shade was 89.6°F and soil temperature one-fourth inch beneath the unshaded, nearly barren ground surface was 141.8°F. The temperature inside a polster of an almost black moss (*Grimmia* sp.) was 143°F. This soil is a very well-developed Podzol and the principal factors in its development are the well-drained site and the coniferous trees which furnished an acid-forming humus. It is interesting to note that the podzol horizon had a pH of 6.6, although in a strongly basic environment, with alkaline horizons both above and below it. The plant species of this site follow.

Relevé of plant community on Podzol Soil, Calico Bluff, Yukon River, interior Alaska.

South-facing slope of 35 to 40 degrees, on bedrock of shale and limestone. Altitude, ca. 1,500 feet. Area, 10 X 10 meters. Observed June 27, 1960.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
Grimmia sp.	r.2
Pleurozium schreberi	3.4

Grasses -

Calamagrostis purpurascens	r.2
Festuca altaica	r.2

Forbs -

Arabis lyrata subsp. kamchatica	+.1
Artemisia frigida	+.2
Bupleurum americanum	+.1
Oxytropis viscida forma albida	+.1

Shrub stratum:

Alnus crispa	+.1
Juniperus communis var. montana	1.3

Tree stratum:

Picea glauca	1.1

The summit of the bluff, which is flat to slightly depressed in places, supported a dense forest of Picea glauca with a Salix species and a few Betula resinifera and Picea mariana. The ground cover was a thick mat of Hylocomium splendens and Rhytidium rugosum, in which three species of small orchids were growing. The soil under this mat was a very dark organic and mineral deposit overlying shallow permafrost, and is classified as a Half-Bog Soil. This sample site was just 17 feet from the previously-described Podzol site, yet the two are in striking contrast. The plant community at the summit bore a great physiognomic resemblance to the one developed over Half-Bog Soil at Mahoney Creek in southernmost Alaska--large conifers furnishing a dense shade, a few shade-tolerant shrub species, a dense moss mat, three species of orchids and very few other forbs, and no grasses and sedges--but all the vascular plants were different species. On the other hand, it bore little physiognomic resemblance to the plant community of the Half-Bog Soil on Yakobi Island, and contained no species in common, with the exception of mosses. A list of species of the bluff summit follows.

Relevé of plant community on Half-Bog Soil, Calico Bluff, Yukon River, interior Alaska.

Dense coniferous forest on flat to gently sloping summit underlain by permafrost. Altitude, ca. 1,500 feet. Area, 10 X 10 meters. Observed June 27, 1960.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
<u>Dicranum majus</u>	+.2
<u>Hylocomium splendens</u>	4.5
<u>Pleurozium schreberi</u>	1.2
<u>Rhytidium rugosum</u>	2.3
Pteridophytes -	
<u>Equisetum arvense</u>	r.2
Grasses and Sedges - (none)	
Forbs -	
<u>Aconitum delphinifolium</u>	+.1
<u>Corallorhiza trifida</u>	r.2
<u>Galium boreale</u>	+.2
<u>Geocaulon lividum</u>	1.2

Goodyera repens var. ophioides	r.1
Linnaea borealis subsp. americana	+.2
Mertensia paniculata	1.3
Platanthera obtusata	+.1
Shrub stratum:	
Rosa acicularis	1.1
Viburnum edule	+.1
Tree stratum:	
Betula resinifera	+.2
Picea glauca	5.4
Picea mariana	+.1
Salix pulchra	+.1

The series of very different Great Soil Groups found on Calico Bluff emphasizes the importance of water relationships in the development of a particular soil. It also illustrates the role of vegetation in determining the soil type. The major processes in the formation of these soils are calcification, podzolization, and gleization, all of which occurred within a short distance of each other. The first of these processes operated under the strong influence of the grass species and other basic humus forming species, the second depended on the acid humus from coniferous trees, and the third was promoted by the organic accumulation of the moss mat and the dense forest. It is obvious that at these sites the soil type does not determine the vegetation type, but that the vegetation responded to the different microclimates by determining the final soil type that is produced.

The early history of these sites, when they were first available for plant colonization and soil formation, is a matter of conjecture in respect to which factor was more important in directing the development toward its present state. These soils and plant communities appear to be relatively static at present--there is no indication of a further developmental tendency, for the topography dominates these developmental processes through its effect on microclimate, and significant changes in topography by aggradation is a slow process. These Soil Groups and plant communities appear to have sufficient stability and permanency to be designated physiographic climaxes.

d. Podzol, Subarctic Brown Forest, Half-Bog, and Bog Soils at Red Devil on the Kuskokwim River, Alaska. The soils of this region are of interest in that they are derived principally from a deep loess deposit, therefore the upper horizons ordinarily have but little relationship to bedrock. The climate here is subarctic, with short and rather wet summers and long, dry, cold winters. Weather observations at Sleetmute, about 6 miles southeast of Red Devil, show a mean annual temperature of 26.3°F, with means in the 50's during summer and near zero in the winter. An absolute maximum of 90°F and a minimum of -58°F have been recorded. The mean annual precipitation is about 22 inches, over half of which falls in July, August, and September (U. S. Weather Bureau, 1943).

A profile of a Podzol Soil in this region is illustrated by Figures 28 and 29. This is not the most common soil type found in the region; Half-Bog Soils cover most of the slopes and Podzols are found only near the summits of the low hills, under the influence of

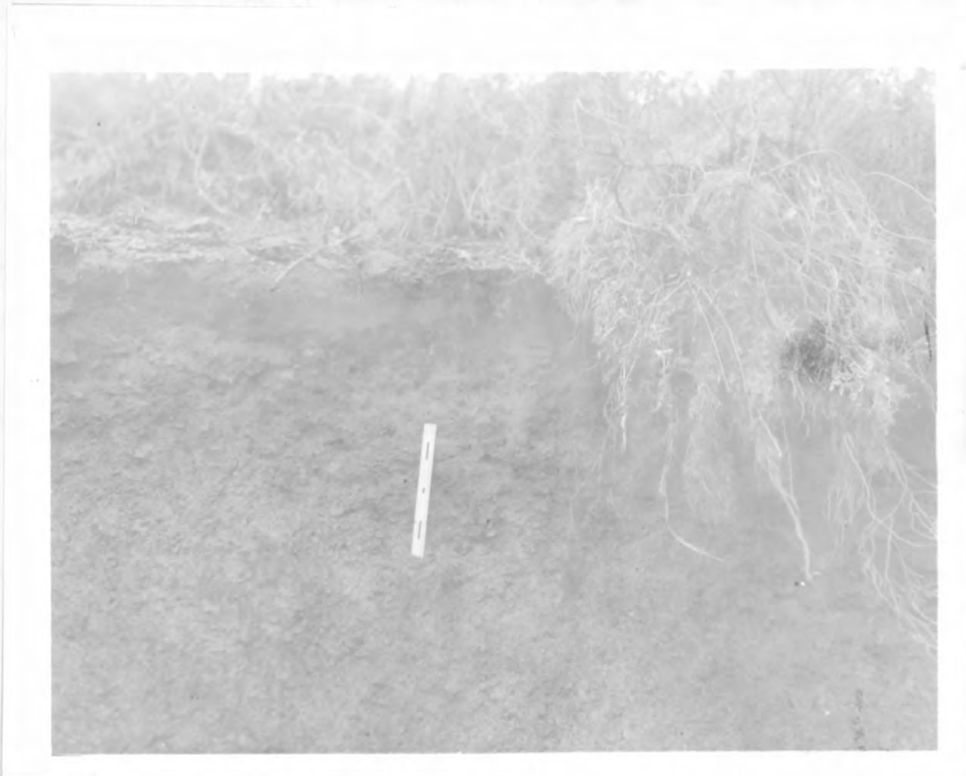


Figure 28. Podzol soil profile in loess, Alice and Bessie claim, Red Devil on the Kuskokwim River, Alaska. A flaky A_0 horizon of humus is shown on the soil surface from which the vegetation mat has been removed. The lower portion of the A horizon leached to form the podzol zone. A deep B horizon, composed principally of loessial silt that has been altered by soil-forming processes overlays a light yellow loess and bedrock mixture (beginning at bottom of ruler). This soil was formed on a well-drained slope under the influence of a Picea glauca forest (since removed by cutting and burning) and occasional colonies of Polytrichum. July 8, 1958.

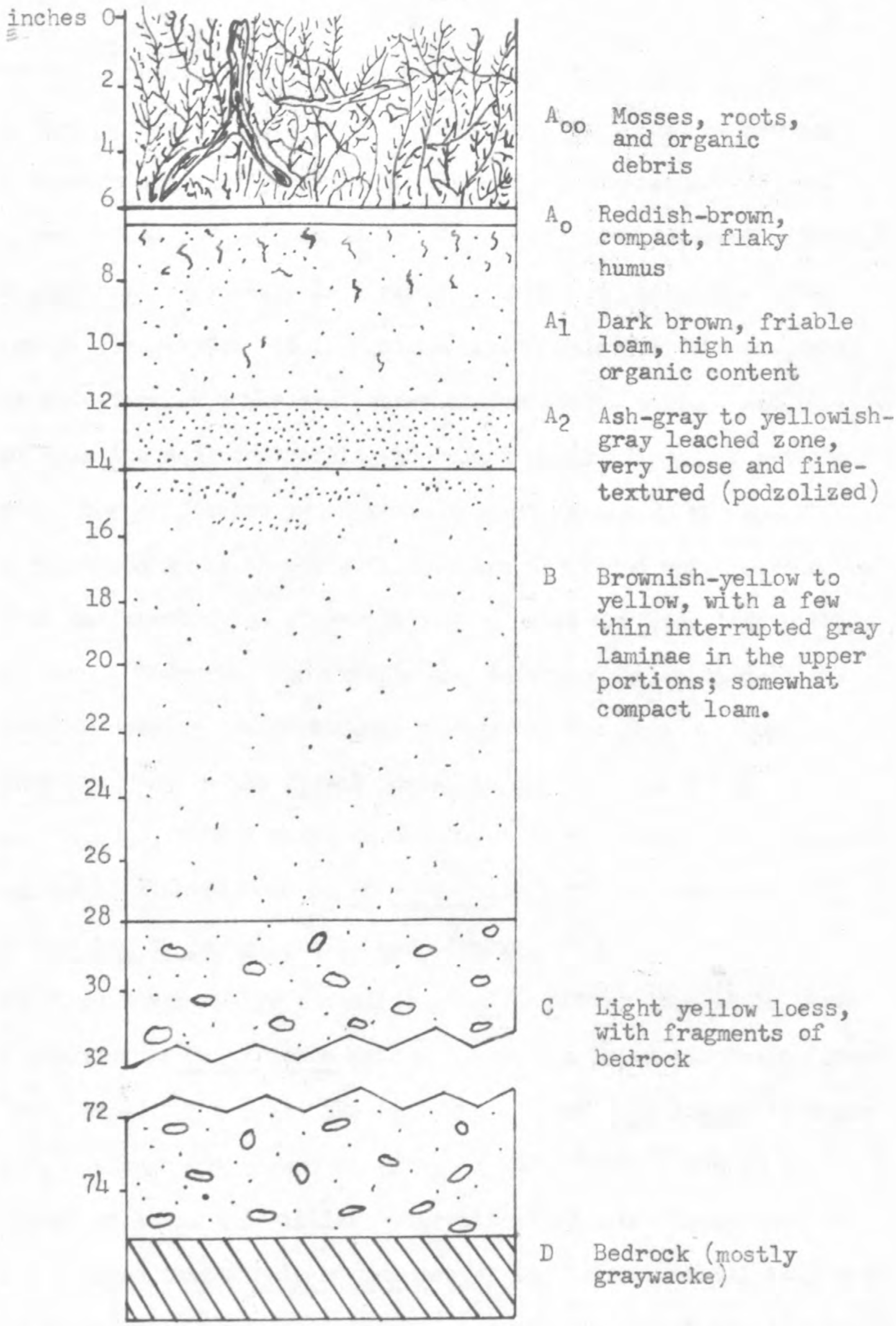


Figure 29. Soil profile diagram, Podzol Soil, Red Devil Mine area, Kuskokwim River, Alaska. Observed July 8, 1958.

Polytrichum species and *Picea glauca*. Podzols may occur in aspen-white birch forests if the ground cover is *Polytrichum*, otherwise these forests ordinarily have a Subarctic Brown Forest Soil. However, some present disclimax deciduous forests have a podzol, although no *Polytrichum* is present, as a relic of former white spruce site occupancy (Figure 30). It is again apparent that adequate drainage and an acid-forming humus are essential for podzolization, and that rather than the soil controlling the plant communities, the reverse is true. The difficulty in this simple explanation of the soil-plant relationship is that the factors are not known which caused the original differentiation of vegetation on sites now underlain with Podzol Soil. There is, for example, no definite explanation of why *Polytrichum* species occur randomly throughout the area, in some instances on what is now Podzol Soils, in others on Half-Bog or Bog Soils. However, Podzol Soils do not develop on underdrained sites, regardless of the presence of *Polytrichum*. This same relationship of *Polytrichum* to podzolization was observed at a site near Eagle, on the Yukon River, where podzolized soils occurred in a white birch forest only under *Polytrichum* mats--otherwise a Subarctic Brown Forest Soil was formed. The pH of the A_1 horizon under *Polytrichum* at Eagle was 4.6, although the parent material of the C horizon was pH 7.

Based on these and similar observations at other localities the writer believes that a *Polytrichum* mat of long duration will in itself direct pedogenesis to podzolization. However, the vegetational history of a site is usually difficult to determine; preceding coniferous forests may have initiated podzolization, and *Polytrichum* merely continued it.

Figure 30. Podzol soil profile on serpentine slope at West Fork near Livengood, Alaska. Although the site is now occupied by a disclimax forest of Betula resinifera and Populus tremuloides, this relic podzol soil is additional evidence of former Picea glauca occupancy. The remains of burned and rotted spruce trees which are still visible at this site show by their size that a well-developed coniferous forest once covered this slope. The serpentine parent material had no apparent influence on either the vegetation or soils developed here, and the process of podzolization under an acid humus here is just as evident as that of the Red Devil site on loess parent material. June 20, 1960.

Relevé of plant community on Podzol Soil at Red Devil, Kuskokwim River, Lower Yukon River district, Alaska.

Low loess hill vegetated with white birch and white spruce. Site is well drained; no permafrost encountered. Altitude, 500 feet. Area, 10 X 10 meters. Observed July 10, 1958.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Anisothecium crispum	r.1
Ceratodon purpureus	1.2
Dicranum majus	r.3
Ditrichum homomallium	+.2
Isopaches bicrenatus	r.2
Plagiothecium laetum	r.1
Pogonatum capillare	1.2
Pohlia nutans	+.2
Pohlia vexans	+.2
Polytrichum commune	1.3
Polytrichum juniperinum	5.4
Oligotrichum laevigatum	r.1
Pteridophytes -	
Dryopteris phegopteris	r.2
Lycopodium complanatum	r.2

Grasses -

Agrostis scabra	+.2
Calamagrostis canadensis	+.2

Forbs -

Boschniakia rossica	+.1
Geocaulon lividum	1.2
Linnaea borealis	2.2
Mertensia paniculata	+.2
Polygonum alaskanum	+.1
Rorippa hispida	+.1

Shrubs and Semi-shrubs -

Cornus canadensis x suecica (?)	1.3
Empetrum nigrum	+.2
Rubus chamaemorus	1.2

Shrub stratum:

Ledum palustre subsp. decumbens	2.3
Vaccinium uliginosum	1.3

Tree stratum:

Betula resinifera	4.4
Picea glauca	1.2

At other sites of Podzol Soils in the vicinity Polytrichum species were scarce or absent, and Picea glauca provided the acid-forming humus necessary for the formation of this soil type.

The Half-Bog Soils of this region support essentially the same species of plants as are found on similar soils throughout interior Alaska. These plant communities of mountain slopes, usually underlain by permafrost, are called by the writer "mountain tundra" communities to distinguish them from the communities of soligenous bogs, which have been termed "muskeg" communities. The contrast between the hanging bogs over permafrost and mountain tundras have been discussed in Chapter III, Section E. A mountain tundra community over Half-Bog Soil on the Barometer Prospect at Red Devil was selected for study (Figures 31 and 32), where the following relevé was made:

Relevé of plant community on Half-Bog Soil at Red Devil, Kuskokwim River, Lower Yukon River district, Alaska.

Mountain tundra community over loess, with sporadic permafrost. Altitude ca. 450 feet. Area, 10 X 20 meters. Observed June 27, 1958.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
Brachythecium bestii	+.2
Dicranum fuscescens	+.3
Dicranum majus	+.3
Drepanocladus uncinatus	+.2
Mylia anomala	r.2
Pohlia nutans	+.2
Pleurozium schreberi	5.5
Polytrichum commune	2.4

Figure 31. Plant community on Half-Bog soil, Alice and Bessie claim, Red Devil on the Kuskokwim River, Alaska. The most abundant plant in this community is Betula nana subsp. exilis, followed in abundance by Vaccinium uliginosum. The dead Picea mariana trees in the foreground were killed by fire. Sporadic permafrost underlies this slope; the approximate upper limit is indicated by the Betula resinifera forest in the background. The organic mat and soil of this mountain tundra community is near saturation. June 27, 1958.

Figure 32. Very wet portion of Half-Bog plant community, Alice and Bessie claim, Red Devil on the Kuskokwim River, Alaska. Isolated well-developed specimens of Salix pulchra (shown above) and S. richardsoni (not shown) mark these wet areas, which are caused by the slight drainage features or "swamping" by Sphagnum fuscum and other sphagnum species. The principal ground cover here is Ledum palustre subsp. decumbens, although other species of shrubs are also present. June 27, 1958.

Polytrichum strictum	1.3
Rhytidium rugosum	1.2
Sphagnum fuscum	2.5
Pteridophytes -	
Athyrium filix-femina subsp. *cyclosorum*	r.1
Lycopodium complanatum	+.2
Grasses and Sedges -	
Agrostis scabra	r.2
Calamagrostis canadensis	r.2
Carex loliaceae	+.2
Carex norvegica subsp. *inferalpina*	+.2
Forbs -	
Epilobium angustifolium	1.1
Parnassia palustris	+.2
Petasites frigidus	+.2
Pyrola grandiflora	+.1
Pyrola minor	r.1
Ranunculus lapponicus	r.1
Sanguisorba sitchensis	+.2
Saxifraga punctata subsp. *insularis*	1.1
Thalictrum sparsiflorum	r.1
Trientalis europea	+.2
Viola epipsila subsp. *repens*	r.1

Shrubs and Semi-Shrubs -

Cornus canadensis x suecica (?)	1.3
Empetrum nigrum	+.2
Oxycoccus microcarpus	+.1
Rubus arcticus	+.2
Rubus chamaemorus	1.2
Vaccinium vitis-idaea	1.3

Shrub stratum:

Alnus crispa	1.3
Betula nana subsp. exilis	4.5
Chamaedaphne calyculata	+.1
Ledum palustre subsp. decumbens	2.3
Salix arbusculoides	+.2
Salix pulchra	+.1
Salix richardsonii	+.1
Spiraea beauvardiana	+.1
Vaccinium uliginosum	3.3

Tree stratum:

Betula resinifera	r.1
Picea glauca	r.1
Picea mariana	1.1

Well-drained ravines and sheltered mountain slopes of this region often support a forest that is predominantly Betula resinifera, intermixed with a sparse growth of Picea glauca and Alnus crispa. The forest litter consists mostly of the birch leaves, which on decomposition develop a circumneutral humus. Under the influence of this humus and the adequate drainage that prevails a Subarctic Brown Forest Soil ordinarily develops. The plant community here is characterized by its many bryophyte, pteridophyte, and forb species, few tree and shrub species, and very few grasses and sedges. This soil, and the plant community that it supports, are considered by some writers to be successional and developmental processes leading to the formation of Podzol Soil. Kellogg and Nygard (1951, p. 58) comment on this process as follows: "Although these soils appear to occupy a stage of immaturity before Podzol, and are placed in the intrazonal order, it is not possible to say definitely that they are simply younger soils. The Subarctic Brown Forest soils appear to be reasonably stable in this region. That is, given the parent materials and geomorphological processes of the landscapes of which they are a part, it cannot be postulated that they will in time become Podzols. Yet some of them may." The present writer is of the opinion that they should be classified as Zonal Soils, and they are so included in the soil key at the beginning of this section. If they are to pass from this so-called stage of "immaturity" that they are said to be in now it must occur by the replacement of the birch trees by white spruce, or by extensive colonization by <u>Polytrichum</u> mosses or other acid-humus forming plants. This process did not appear to be occurring--the communities of Podzol soils were always found by the writer on overdrained slopes, and it does not seem possible that the plant communities can overcome this dominant influence of a physiographic factor.

Relevé of plant community on Subarctic Brown Forest Soil at

Red Devil, Kuskokwim River, Lower Yukon River district, Alaska.

Birch forest on the slopes of a slight ravine, northwest exposure having no evidence of fire damage or logging operations. Altitude, ca. 400 feet. Area, 10 X 20 meters. Examined July 2, 1958.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Aulacomnium palustre	+.2
Dicranum fragilifolium	r.3
Dicranum majus	+.3
Hypnum subplicatile	+.2
Lophozia ventricosa	+.2
Mnium rugicum	+.2
Plagiothecium denticulatum	+.1
Pohlia cruda	+.2
Pohlia nutans	+.2
Ptilidium ciliare	r.2
Ptilidium pulcherrimum	r.2
Ptilium crista-castrensis	r.2
Rhytidiadelphus triquetrus	+.2
Tetraphis pellucida	r.2
Tetraplodon angustatus	r.2
Pteridophytes -	
Cystopteris fragilis	+.2
Cystopteris montana	+.2

Dryopteris austriaca	1.1
Dryopteris linnaeana	+.1
Dryopteris phegopteris	+.1
Equisetum scirpoides	+.3
Lycopodium annotinum	+.2

Grasses and Sedges - (a very few non-fruiting specimens were seen)

Forbs -

Aconitum delphinifolium subsp. *chamissonianum*	+.1
Actaea rubra	+.1
Boschniakia rossica	+.1
Cardamine pratensis	1.1
Corydalis pauciflora	+.1
Erysimum cheiranthoides	+.1
Galium trifidum	1.2
Impatiens noli-tangere	+.2
Linnaea borealis	+.2
Mertensia paniculata	2.2
Moneses uniflora	+.1
Polemonium acutiflorum	+.2
Pyrola minor	+.1
Stellaria alaskana	+.1
Valeriana capitata	1.1

Shrub stratum:

Alnus crispa	+.1
Rosa acicularis	3.1
Viburnum edule	+.1

Tree stratum:

Betula resinifera	5.4
Picea glauca	2.1
Populus tremuloides	+.1

Near the mouth of Barometer Creek, in the Red Devil area, a large soligenous bog is formed on a terrace of the Kuskokwim River. This bog is characterized by mats of sedges growing in the soil near the edge of the bog lake, but free-floating farther into the lake. A discussion of this bog has been given by Persson and Shacklette (1959) in their report of a new distribution record of a moss species. The list of plants of this bog may be compared with that of the Yakobi Island bog, and it will be seen that the former is a sedge bog, whereas in the latter bryophytes predominate. Yet the soil that is formed in the two bogs is defined as the same--a Bog Soil--although the two soils are somewhat different in texture. The principal floristic resemblance of the two bogs is only that aquatic and paludal species are most abundant, but generally they are not the same species in both bogs.

Relevé of plant community on Bog Soil at Red Devil, Kuskokwim River, Lower Yukon River district, Alaska.

Sedge bog around lake margin at the mouth of a small creek; inner portion of bog mat free-floating. Altitude, ca. 350 feet. Area, 10 X 10 meters. Examined July 14, 1958.

Species	Abundance-Cover and Sociability Values

Ground stratum:

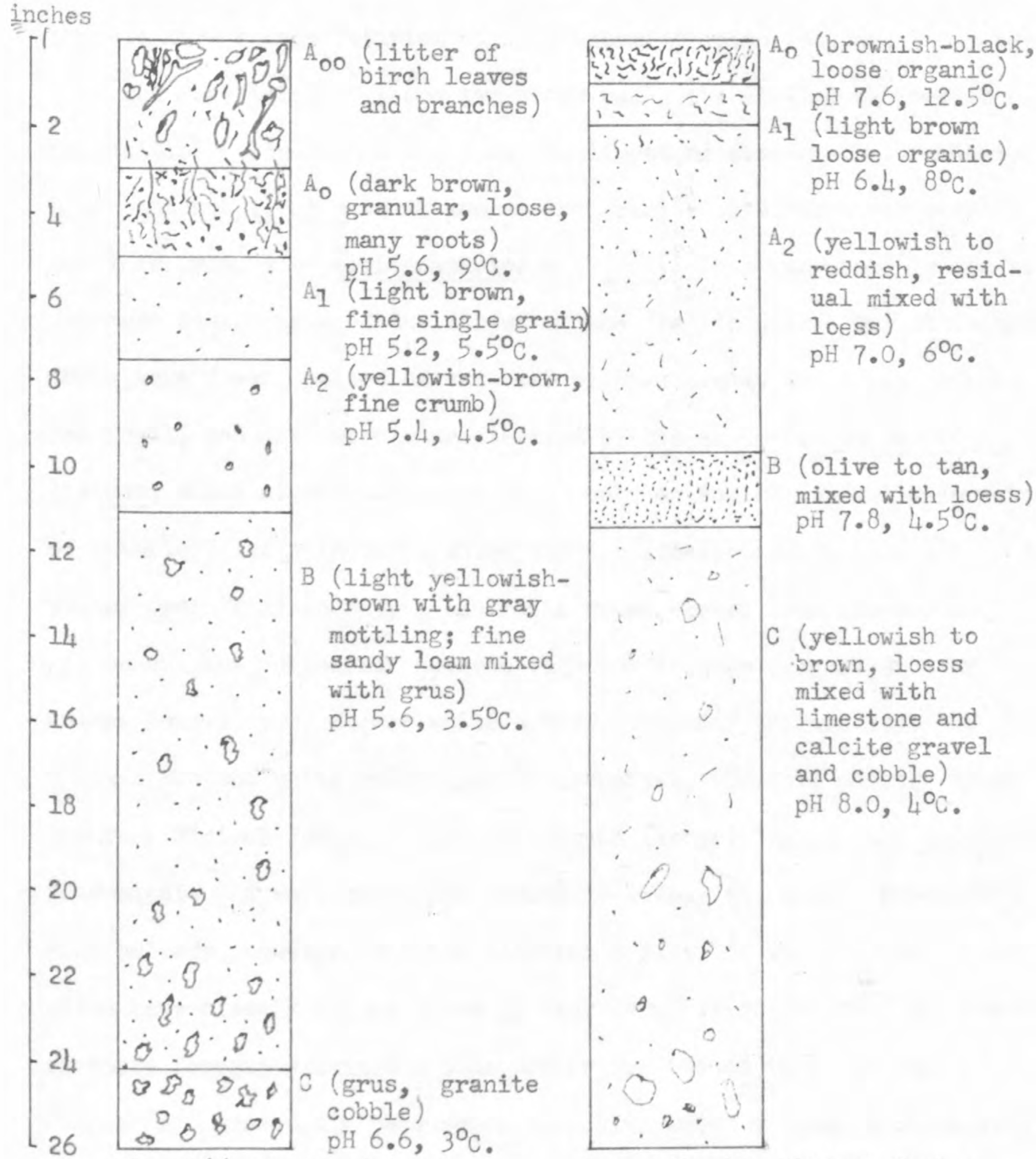
Bryophytes -

Bryum pseudotriquetrum	+.2
Calliergon megalophyllum	1.2
Drepanocladus trichophyllus (first report for North America)	r.2
Drepanocladus tundrae	1.2
Drepanocladus uncinatus	1.3
Hypnum lindbergii	r.2
Mnium pseudopunctatum	+.2
Mnium rugicum	+.2
Pteridophytes -	
Equisetum limosum	3.4
Grasses and Sedges -	
Beckmannia syzigachne	+.2
Carex aquatilis	4.4
Carex rostrata	+.3
Eleocharis acicularis	+.3
Eriophorum vaginatum	1.3
Juncus alpinus subsp. *nodulosus*	1.3
Juncus arcticus subsp. *alaskanus*	1.3
Forbs -	
Calla palustris	1.2
Callitriche verna	+.2
Cicuta mackenziana	3.4
Potentilla palustris	1.2
Ranunculus pennsylvanicus	+.1
Senecio congestus	+.1
Stellaria calycantha subsp. *interior*	+.2

Shrub stratum:

Potentilla fruticosa	1.3
Vaccinium uliginosum	r.2

e. Subarctic Brown Forest Soils of interior Alaska on different parent materials. A principle generally accepted by pedologists is that the development of a soil type is largely independent of the nature of the parent material--that if given enough time, the dominant effects of climate and vegetation will prevail. In order to test this principle as applied to a particular Soil Group, the Subarctic Brown Forest, profiles of this soil were studied which had developed over schist, serpentine, loess, granite, and limestone. Figure 33 gives a comparison of the profiles derived from the two latter rock types. Both were in a forest of Betula resinifera, and were on well-drained, but not over-drained, sites. It can be seen from the profile diagrams that the soil derived from granite is more acid throughout. Another difference is the rather deep litter accumulation in the A_{oo} horizon of the granite-derived soil, whereas there is no appreciable A_{oo} horizon of the limestone-derived soil. The explanation of this difference may be that the alkalinity of the latter soil favors rapid bacterial decomposition so that the litter quickly looses its particulate identity and forms the A_o horizon. Both soils are of higher pH in the C horizon than in the other horizons; the effect here of the so-called "base-forming litter" is not that of making the upper horizons basic--this litter merely prevents very high acidity developing in these horizons, which occurs as the normal



Site 265, Deadwood Creek,
Circle Hot Springs area.
Examined July 8, 1960.

Site Mile 29, Elliott Highway,
Livengood area.
Examined June 21, 1960.

Figure 33. Soil profile diagrams of Subarctic Brown Forest Soils that have developed from contrasting rock types, both in the Central Yukon district and in Betula resinifera forests.

process in the decomposition of "acid-forming" plant litter.

The vegetation of these two sites was quite similar in species composition. The ground cover at the limestone site was not dominated by Hypnum subplicatile as it was at the granite site, but this species was intergrown with Arctostaphylos uva-ursi. This was probably due to the more dense shade of the forest at the granite site. At both sites there were fewer species of vascular plants than at the loess site at Red Devil, and both were characterized by the abundance of Geocaulon lividum, which at Red Devil was found only on Podzol Soil. The forests of interior Alaska in which white birch predominates are believed by the writer ordinarily to have a Subarctic Brown Forest Soil unless the ground surface is densely covered with Polytrichum (Figure 34), or unless on a site of former white spruce occupancy (Figure 30). If white birch and white spruce occur intermixed, the soil usually trends toward a Minimal Podzol. If white spruce (especially if with Polytrichum) predominates, a well-developed Podzol is likely to occur. Exceptions must be made, however, for the alluvial forests of white spruce, which often have closely spaced trees of very large size (Figure 35). Soils of these forests examined by the writer were found to be Azonal or Intrazonal, presumably because of excessive water so that podzolization cannot occur although there is an abundance of acid-forming humus.

These observations indicate that the formation of Subarctic Brown Forest Soil is independent of the type of rock from which it is derived, but that all soils placed in this category do not have the same properties. There is a recognizable difference in the plant communities developed

Figure 34. Discontinuous Betula resinifera forest on a chert rubble slope, Money Knob near Livengood, Alaska. The rocky area in the foreground supports a lithosol plant community which may eventually develop into a deciduous forest of white birch having Subarctic Brown Forest Soil. The development of this soil type is largely independent of the nature of the parent material. June 17, 1960.

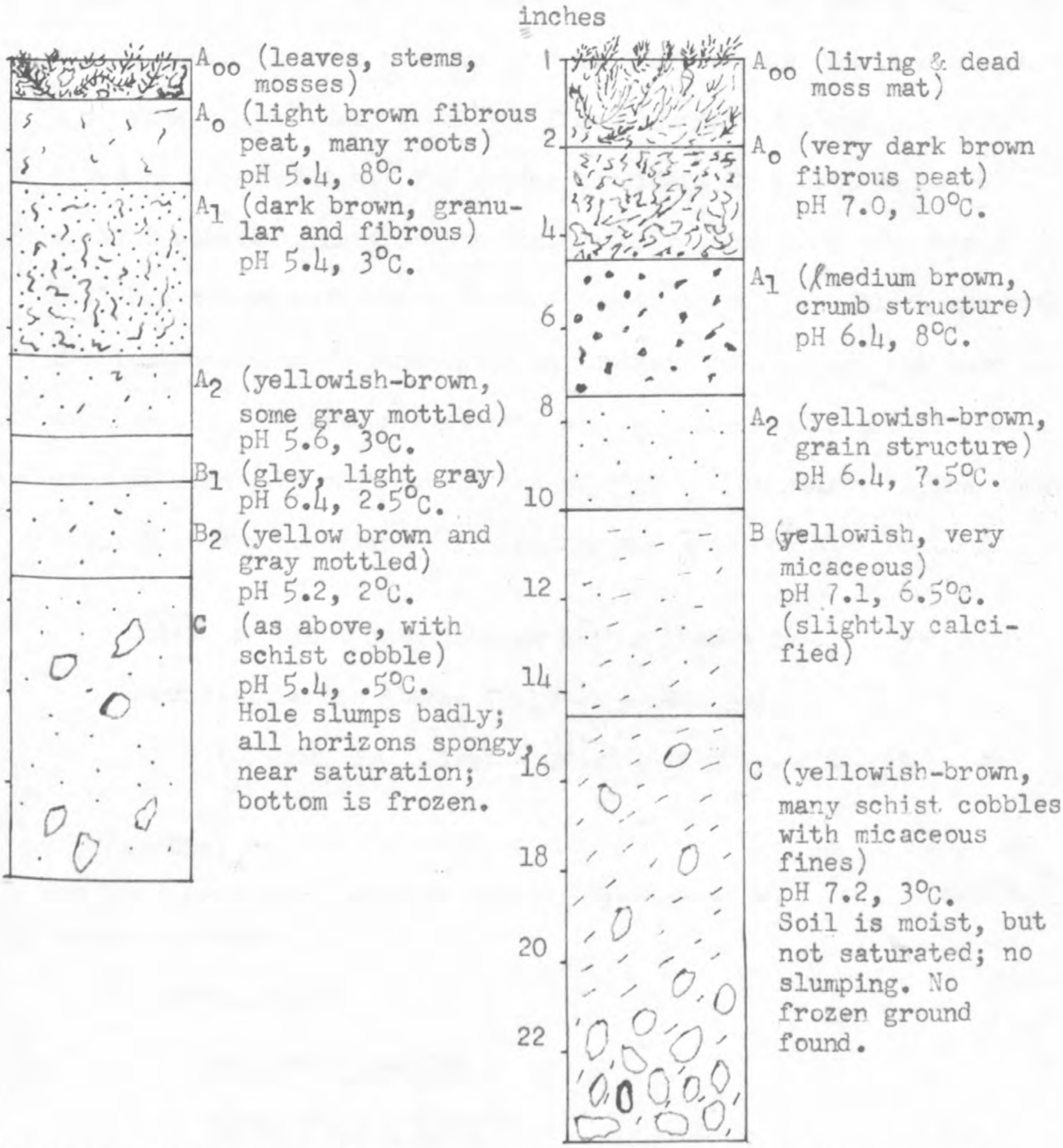
Figure 35. Upper limit of the alluvial forest on terraces of the Kuskokwim River at Barometer prospect, near Red Devil. The *Betula resinifera* forest of the slope (foreground) abruptly terminates on the nearly-level alluvial terrace and is replaced by a dense alluvial forest in which *Picea glauca*, often of very large size, is most abundant. *Picea mariana*, *Alnus crispa*, *Salix* spp., and *Populus tacamahacca* also occur here. June 29, 1958.

thereon as the result of the influence of soil parent material or some other factors of the environment. Further studies are needed to identify and evaluate these differences more accurately.

f. A comparison of Alpine Tundra and Alpine Meadow Soils and plant communities. The ordinary altitudinal succession of soil groups in interior Alaska begins with Bog or Alluvial, and proceeds upward through Half-Bog, Alpine Meadow, Alpine Tundra, to the Lithosols or Regosols of the mountain summits (Figure 37), according to the observations of the writer. Two sites were selected for study on Twelve Mile Summit, one having an Alpine Meadow Soil (altitude, 3,025 feet) and the other an Alpine Tundra Soil (altitude, 3,100 feet), both being underlain by schist bedrock (Figures 36 and 38). At the time of observation, July 4, 1960, the aspect of the alpine meadow was that of an almost continuous carpet of flowers, whereas the alpine tundra bore only scattered flowers. The alpine meadow was on a terrace below a large solifluction lobe, and the alpine tundra was at the summit of the mountain with no protection afforded by landscape features. Both communities were above the limit of trees. The soil of the alpine meadow was well drained through the unfrozen schist cobble C horizon; the slope of the surface also favored runoff. The alpine tundra had but little relief except on northerly facing slopes and was underlain by frozen ground at a depth of 18 inches, which with the low relief made the soil almost completely saturated. The boundaries of the two plant communities were rather sharply delimited, probably due to wetness associated with shallow ground ice. These boundaries were most abrupt where the almost level ground surface met a south facing slope. If the elevation gradient was gradual the tension zone was more

Figure 36. Solifluction ridge in alpine tundra at Twelve Mile Summit, Steese Highway, Alaska. This ridge was covered with a tough, dense organic mat overlying ground ice about 18 inches below the surface. When this mat was punctured with a probe, water flowed freely from the hole. Salix arbusculoides, which grows 2 to 3 feet tall (left center), commonly outlines these ridges, making them conspicuous from a distance. Salix chamissonis is also common on the ridges, but is decumbent and trails down the ridge sides. The area in the foreground is an alpine meadow plant community; here no ground ice was encountered at bedrock which was 2.5 feet from the surface. July 4, 1960.

Figure 37. Vegetation transition at "tree line" on Eagle Summit, Steese Highway, Alaska. The spruce forest at the left develops a podzol soil, which as the altitudinal limit of trees is approached, gradually changes to a Half-Bog soil formed under the mountain tundra community in the right half of the picture. Further increase in altitude is accompanied by a transition to alpine meadow, alpine tundra, and alpine lithosol communities, with corresponding soil types developed under them. "Tree line" here is at about 2,800 to 3,000 feet altitude. July 5, 1960.



Site 259. Alpine Tundra Soil

Site 260. Alpine Meadow Soil

Figure 38. Profile diagrams of adjacent soils, Twelve Mile Summit, Steese Highway, Central Yukon district. Observed July 4, 1960.

extensive. Alpine Tundra Soil can be characterized as largely organic, if the usually abundant rocks of gravel and cobble size are discounted, with some mineral soil resulting from slow rock disintegration intermixed by frost action. The writer considers this soil to be only an altitudinal variety of the Arctic Tundra soils. Alpine Meadow Soil has a more definite structure, more mineral particles, and rather distinct horizons as contrasted to tundra soils. There was some slight calcification in evidence at this site and the entire profile was circumneutral, in contrast to the acidity of the nearby Alpine Tundra Soil, although both were derived from the same schist formation.

Relevé of plant community on Alpine Meadow Soil, Twelve Mile Summit, interior Alaska. (Figures 36 and 39).

Altitude, 3,025 feet. Area, 10 X 10 meters. Observed July 4, 1960.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
Dicranum elongatum	1.3
Dicranum fuscescens	r.3
Dicranum majus	2.3
Distichium capillaceum	+.3
Ditrichum flexicaule	+.3
Drepanocladus uncinatus	1.2
Hylocomium splendens	r.2

Figure 39. Vegetation of alpine meadow at Twelve Mile Summit, Steese Highway, Alaska. This plant community is rich in species of forbs and low shrubs, the most abundant being *Dryas alaskensis*, *Anemone parviflora*, and *Salix reticulata* shown in this close-up view. July 4, 1960.

Isopterygium pulchellum	+.3
Pleurozium schreberi	1.3
Pogonatum alpinum	+.2
Rhytidium rugosum	3.4
Pteridophytes -	
Equisetum pratense	+.2
Lycopodium alpinum	+.1
Lycopodium selago	+.1
Grasses and Sedges -	
(non-fruiting plants only were observed, and were a relatively minor part of the vegetation)	
Forbs -	
Astragalus umbellatus	+.1
Claytonia sarmentosa	r.1
Dodecatheon frigidum	1.1
Dryas alaskensis	4.4
Lagotis glauca var. stelleri	+.1
Mertensia eastwoodae	1.3
Myosotis alpestris subsp. asiatica	1.2
Parrya nudicaulis subsp. interior var. grandiflora	3.4
Pedicularis capitata	+.1
Pedicularis langsdorfii subsp. arctica	+.1
Pedicularis oederi	+.1
Saxifraga punctata subsp. nelsoniana	1.2
Silene acaulis	+.3

Viola biflora	r.2
Viola epipsila subsp. repens	r.2
Shrubs -	
Cassiope tetragona	1.3
Loiseleuria procumbens	r.2
Salix reticulata	1.3
Shrub stratum:	
Betula nana subsp. exilis	1.2
Salix arbusculoides	1.3
Salix chamissonis	1.3
Vaccinium uliginosum	1.2

Relevé of plant community on Alpine Tundra Soil, Twelve Mile Summit, interior Alaska (Figure 40).

Altitude, 3,100 feet. Area, 10 X 10 meters. Observed July 4, 1960.

Species	Abundance-Cover and Sociability Values
Ground stratum:	
Bryophytes -	
Aulacomnium palustre	3.2
Aulacomnium turgidum	1.2
Brachythecium turgidum	1.3
Bryum cirratum	+.3
Calliergon sarmentosum	1.2
Calliergon cordifolium	2.2
Dicranum majus	1.3

Ditrichum flexicaule	+.3
Drepanocladus uncinatus	1.2
Hylocomium splendens	r.2
Orthothecium chryseum	r.3
Sphagnum teres	2.3
Pteridophytes -	
Lycopodium selago	r.1
Grasses and Sedges -	
Carex bigelowii	1.1
Carex membranacea	+.2
Eriophorum angustifolium	r.2
Eriophorum scheuchzeri	+.2
Festuca brachyphylla subsp. *saximontana*	1.2
Forbs -	
Arnica lessingii	+.2
Campanula lasiocarpa	r.2
Castilleja hyperborea	+.2
Oxytropis nigrescens subsp. *bryophila*	r.1
Petasites frigidus	+.3
Polygonum bistortum subsp. *plumosum*	+.1
Polygonum viviparum	+.1
Stellaria laxmanni	1.3
Shrubs -	
Empetrum nigrum	1.3
Salix reticulata	1.3

Figure 40. Upper limits of alpine tundra at Twelve Mile Summit, Steese Highway, Alaska. The vegetation cover is broken by frost scars (lower left corner) and solifluction features. Slightly protected sites support shrubby willows (left background) and young *Picea glauca* may persist for a few years (right, above center). If the altitude is sufficiently high, the alpine tundra gives way to an alpine lithosol community (upper left corner) having very few species of flowering plants and bryophytes. July 4, 1960.

Shrub stratum:

Betula nana subsp. exilis (some specimens are in the ground stratum)	2.3
Salix arbusculoides	+.2
Vaccinium uliginosum (some specimens are in the ground stratum)	1.2

A comparison of the two relevés shows rather distinct plant communities on each of the two soil types. The bryophyte species may be divided into three ecological groups: (1) those of wide ecological amplitude, found at both sites (e.g., Hylocomium splendens, Dicranum majus, Drepanocladus uncinatus) but generally having different abundance-cover values on the two sites), (2) mosses that characteristically are "dominant" on more mesic sites and form the major portion of the bryophyte cover (e.g., Rhytidium rugosum), and (3) those that are best adapted to a wet substrate and there form the major component of the moss stratum (e.g., Calliergon cordifolium, Aulacomnium palustre, Sphagnum teres). There are also a few "exclusive" species that are quite or almost entirely absent from one community or the other. Examples of the latter are Pleurozium schreberi, which is ordinarily the dominant species in mountain tundra communities, reaching its moisture or altitudinal limit in the alpine meadow, and Aulacomnium turgidum, which requires a wetter substrate than is usually found in the alpine meadow and which is common in the alpine tundra up to the alpine lithosol communities.

The vascular plants of the two communities show environmental tendencies parallel to those of bryophytes. The minor importance of grasses in this alpine meadow is not believed to be a typical condition, and no reason for the low importance value of these plants here is apparent to the writer. The most constant species of the alpine tundra, as here described, are thought to be Petasites frigidus, Polygonum bistortum subsp. plumosum, Polygonum viviparum, and Carex bigelowii. The presence of these species shows the ecological relationship of this community to the arctic tundra community.

As with the bryophytes, we see certain vascular species that are too mesophytic to grow in this alpine tundra community on wet soil (e.g., Mertensia eastwoodae, Parrya nudicaulis subsp. interior var. grandiflora, Myosotis alpestris subsp. asiatica, Dryas alaskensis)--species that form the most conspicuous elements of the alpine meadow. Some species of wide ecological amplitude grow in both communities (e.g., Betula nana subsp. exilis, Salix reticulata, Vaccinium uliginosum) but may have different abundance-cover values at the two sites.

The phytosociological distinctiveness of these two communities on adjacent sites is believed by the writer to closely relate to the different properties of the two soil types, although the direct effect of microclimatic differences cannot be entirely discounted. The primary differentiating soil factor is thought to be degree of wetness, and associated with this water relationship, a difference in soil pH. The nature of the soil parent material (schist) does not seem to be a factor in the development of the distinctiveness shown by these soils and plant communities.

g. Characteristics and development of Lithosols. This Great Soil Group, as well as Regosols, are so lacking in specific characterization, and include such a wide variety of very different parent materials that it is difficult to relate specific plant communities to them, if it can be done at all. In a given climatic region on a specific rock type a local Lithosol may be quite constant in the plant community that it supports. The schist Lithosols of Yakobi Island and those of the Alaska mainland near Juneau have very similar plant communities. These communities, however, bear but very little relationship to those of a slate, granite or even schist Lithosol of the Alaska Range or interior Alaska. The same condition obtains in relating Regosols and Alluvial Soils to their plant communities. These categories of soils are scarcely comparable to the Zonal and Intrazonal Soils, although both groups are at the same hierarchical level. The Lithosols are classified on the basis of their origin; the latter two on the basis of complex interactions of climate, parent material, and plants operating over a long period of time.

Of this group of Azonal Soils, Lithosols are selected to illustrate some processes of development and to show the influence of parent material on the soil that is formed and the plant community that results.

A Lithosol derived from granite at the ridge crest (altitude ca. 2,100 feet) between Half Dollar and Portage Creeks, near Circle Hot Springs, Central Yukon district illustrates an effect of vegetation on soil development (Figure 42). The surface horizon is a grus and granite cobble mixture with organic material derived from a very sparse vegetation--an indication that congeliturbation is very active on this exposed crest. Two soil profiles were studied that were only six feet apart with similar almost level surfaces; one had a very thin cover of Cladonia sp. and Polytrichum piliferum, the other was covered with a well-developed Empetrum nigrum mat having evidence of considerable age (Figure 41). The first had such weakly developed horizons that it is considered best to use only descriptive terms in their designation and to consider the soil a Lithosol. The profile under the Empetrum mat had weak but discernible horizon differentiations, including a zone of minimal podzolization overlying a definitely illuviated B horizon. There was a small, but significant, difference of pH at corresponding levels of the two soils. This difference is attributed to the acid-producing humus under the Empetrum mat, which by eluviation had provided a change in acidity of the entire soil profile. The greater depth of the surface organic layer is also owing to the growth of Empetrum, which provided the organic eluviate that has influenced horizon development. Other factors, such as more uniform temperature and less evaporation (which were influenced by the shrub mat) may also have been important.

The plant community surrounding these soil sample sites included more than just these three species already mentioned, but they were having no apparent effect on these soils due to their isolation by distance from the sites. However, they will be listed for comparison with other lithosol communities.

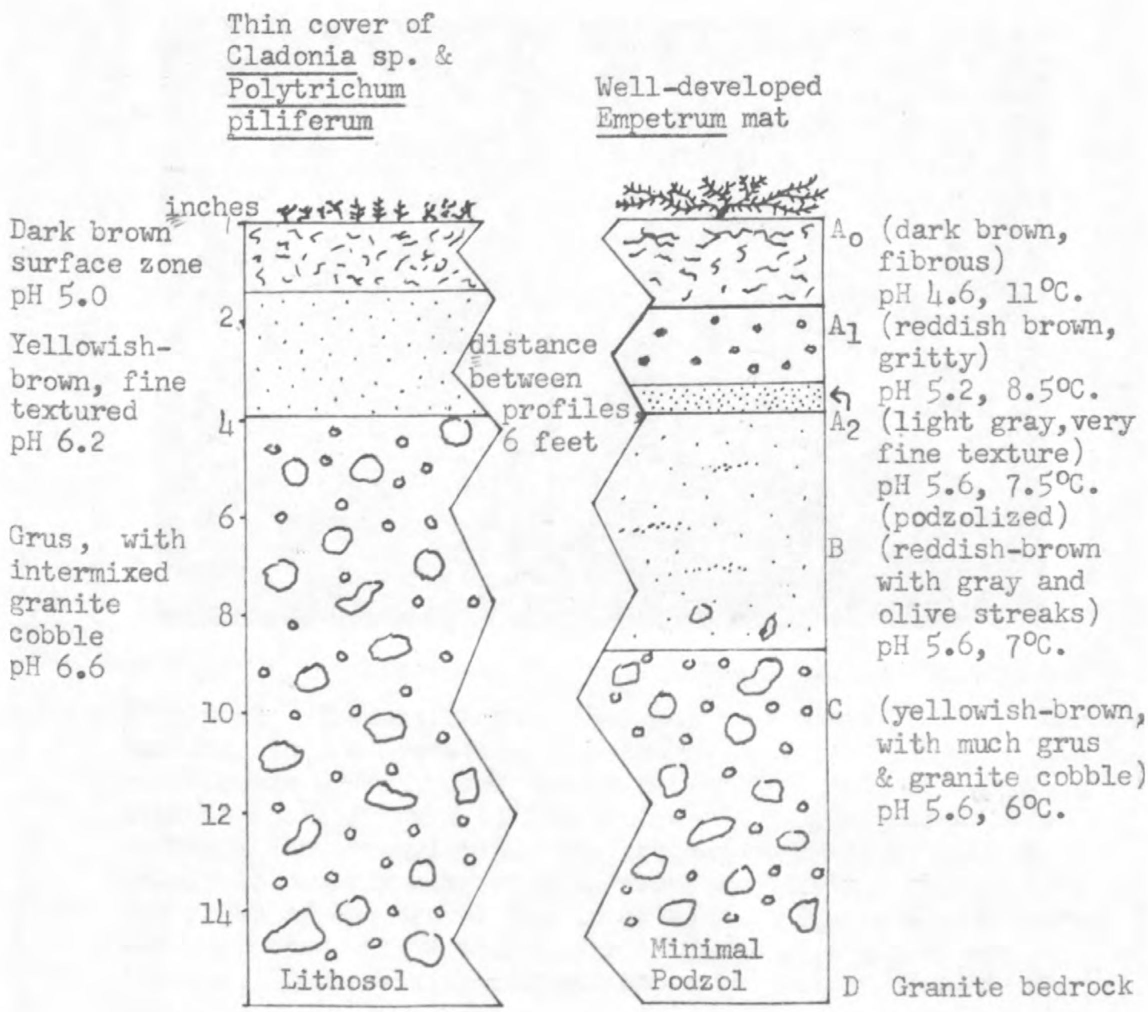


Figure 41. Soil and vegetation profile diagram, granite Lithosol grading to Minimal Podzol. Ridge crest of divide between Half Dollar and Portage Creeks, Circle Hot Springs area, Central Yukon district. Observed July 7, 1960.

Figure 42. Transition from Lithosol to Minimal Podzol under the influence of vegetation on the ridge between Half Dollar and Portage Creeks, near Circle Hot Springs, Alaska. The soil in the left half of the picture is weakly podzolized, ending at the trowel tip. The surface above this soil is thinly to densely covered with vascular plants. The soil to the right of the trowel tip is an essentially azonal Lithosol and supported only a thin cover of one moss species and lichens. Compare with diagram shown in Figure 35. July 7, 1960.

Relevé of plant community on Lithosol at ridge crest between Half Dollar and Portage Creeks, Central Yukon district, Alaska

Altitude, ca. 2,100 feet. Area, 10 X 10 meters. Observed July 7, 1960.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Polytrichum piliferum	2.2
Grasses -	
Calamagrostis purpurascens	r.2
Festuca altaica	r.2
Forbs -	
Arnica louiseana subsp. frigida	+.2
Campanula lasiocarpa	+.2
Epilobium angustifolium	+.1
Saxifraga tricuspidata	+.2
Shrubs -	
Arctostaphylos uva-ursi	+.3
Empetrum nigrum	1.3
Vaccinium vitis-idaea	+.2
Shrub stratum:	
Betula nana subsp. exilis	4.4
Spiraea beauvardiana	+.1
Vaccinium uliginosum	+.2

Lithosols derived from schist and from serpentine are compared by two soil profile diagrams in Figure 44. The schist Lithosol occurred at Eagle Summit on the Steese Highway, at an altitude of 3,900 feet (Figure 43) and the serpentine Lithosol was found at West Fork near Livengood at an altitude of about 900 feet (Figure 45). The differences of the two soil profiles are due partly to differences in bedrock and partly to the difference in the climate in its effect on rate of weathering. In these northern regions weathering of rock is largely a physical process and changes in extremes of temperature have a great effect on rate of fragmentation. The schist Lithosol is in a more severe climate, and probably less protected by a snow cover. On the other hand, the lower altitude of the serpentine outcrop had permitted it to have been formerly forested, which should increase rock disintegration by root action. The schist Lithosol is at an altitude higher than tree line. Thus the two rock types in such different environments are not directly comparable in regard to rate of weathering and Lithosol formation, but the observation here, as well as at other sites, is that serpentine ordinarily develops a shallower Lithosol than does schist or other rock types (compare with Figure 41).

There was no frozen ground encountered at either site as deep as could be dug, which was to bedrock or to large schist blocks. Both sites are well-drained to over-drained; however the schist site is the wetter due to climatic differences caused by the higher altitude. In the surface zones of both soils congeliturbation played

Figure 43. Road cut through a schist lithosol at Eagle Summit, Steese Highway, Alaska. The D horizon consists of schist blocks rather than bedrock; slumping of the soil over this horizon gives a false impression of soil depth in this picture. The actual depth of the solum is shown just beneath the organic mat in the center of the picture. There was no ground ice found in the solum; however the D horizon is probably frozen where undisturbed. July 5, 1960.

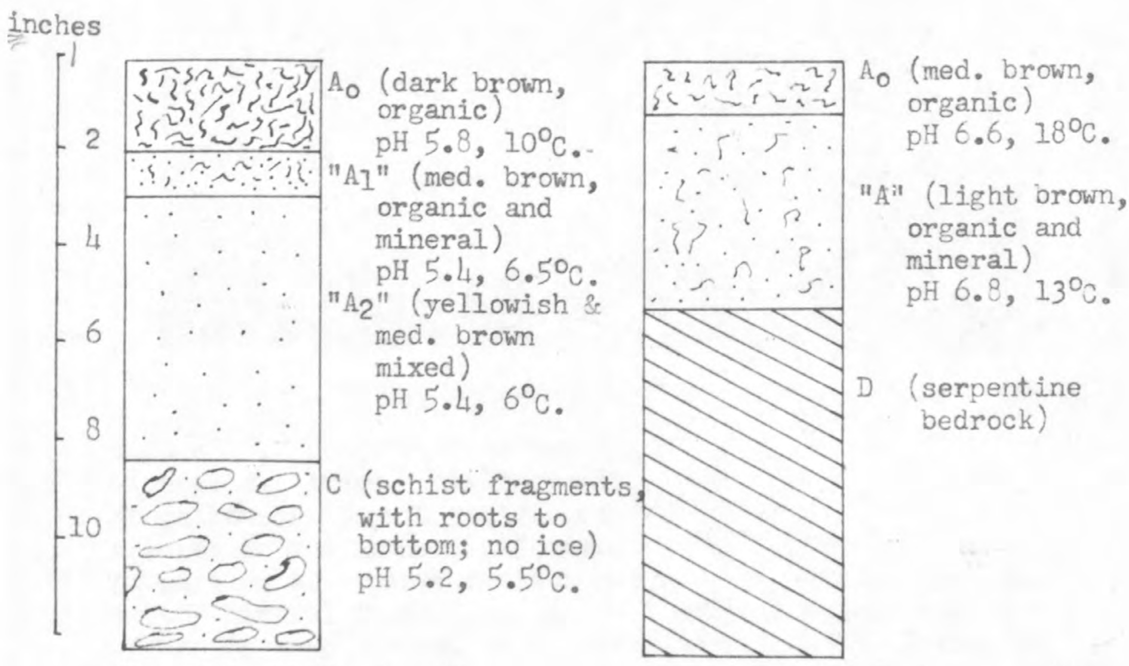


Figure 44. Soil profile diagrams of Lithosols derived from schist and from serpentine, Central Yukon district. (Compare with Figure 6, Lithosol derived from granite)

Figure 45. Profile of serpentine Lithosol at West Fork near Livengood, Alaska. Shallow soil, sparse vegetation, and congeliturbation all contribute to lack of zonality. The changes in the soil with increasing depth are a decrease in proportion of organic content and a corresponding increase in the mineral fraction, and the increased decomposition of the organic matter. The grass shown in this picture is *Festuca altaica*. June 20, 1960.

an important part in mixing the rock fragments and the organic matter. However, the total amount of organic material is greater in the Eagle Summit Lithosol.

The differences in the plant communities cannot be attributed only, if at all, to differences in parent materials of the two soils. The greatest difference in the two sites, in their effect on plant species occupancy, is undoubtedly that of climate. This again emphasizes the lack of relationship of a named soil category and a specific plant community type. These two types of lithosol plant communities have been designated "high altitude lithosol" and "low altitude lithosol" in this report, for convenience of study. The high altitude lithosol plant communities more closely resemble an arctic coastal or arctic lithosol plant community than a low altitude lithosol community.

Relevé of a plant community on serpentine Lithosol at West Fork near Livengood, Central Yukon district, Alaska.

Southerly facing slope having extensive frost action. Center of sample plot mostly with a ground stratum only, but surrounded by shrub and tree strata. Altitude ca. 900 feet. Area, 10 X 20 meters. Observed June 20, 1960.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Abietinella abietina	+.3
Ceratodon purpureus	1.2
Dicranum undulatum	+.3

Eurhynchium pulchellum	r.2
Hedwigia ciliata	2.4
Polytrichum piliferum	2.2
Rhytidium rugosum	+.3
Schistidium strictum	1.3
Weissia viridula	+.2
Pteridophytes -	
Dryopteris fragrans	+.1
Polypodium vulgare subsp. *occidentale*	r.2
Selaginella sibirica	4.4
Grasses -	
Calamagrostis purpurascens	1.2
Festuca altaica	1.2
Forbs -	
Aconitum delphinifolium subsp. *chamissonianum*	+.1
Bupleurum americanum	+.1
Rumex acetosa subsp. *alpestris*	2.1
Saxifraga tricuspidata	+.2
Silene williamsii	+.1
Solidago multiradiata	1.1
Solidago (anomalous form)	r.2
Zygadenus elegans	+.1
Shrubs -	
Arctostaphylos uva-ursi	2.3

Shrub stratum:

Juniperus communis var. *montana*	1.3
Vaccinium uliginosum	+.2

Tree stratum:

Betula resinifera	+.1
Picea glauca	+.1

Relevé of plant community on schist Lithosol at Eagle Summit, Steese Highway, Central Yukon district, Alaska.

Southeasterly facing slope, congeliturbation prominent. Altitude ca. 3,900 feet. Area, 10 X 10 meters. Observed July 5, 1960.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Bryum cirratum	+.2
Dicranum majus	2.3
Polytrichum juniperinum (?)	+.3
Polytrichum piliferum	3.3
Rhacomitrium lanuginosum	1.3
Rhytidium rugosum	+.3
Pteridophytes -	
Lycopodium selago	r.1
Grasses and Sedges -	
Carex bigelowii	+.2
Festuca brachyphylla subsp. *saximontana*	2.2
Luzula nivalis subsp. *latifolia*	+.2
Poa sp.	1.1

Forbs -

Arnica louiseana subsp. frigida	+.2
Campanula lasiocarpa	+.2
Castilleja hyperborea	+.1
Dryas alaskana	2.2
Ligusticum mutellinoides subsp. alpinum	+.1
Minuartia arctica	+.2
Minuartia macrocarpa	1.3
Oxytropis nigrescens subsp. bryophila	+.1
Pedicularis labradorica	+.1
Pedicularis lanata	+.1
Polemonium acutiflorum	r.1
Polygonum bistorta subsp. plumosum	+.1

Shrubs -

Betula nana subsp. exilis (appressed form)	+.2
Diapensia lapponica subsp. obovata	+.3
Loiseleuria procumbens	+.3
Salix phlebophylla	+.2

h. Soils of the tundra regions. These soils have been described by Kellogg and Nygard (1951), and more recently in detailed studies of Tedrow and Hill (1955), Tedrow, Drew, Hill, and Douglas (1958), Tedrow and Cantlon (1958), and Brown and Tedrow (1958). Intense frost action and excessive wetness associated with the cold climate are the major factors in soil formation, and a very complicated pattern of soils has resulted. These various individual soils may be placed in two Great Soil Groups, (1) Tundra Soils of the areas of low relief, characterized by high organic content, extreme wetness, and poor horizon development over near-surface ground ice, and (2) Arctic Brown Soils, which occur on the well-drained sites across valley and mountain gradients. A third soil type has been recognized by several investigators, including the writer, but it has not yet been formally described. It is said by Brown (1962) to have montmorillonite in the A_2 horizon, and that its development is facilitated by acid parent materials, dwarf birch-heath vegetation, and protected microrelief positions. The observations of the present writer indicate that in addition to these favorable influences, good drainage above the permafrost zone is also important. This soil is designated "arctic Minimal Podzol" in this report.

Three soil profile diagrams are given (Figure 46) to illustrate these soil types--Arctic Tundra and Arctic Brown Soils at Nome, Bering Sea coast, and "Arctic Minimal Podzol" at Cape Krusenstern near Kotzebue, on the Arctic Sea coast. The Arctic Tundra Soil resembles a Bog Soil of more southern regions, in which the excess of water has prevented normal horizon development, and has caused the formation of a gley zone by eluviation of the organic deposit. It differs from the Bog Soil in its instability due to congeliturbation, which results in considerable mixing of the mineral fraction of the C horizon with the upper layers. This process is described in detail by Hopkins and Sigafoos (1951), and its effects on soil horizon development is presented by Douglas and Tedrow (1960, p. 300).

The underlying parent material of the Arctic Tundra Soil site

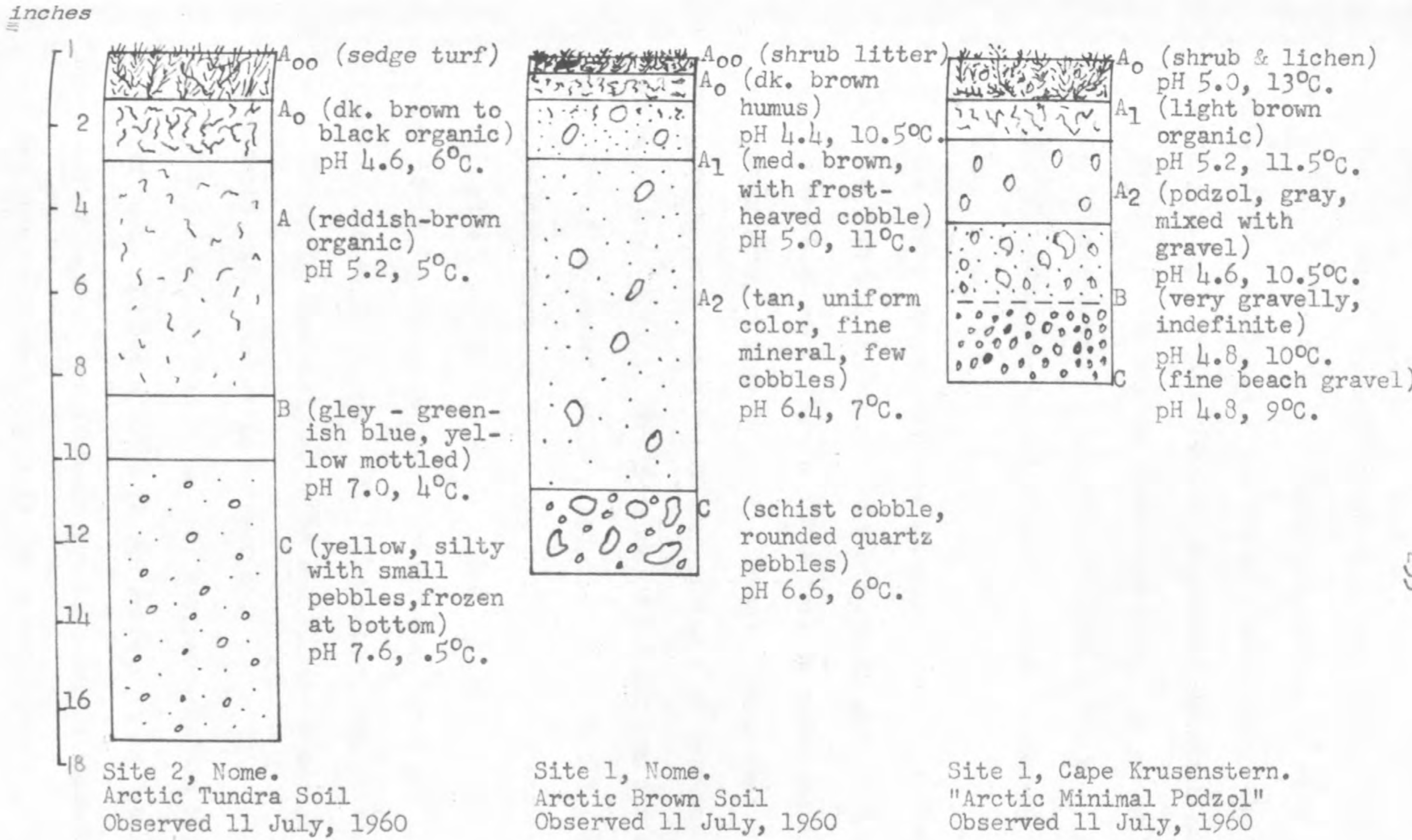


Figure 46. Soil profile diagrams of three soils of the Arctic Tundra region. The three different Soil Groups are formed under similar climatic conditions.

at Nome is mapped by Hopkins, Macneil, and Leopold (1960, p. 48) as till and outwash of Nome River glaciation, is basic in reaction, and is frozen to within 17 inches of the surface. The A horizon is strongly acid, changing abruptly to neutral in the B horizon. The same profile pH tendencies were observed by the writer to be present in Bog Soils--however, the reaction of the lower bog horizons is largely dependent on the nature of the parent material of the C horizon.

The Arctic Brown Soil site at Nome is about 150 feet upslope from the former site, and is over bedrock mapped as Paleozoic schist by the above authors (ibid.). This soil is quite shallow (bedrock was encountered at a depth of 13 inches), and of medium to low moisture content. Differentiation of the A horizon was distinct in spite of frost action. The absence of a B horizon indicates the lack of illuviation caused by low precipitation (7 to 8 inches annually, U. S. Weather Bureau, 1943). The shallow profile and the location of this site on a bedrock ridge relate this soil to a Lithosol, from which it is suggested to have been derived. However, the definite zonation places it in the Zonal Soils rather than in the Azonal to which Lithosols are assigned. The soil horizons decrease in acidity with depth, but remain acid to bedrock.

The "Arctic Minimal Podzol" site represented in Figure 46 is located on an old beach ridge (2,900 years old, as determined by radiocarbon dating, verbal communication, Dr. J. Louis Giddings), and has unconsolidated gravel as the parent material. The thin organic and organic-mineral horizons A_0 and A_1 are on a distinct podzolized A_2 horizon of a gray color and mixed with abundant gravel. The distinction between the B and C horizons is not sharp--the gravel content gradually increased to pure gravel at the bottom of the sample hole. The highly acid organic litter (pH 5.0) and the adequate drainage provided by the gravel of the C zone on the slightly elevated beach ridge promoted the process of podzolization which apparently occurred at a low rate, probably because of the cold climate (the soil temperature was 9 to 13 degrees C.). Adjacent profiles, but in the swales instead of on the ridges, did not have this podzol horizon, but were characterized by a reddish iron oxide (determined by chemical analysis) deposit 1 to 4 inches thick. This iron deposit most likely was caused by the rod-shaped (iron reducing?) microorganisms that the writer found by microscopic examination to be abundant in the water which periodically submerged the swales. This process was observed to be currently in operation in these pools, the shallow water having an abundance of orange-red floccules in suspension. The soil of the swales does not seem to correspond to any described soil type, and more study is needed of its occurrence and characteristics.

The vegetation of the arctic tundra has been described by Steere (1947, 1954), Polunin (1948), Hopkins and Sigafoos (1951), Wiggins (1951), Spetzman (1959), Sjörs (1959), and others. The complexities of tundra soil and vegetation patterns are well known but imperfectly understood. The major distinction of the development of these three soil types appears to be the degree of wetness and the amount of congeliturbation. Likewise, the major distinctions in plant communities of this region probably is in the adaptation of the component species to a moisture requirement or tolerance and their ability to withstand severe frost action. These studies were not sufficiently detailed in the arctic regions to more definitely establish the relationships of plant communities and soil types. The difficulties in field studies of this region involve the determination of just what is a specific plant community, and what are the limits of a soil type. Until both categories, as they exist in this region that was studied, can be more precisely defined it is impossible to make an accurate appraisal of their spatial correspondence.

Relevé of plant community on Arctic Tundra Soil, Nome, Alaska.

Altitude, near sea level. Area, 10 X 10 meters. Observed July 10, 1960.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
<u>Anisothecium crispum</u>	1.3
<u>Aulacomnium palustre</u>	+.2
<u>Aulacomnium turgidum</u>	+.2
<u>Drepanocladus uncinatus</u>	1.3
<u>Drepanocladus revolvens</u>	1.2
<u>Mnium andrewsianum</u>	r.1
<u>Oligotrichum cavifolium</u> (fruiting abundantly)	4.4
<u>Oncophorus wahlenbergii</u>	+.2
<u>Pogonatum capillare</u>	+.2
<u>Polytrichum juniperinum</u>	2.4
<u>Polytrichum piliferum</u>	+.3
<u>Sphagnum fimbriatum</u>	1.4

Sedges -

Carex bigelowii	4.5
Eriophorum sp. (immature)	3.4

Forbs -

Petasites frigidus	+.2
Pinguicula vulgaris	r.2
Saxifraga hieracifolia	+.1
Saxifraga hirculus	+.2

Shrubs -

Empetrum nigrum	+.3
Salix reticulata	+.2

Shrub stratum:

Betula nana subsp. exilis	+.2

This very wet site had the appearance of a sedge meadow. Only one Carex was fruiting and could be identified; other species of similar vegetative appearance may have been present. This community had only a very small percent of the total number of species known to grow on this soil type as observed by the writer at Barrow, and elsewhere. It is noteworthy that all vascular species listed above (except Pinguicula vulgaris) were found by the writer on Alpine Tundra soils of interior Alaska.

Relevé of plant community on Arctic Brown Soil, Nome, Alaska.

Altitude, ca. 75 feet. Area, 10 X 10 meters. Observed July 10, 1960.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Anisothecium crispum	1.3
Brachythecium albicans	+.2
Cephaloziella arctica	r.1
Pleurozium schreberi	3.4
Sedges -	
Carex cf. *bigelowii* (fruiting poorly)	+.2
Carex nesophila	+.2
Luzula nivalis var. *latifolia*	3.2
Forbs - (none)	
Shrubs -	
Empetrum nigrum	3.3
Loiseleurea procumbens	3.3
Vaccinium vitis-idaea	+.3
Shrub stratum:	
Betula nana subsp. *exilis*	+.1
Ledum palustre var. *decumbens*	2.3
Salix pulchra	+.2
Salix phlebophylla	+.2

The vegetation of this rather dry ridge was characterized by a shrub community of low, matted growth. The shrubs were depauperate and grew from a usually large stem base resembling a caudex, which indicated slow growth and great age for many of the plants. If the area of the relevé had been enlarged, probably some forbs would have been found; however, none was seen on this entire ridge. The sedges (excluding Luzula) were barely existing at this site and scarcely if at all fruiting.

Relevé of plant community on "Arctic Minimal Podzol" Soil at Cape Krusenstern near Kotzebue, Arctic coast (Figure 47).

Altitude, near sea level. Area, 10 X 10 meters. Observed July 12, 1960.

Species	Abundance-Cover and Sociability Value
Ground stratum:	
Bryophytes -	
Anisothecium crispum	1.3
Polytrichum piliferum	3.4
Grasses and Sedges -	
Festuca brachyphylla	1.2
Hierochloe alpina	1.1
Luzula confusa	+.2
Luzula multiflora var. frigida	+.2
Forbs -	
Astragalus alpinus subsp. arcticus	r.1

Figure 47. Plant community on old beach ridges at Cape Krusenstern, about twenty miles north of Kotzebue, Alaska. The slight elevation of these ridges and their gravel D horizon permit free drainage when unfrozen. The thin vegetation cover produces an acid humus, which results in a zone of minimal podzolization at the base of the A horizon. This previously-undescribed soil is tentatively referred to as "Arctic Minimal Podzol." July 12, 1960.

Draba hirta	+.1
Erysimum pallasii	+.1
Minuartia macrocarpa	1.2
Potentilla ledebouriana	+.1
Saxifraga hieracifolia	+.1
Tofieldia pusilla	r.2
Shrubs -	
Vaccinium vitis-idaea	r.1
Shrub stratum:	
Betula nana subsp. exilis	+.1
Ledum palustre var. decumbens	r.1
Vaccinium uliginosum	+.1

Grasses and forbs were the most prominent elements in these old beach ridge communities; the shrubs were very depauperate and scarce. In contrast, the swales between the ridges were often conspicuous by their dense growth of shrub willows (Salix ovalifolia and S. flagellaris) and had a greater number of forb and moss species. The differences in these immediately adjacent communities appeared to be due to the amount of water, frost action, and exposure to wind.

3. Summary and conclusions.

The writer concludes that, on the whole, these Soil Groups cannot be definitely and precisely identified with a specific plant community (which must still be descriptive rather than taxonomic). One reason for this non-conformity is the lack of specificity and precision in establishing the units of soils and plants to be compared. However, as now defined, the range of climate and parent material allowed in a soil category is greater than the range in climate and substrate of a logically-describable plant community. The correspondence of the two could be increased by broadening the definition of the plant community to include the variations of plant associations found throughout the extent of the Soil Group. This would result, however, in such heterogeneity in the named plant community that the species composition in different regions of its occurrence would have little relevancy. The fundamental difference in the two is in the range of generalizations allowable in each.

There are certain species associated only with a certain Soil Group--not because of the species' dependence on the properties of the soil of the Group but because climatic and other environmental conditions favorable to both fortuitously coexist. In describing some plant communities of the arctic tundra of Alaska and their occurrence on certain soils, Bliss (1956, p. 306) concludes, "Soil group-plant community relationships are not always as clear cut as described above, for gradations of all types appear." The properties of a soil cannot be disassociated from the species of plants that it supports, but the naming of a Soil Group is not entirely based on its properties. Thus we find an inconsistant degree of relationships between the two, for the characterizations of the two units are not based on the same system. It is therefore futile to try to harmonize the two as a matter of principle; such correspondence as does occur is due to an overlap that is not a fundamental of either system.

It is shown in these studies that the genesis of a soil, particularly if the soil is Zonal, is largely determined by climate directly, and by plants both directly and indirectly. With these soils it is more accurate to say that plants control soil development, rather than the reverse. Once a soil is formed, or as it is being formed, by whatever combination of climatic, geologic, chemical, and biological processes, it does exercise a degree of control on the species that can occupy it. The importance of this control in the plant community varies with the species of plant in accordance with its general ecological amplitude, and is only one of the controlling factors of the environment--exposure, water relationships, frost action, temperature characteristics, and other factors all combine to make the environment holocoenotic. The precise effect of one factor relative to another in a plant community can best be appraised by detailed autecological studies of each component species.

C. Evidence of the Control of Bryophyte Communities by Soil and Other Substrates.

1. Reaction to the environment. Bryophytes are said to be generally very sensitive to the many factors of their environment. In the field work of this study special attention was given to recording the environmental factors associated with each specimen collection because the effects of one factor, such as substrate influence, are dependent on the combined effects of others. In this way an evaluation of the ecological amplitude of bryophyte species of this region could be made, also an appraisal could be had of the effects of the several

environmental factors themselves.

Richards (1932, p. 369) in discussing the ecological amplitude of bryophytes writes, "Among bryophyta, as among other plants, species differ very much in the range of conditions under which they live. There are a few wide-ranging species found in a great variety of habitats, such as Hypnum cupressiforme and Ceratodon purpureus. In one form or another, the latter extends all over the world, grows on wood, stone and soil, and in all kinds of situations. It is said to tolerate hydrogen ion concentrations from pH 4.6 to 7.6, though it prefers acid substrata . . . At the other extreme are species with very specialized habitats, such as Anacamptodon splachnoides (in rot-holes of trees, usually Fagus) and Philophyllum spp. (in the "tanks" of Bromeliaceae only).

"On the whole, however it is true to say that most bryophytes have a sharply defined and rather narrow ecological range. This gives them great value as indicators of certain habitat conditions, probably greater than most flowering plants. It must be remembered however that the habitat of a bryophyte is usually a very small space. Thus moss indicators will only give information about the top-most layers of the soil."

In view of this extreme variation in ecological amplitude in respect to substrates, from single, specific ones to almost any type supporting medium, if bryophytes of a region are to be studied from this standpoint individual species preferences must be determined. These substrate occurrences must then be treated statistically if generalized tendencies are to be derived and if the question of whether bryophytes as a group are, in fact, peculiarly limited to a narrow ecological range is to be answered. This information not only relates to an appraisal of their general indicator value, but also shows the proportion of species having specialized environments to those of general distribution in the region.

2. Methods of study. The analysis of any ecological situation is very difficult because of the single effects of the great number of environmental factors known (in addition to those unknown which may exist) and their multiple or different effects when in almost endless combination. This latter effect is included in Mayr's (1961, p. 1,505) reasons for indeterminancy in biology as "emergence of new qualities at higher levels of integration." This author states further (ibid), "As is true in many other branches of science, the validity of predictions for biological phenomena (except for a few chemical or physical unit processes) is nearly always statistical."

If bryophytes are to be related to the effects of substrate factors the effects of the other environment factors (such as light, altitude, temperature, water relationships) must be observed, then the attempt made to differentiate by statistical analysis the two classes of effects. The validity of data derived statistically is founded on the sampling accuracy. In field studies of plant species of a large area having greatly varied ecological conditions only the most intensive sampling program would insure a high degree of accuracy in evaluating the ecological amplitude of the individual species. This accuracy ordinarily is expected to increase with the increased number of occurrences recorded for the species. In the writer's surveys of vegetation in Alaska (see Figure 1) many bryophyte species were found at only one location, which may mean (1) that the species occurs in only one specific combination of environmental factors, (2) that one factor of the environment exercises a controlling effect within the general range of the other factors of the region, (3) the species was present at other sites but was not recognized due to the difficulty of its field identification, and (4) that insufficient sites were examined to cover the range of ecological amplitude of the species. Therefore but little significance can be attached to the apparently narrow range in ecological amplitude of a particular species that was found but once if its specific limiting requirement is unknown. However, a different and more definite interpretation can be placed on the limitation of a species or group to a particular known factor of the environment. For example, in these studies the members of the family Splachnaceae were found entirely restricted to substrates of animal organic matter, which is in accord with world-wide observations on this group. There is a high degree of reliability in this substrate requirement of these mosses, but the predictability of their actual occurrence is of a low order. Other environmental factors must also be favorable, in addition to the basic substrate requirement; these first requirements are not often met, as deduced from the general rarity of these mosses, although the basic requirement is generally abundant. The only positive interpretation that can be given from the single occurrence of a species is that it is capable of growing in the environment of that site, although all factors of this environment may not be discernable; the assumption that it is restricted to environments of this type is not warranted without extensive sampling.

In contrast to the statements above, some bryophyte species were collected at many sites under the influence of greatly varying environments. Some questions also arise in the interpretation of this multiple occurrence--was the species actually occurring at more sites than was some other species, was it a more "dominant" species and therefore its presence more obvious, was there bias in collecting species from a site so that some were favored over others (for example, those species better known by the collector), or did the selection of sites intentionally or unintentionally favor the frequent occurrence of this species? These factors were kept in mind when these collections were made, and some degree of control over them was attempted. However, it is not claimed that these collections are entirely free from sampling bias. Random sampling was not done; however, the mixed occurrence of many species in a "micro-community" of bryophytes gave a certain degree of randomness to the single collections having a number of species that were not detected until laboratory studies were made. In each collection every recognizable species was recorded, even though represented only by fragments. For this painstaking search for all species in a collection the writer is greatly indebted to Dr. Herman Persson, without whose help many small or fragmentary plants, or rare species, would have been overlooked.

The field method of collecting used was that of having selected a sample site of a more or less distinct habitat type, to collect all recognizable species at the site. The sites were not randomly chosen, as indicated above; if this had been done, it is probable that many significant micro-communities would not have been included in the study. The completeness that was sought was that of sampling habitat types within a particular region and of obtaining all species occurring in each habitat type. How well this was achieved cannot be evaluated from this study itself.

In all, 1,750 bryophyte collections were made and identified (by the term "collection" is here meant one species from one site). The data for each collection was entered on a species card, and the cards were filed alphabetically by genera and species, keeping the mosses (including the genera of questionable taxonomic position *Sphagnum*, *Andreaea*, and *Oedopodium*) separate from the liverworts. Using this card file to establish the categories of environmental factors that were actually found to pertain to these Alaskan species, a large chart was made having 116 individual environment categories on which the 397 bryophyte species were listed, with mosses and liverworts kept separate. Then each species card was examined, and the occurrence of the species in relation to each environment category was noted. This required a theoretical total of 46,052 trials for category fit, although the actual number was less because some of the larger categories could be eliminated for certain species. The information derived from this master chart was used in the preparation of Tables II through IV.

The division of the environmental factors into categories on this chart may be a source of misleading or incorrect conclusions that are statistically derived from it. The rather arbitrary and perhaps somewhat subjective nature of some of these divisions is not denied. Further testing and perhaps modifications of this categorization is to be desired. The substrate categories used in this master chart are given in Table II. The "non-substrate" ecological factors that were used on the master chart are given below, with the specific categories numbered consecutively:

LIGHT:
1. full exposure
2. reduced
3. greatly reduced

WATER:
Submerged -
4. stream
5. rapids
6. bog and tundra pools
7. other pools
8. salt water

Emergent -
9. bog
10. other

Spray -
11. fresh
12. salt

Substrate -
13. medium drained
14. overdrained
15. underdrained
16. washed
17. thermal spring

ALTITUDE:
18. sea level to 999 feet
19. 1000 to 1999 feet
20. 2000 to 2999 feet
21. 3000 to 3999 feet
22. 4000 to 4999 feet
23. 5000 feet and higher

PLANT COMMUNITY:

24. chasmophyte
25. rock surface
26. talus
27. shingle or scree
28. bog
29. muskeg
30. sedge tussock meadow
31. alpine meadow
32. mountain tundra
33. alpine tundra
34. arctic tundra
35. deciduous forest
36. coniferous forest
37. mixed forest
38. littoral, salt water
39. littoral, fresh water
40. frost mound
41. frost scar
42. epiphyte
43. aquatic
44. ruderal
45. alluvial
46. fire disclimax
47. other disclimax
48. nitrophilous
49. calcicolous

PHYTOGEOGRAPHIC DISTRICTS:

50. Eastern Pacific Coast
51. Central Pacific Coast
52. Alaska Range
53. Lower Yukon River
54. Central Yukon River
55. Bering Strait
56. Arctic Coast

3. Statistical analysis of bryophyte substrates (Table II.). Because of the special emphasis in this study on soil or other substrate effects on vegetation the substrate categories were summarized to show the number of bryophyte species found on or near each substrate, and the percentage that this number represents of the total species of mosses or liverworts. In this way a comparison of mosses and liverworts

Table II. Statistical Analysis of Bryophyte Substrates

S-O = Species-Occurrence, i.e., number of occurrences ÷ total number of species.
Percentages are of total number of moss or liverwort species.
Other numbers are total occurrences on the substrate.

Kind of Substrate	Mosses, including Sphagnum (301 species)	Liverworts, leafy & thallose (96 species)
I. ROCKS & MINERALS	(S-O on & near, 122)	(S-O on & near, 99)
1. Rocks	(S-O 82 on; 19 near)	(S-O 52 on; 16 near)
A. Sedimentary	(S-O 8 on; 2 near)	(S-O 3 on; 0 near)
a. limestone	22 (7%) on; 0 near	3 (3%) on; 0 near
b. shale	1 (.3%) on; 0 near	- - - - - - - - - -
c. chert	0 on; 2 (.7%) near	- - - - - - - - - -
B. Igneous	(S-O 21 on; 1 near)	(S-O 9 on; 2 near)
a. granite	6 (2%) on; 0 near	1 (1%) on; 0 near
b. diorite	6 (2%) on; 0 near	- - - - - - - - - -
c. gabbro	15 (5%) on; 0 near	1 (1%) on; 0 near
d. norite	4 (1%) on; 2 (.6%) nr.	- - - - - - - - - -
e. serpentine	1 (.3%) on; 2 (.6%)nr.	3 (3%) on; 1 (1%) nr.
f. rhyolite	5 (2%) on; 0 near	0 on; 1 (1%) near
g. basalt	25 (8%) on; 0 near	4 (4%) on; 0 near
C. Metamorphic	(S-O 54 on; 17 near)	(S-O 40 on; 14 near)
a. argillite	1 (.3%) on; 0 near	- - - - - - - - - -
b. slate	47 (16%) on; 14(5%)nr.	14 (5%) on; 4 (4%) nr.
c. schist	82 (28%)on;34 (11%)nr.	16 (11%) on; 9 (9%)nr.
d. gneiss	1 (.3%) on; 0 near	- - - - - - - - - -
e. quartzite	1 (.3%) on; 0 near	- - - - - - - - - -
f. graywacke	13 (4%) on; 4 (1%) nr.	5 (5%) on; 0 near
g. soapstone	1 (.3%) on; 0 near	- - - - - - - - - -
h. other	16 (5%) on; 0 near	3 (3%) on; 0 near

Table II. Statistical Analysis of Bryophyte Substrates (continued)

Kind of Substrate	Mosses, including Sphagnum (301 species)	Liverworts, leafy & thallose (96 species)
2. Minerals	(S-0 13 on; 8 near)	(S-0 23 on; 8 near)
A. copper minerals	3 (1%) on; 11 (4%) near	2 (2%) on; 2 (2%) near
B. galena	3 (1%) on; 4 (1%) near	3 (3%) on; 3 (3%) near
C. sphalerite	4 (1%) on; 2 (.6%)near	3 (3%) on; 3 (3%) near
D. quartz	4 (1%) on; 2 (.6%)near	1 (1%) on; 0 near
E. calcite	2 (.6%) on; 0 near	2 (2%) on; 0 near
F. calcareous tufa	7 (2%) on; 0 near	4 (4%) on; 0 near
G. gypsum	2 (.6%) on; 0 near	2 (2%) on; 0 near
H. pyrite	5 (2%) on; 2 (.6%)near	4 (4%) on; 0 near
I. other	9 (3%) on; 2 (.6%)near	4 (4%) on; 0 near
II. OTHER SUBSTRATES		
1. Mineral Soil	(S-0, 54)	(S-0, 33)
A. sand to sandy	21 (7%)	- - - - - - - - - -
B. silt or loess	47 (16%)	11 (11%)
C. lithosol	61 (20%)	19 (19%)
D. fine glacial	13 (4%)	1 (1%)
E. alluvium	8 (3%)	1 (1%)
F. gravel or scree	14 (5%)	- - - - - - - - - -
2. Mixed Mineral & Organic Soil	(S-0, 21)	(S-0, 14)
A. muck	23 (8%)	9 (9%)
B. peat-loess	5 (2%)	- - - - - - - - - -
C. peat-sandy	35 (12%)	4 (4%)

Table II. Statistical Analysis of Bryophyte Substrates (continued)

Kind of Substrate	Mosses, including Sphagnum (301 species)	Liverworts, leafy & thallose (96 species)
3. Organic	(S-O, 125)	(S-O, 106)
A. tree or shrub	(S-O, 40)	(S-O, 46)
a. angiosperm	31 (10%)	3 (3%)
b. gymnosperm	27 (9%)	16 (16%)
c. living	(S-O, 18)	(S-O, 46)
(1) base	15 (5%)	- - - - - - - - - -
(2) trunk	16 (5%)	6 (6%)
(3) branch	11 (4%)	3 (3%)
(4) root	12 (4%)	2 (2%)
d. dead	(S-O, 22)	(S-O, 8)
(1) "sound"	14 (5%)	7 (7%)
(2) charcoal	5 (2%)	1 (1%)
(3) rotten wood	47 (16%)	25 (25%)
B. Peat & Other Loose Organic	(S-O, 58)	(S-O, 58)
a. miscel. peat	101 (34%)	36 (36%)
b. liverwort peat	2 (.6%)	4 (4%)
c. sedge peat	4 (1%)	- - - - - - - - - -
d. raw humus mat	33 (11%)	10 (10%)
e. leaf mold	10 (3%)	1 (1%)
f. conifer needles	16 (5%)	2 (2%)
g. turf	8 (3%)	3 (3%)
C. Animal	(S-O, 8)	(S-O, 2)
a. dung	13 (4%)	1 (1%)
b. bone	6 (2%)	- - - - - - - - - -
c. carcass	2 (.6%)	- - - - - - - - - -
d. other	2 (.6%)	- - - - - - - - - -
D. Other	1 (.3%)	1 (1%)

could be made in respect to their substrate occurrences. The category "on" was held to mean that the bryophyte species was observed to be in actual contact with the rock or mineral surface. The designation "near" was used to signify that although the species was not actually in contact, it was on material immediately derived from the rock or mineral, or otherwise so situated that it was reasonable to assume that the dominant substrate influence was that of the rock or mineral listed.

On examination of Table II the fact is at once evident that moss species predominate on the common rocks and minerals; liverworts, in contrast, show a slight predominance on the more uncommon ones, as serpentine, copper minerals, galena, sphalerite, calcite, calcareous tufa, gypsum, and pyrite. This supports the prior evidence given of the generally great range of tolerance to anomalous substrate chemical concentrations among liverwort species. Mosses have a greater percent of species on mineral soils and on soils of mixed mineral and organic composition. Liverworts were notably absent from sand to sandy soil, gravel or scree, and mixed peat-loess soil. The first two above observations are believed to be correct, whereas the last is probably sampling error.

Of the organic substrates, liverwort species are significantly more abundant on rotten wood than are mosses, and the converse is true in regard to "sound" (non-rotten, but "non-living") wood. Charcoal as a substrate is favored more by mosses; it is believed that the one liverwort occurrence was merely fortuitous. The adaptation to animal organic matter as a substrate is believed to be a peculiar property of certain mosses--the one liverwort occurrence is believed again to be a factor of chance, for this liverwort species was not restricted to this type of substrate whereas the moss species were so restricted.

Results that may be somewhat surprising are the differences in occurrence of bryophytes on gymnosperm and angiosperm species of trees and shrubs. Although as forest trees gymnosperms are much more abundant in most parts of Alaska than are angiosperms, yet mosses showed an almost equal percentage occurrence on the two. Liverwort species, on the other hand, were much more abundant on gymnosperm species. The general preference of mosses for angiosperm trees and their rarity on gymnosperms has often been recognized, but no previous reports have been found of this contrary tendency of liverworts.

In order to compare the subdivided categories of substrate factors the term "Species-Occurrence" was devised (abbreviated S-O). Because a single species was frequently found on several of the substrate subdivisions of a category, the summation of the occurrences on the substrate does not conform to the total number of different species of mosses or liverworts, but may exceed it. A comparison of major category occurrences of moss and liverwort species is made possible by dividing the total number of species of mosses or liverworts into the total number of occurrences of each. This gives, in effect, percentage values that may be compared for mosses and liverworts, although there are three times as many moss species as liverwort species listed in the table. This process may be expressed as follows:

$$\frac{\text{Number of occurrences on the substrate group (listed in Table II)}}{\text{Total number of species of the plant group (i.e., mosses or liverworts)}} = \text{Species-Occurrence}$$

By the use of this process we can see that mosses have the greater S-O value for all the major substrate categories (rocks and minerals, mineral soils, mixed mineral and organic soils, and organic substrates). In the next lower order of subdivisions mosses have the greater occurrence on rocks, liverworts the greater on minerals and on living trees and shrubs. The S-O value of both plant groups is the same for peat and other loose organic matter, and in the next lower subdivisions of this category the two groups show a remarkable similarity in percentage occurrence.

Although Table II shows the occurrence of bryophytes on limestone and calcite, it does not further evaluate these occurrences. Because of the particular interest in this study of calcicolous plant species, these bryophytes will be considered in more detail. A bryophyte community was studied by the writer which occurred on the limestone and calcite outcrops at Mile 39, Elliott Highway, Central Yukon district. This outcrop is a westward extension of White Mountain which was botanically explored by Dr. Olav Gjaerevoll in 1957. The Mile 39 site supported a bryophyte community composed largely of calcicolous species, which are discussed below.

Mosses:

Abietinella abietina - Reported to be calcicolous (Persson and Gjaerevoll 1957, p. 22). Was found in Alaska also on basalt and schist by the writer.

Amblystegium sprucei - Probably calcicolous; found in Alaska only at this site by the writer.

Ceratodon heterophyllus - Probably calcicolous; found in Alaska only at this site by the writer. A very rare species.

Drepanocladus uncinatus - A species of very wide ecological amplitude, found by the writer throughout Alaska.

Encalypta longicolla - Reported to be an obligate calcicole (ibid, p. 42-43). Found at no other site by the writer. This is the second report of this species for North America.

Grimmia tenuicaulis - This species was found in a calcicolous habitat by Gjaerevoll, and in Alaska only at this site by the writer. This is the second report of this species for North America.

Gymnostomum recurvirostre - Reported to be calcicolous (ibid, p. 46). Found in Alaska by the writer also on slate.

Hypnum vaucheri - Reported to be calcicolous (ibid, p. 49). Found on chlorite schist in Alaska Range by the writer.

Mnium hymenophylloides - Reported to be an obligate calcicole (ibid, p. 54). Found in Alaska only at this site by the writer.

Mnium orthorhynchum - Reported to be calcicolous in Scandinavia (ibid, p. 54). Found by the writer on schist and on rotten wood in the Alaska Range.

Myurella careyana - Probably calcicolous. Found in Alaska only at this site by the writer.

Myurella julacea - Reported to be calcicolous (ibid, p. 55). Found in Alaska also on slate by the writer.

Orthothecium chryseum - Reported to be calcicolous in Scandinavia (ibid, p. 56). Found in Alaska as a tufa-forming species, also on schist and on organic soil of a mountain tundra by the writer.

Orthothecium intricatum - Reported to be calcicolous (ibid, p. 57). Found in Alaska only at this site by the writer.

Schistidium strictum - Found on many other substrates in Alaska by the writer, including basalt and granite.

Tortella fragilis - Reported to be calcicolous (ibid, p. 70). Found by the writer on schist in Alaska.

Tortella tortuosa - Reported by Grout (1938, p. 168) as occurring "principally in calcareous regions." Found by the writer in Alaska only at this site.

Liverwort:

Scapania cuspiduligera - Reported to be calcicolous (Persson and Gjaerevoll, 1957). Found in Alaska by the writer at this site only.

The assemblage of so many obligate or preferential species of bryophytes on a small outcrop represents a decided contrast to the vascular plant community on and around this same outcrop which had no distinctly calcicolous species. A somewhat similar community of bryophytes was examined on a limestone and calcite outcrop on the Taylor Highway near the Canadian-Alaskan boundary. In addition to other calcicolous species, two liverworts (Clevea hyalina and Mannia pilosa) that are reported to be decidedly calcicolous (ibid, p. 13) were found here. This was the only site in Alaska where these species were found by the writer.

In Chapter III the conclusion was made that arctic vascular species were only 3 to 4 percent calcicolous. Table II lists 22 species (7 percent) of mosses and 3 (3 percent) species of liverworts growing directly on limestone. If we subtract the non-calcicolous and the doubtfully-calcicolous species, 15 species remain that are believed to be definitely calcicolous, although occasionally found on non-calcareous substrates. This is approximately 4 percent of the total bryophyte species included in this report. Thus the bryophyte flora and the vascular flora of these northern regions are believed to have about the same percentage of calcicolous species. The outstanding difference between these plant groups, in regard to calcicolous species, is a phytosociological one. Calcicolous bryophyte communities tend to exclude non-calcicolous species from occupancy of the site, whereas vascular plants probably do not occur in such exclusive communities. This difference may be partly due to the greater ability of vascular plants to alter the pH of surficial material over the basic substrate. The calcicolous bryophytes are mostly "pioneer" species of the rock surfaces, and are subjected to the almost unaltered chemical environment of the basic rocks. When a surficial deposit is formed that is sufficiently deep to have a significant change in pH the vascular plants invade the site, and continue the process of substrate acidification. In regions of deep organic accumulations, as in arctic and boreal areas, obligate calcicolous species must ordinarily be "pioneer" species of a basic substrate, otherwise the acidity of the organic deposit that is formed excludes them from occupancy of the site.

It may be concluded that certain bryophyte species are definite indicators of a basic substrate, and that on most such substrates, few other bryophyte species will be found. The primary control of the occurrence of these species is the nature of the substrate, and most of them are adapted to the xerophytic habitats often associated with basic rock outcrops.

4. Summary of ecological amplitudes of bryophyte species (Table III). If the statement of Richards given at the beginning of this section is to be tested by these data at hand, an appraisal of the ecological amplitudes of the individual moss species must be made. These may then be grouped to show the tendency of mosses or liverworts toward a wide or narrow range of ecological amplitudes, and the two classes of bryophytes can be compared in this respect. Accordingly, a system of classes of ecological amplitude (abbreviated E-A) was devised by the writer, as given in Table III, and the number of species and the percent of the total species of each class were tabulated separately under mosses and liverworts.

These E-A classes were established by adding the number of factors relating to substrates (Table II) and the number of "other environmental factors" (pages 271-272), which gave a total of 116 factors, then enumerating the species-occurrences according to their distribution

Table III. Summary of Ecological Amplitudes of Bryophyte Species

Total number of moss species, including Sphagnum, 301.
Total number of leafy and thallose liverwort species, 96.
Total number of ecological factors considered, 114.

Classes of Ecological Amplitude	Mosses		Liverworts	
	Number of species	Percentage of total species	Number of species	Percentage of total species
I. (0- 5%)	116	38.6	47	48.9
II. (6-15%)	150	50.0	42	43.7
III. (16-25%)	30	10.0	7	7.2
IV. (26-35%)	4	1.3	---	---
V. (36-45%)	---	---	---	---

in arbitrarily-derived percentage-of-occurrence classes (i.e., classes of ecological amplitude). As an interpreted example from Table III, we may select E-A Class II and observe that the occurrence of 150 species of mosses ranged between 6 and 15 percent of the total environmental conditions recognized. These 150 species represent approximately 50 percent of the moss species studied, thus we can conclude that about half of the moss species occur under the influence of 6 to 15 percent of the total recognized environmental factors--that is, are rather highly "selective" in habitat. In E-A Class IV we find that only 1.3 percent of the total number of moss species were found to exist under a rather large number of different environmental conditions. Thus this table shows the general tendency of bryophytes toward a narrow E-A range--none extended into the Class V category. This class was established because it is believed that additional sampling will extend some few species into this range, for some closely approached it with the sampling that was done. At the same time, this table shows that a few species have a very wide range of environmental conditions of habitat.

Of the two plant groups, liverworts are shown to have a narrower range of E-A, with the largest group occurring in Class I. These are essentially those species found in only one habitat, many of which are probably rather closely restricted to this habitat. Mosses, in contrast, have more species in Class II than in Class I, showing that the species are not so frequently restricted to one habitat. We may conclude by stating that Richards' statements on the ecological amplitude of bryophytes are supported by this study, and that the statistical evaluations used here express the differences of mosses and liverworts in this respect.

5. Comparative effects of environmental factors (Table IV). The effects of substrate factors on the occurrence of bryophyte species must be separated from those of the other environmental factors if they are to be compared. In this way it can be determined if these plants as a group are more commonly controlled in their occurrence by substrate factors, or if the majority of species are relatively indifferent to the effects of this factor. Table V gives the results of this comparison. The "substrate factors" percentages begin with a lower value than do "other environmental factors" percentages. This is because a species may be found on only one substrate (1 factor of 60 factors = 1.6 percent), whereas under "other environment factors" every species has a minimum of five factors listed (light, water, altitude, plant community, and phytogeographic district) therefore has 5 factors of 56 factors = 8.9 percent.

The very high beginning numbers in each column reflect the fact that many species are represented by one collection only. Because these numbers in the first group of each column are so high and drop so drastically in the second group it is believed that a high environment factor specificity is indicated for many species; it seems improbable that the essentially "mass collection" techniques used, particularly in making liverwort collections, would result in such gross inadequacy of sampling. However, additional sampling would probably reduce the number of species in the first groups.

Table IV. Comparative Effects of Environmental Factors

SUBSTRATE FACTORS (60) (rocks, minerals, mineral soil, mixed mineral & organic, & organic)			OTHER ENVIRONMENT FACTORS (56) (light, water, altitude, plant community, phytogeographic district)		
Percent of factors	Number of species		Percent of factors	Number of species	
	Mosses	Liverworts		Mosses	Liverworts
1.6	97	34			
3.3	61	29			
5.0	43	6			
6.6	23	8			
8.3	21	7	8.9	106	38
10.0	16	2	10.7	9	7
11.6	5	3	12.5	26	6
13.3	8	2	14.2	22	6
15.0	6	0	16.0	25	10
16.6	2	1	17.8	20	3
18.3	1	1	19.6	12	8
20.0	1		21.4	13	3
21.6	0		23.2	14	5
23.3	1		25.0	7	2
25.0	2		26.7	13	1
26.6	1		28.5	3	1
28.3	2		30.3	5	2
30.0	1		32.1	7	1
			33.9	5	0
			35.7	2	1
			37.5	5	0
			39.2	1	0
			41.0	1	1
			42.8	1	0
			44.6	1	1
			46.4	0	
			48.2	0	
			50.0	0	
			51.7	1	
			53.5	0	
			55.3	2	

In comparing the relative importance of substrate factors and other environment factors in their effect on species occurrence Table IV clearly shows the dominating effect of other environment factors, when bryophytes are considered as a whole. Here the same conclusions are reached with bryophytes as a group as were maintained for vascular plants in arctic and boreal environments--that substrate influence is subordinate to other factors of the environment in determining the development and species composition of plant communities. At the same time, a few individual species are found to be closely related in their occurrence to a particular substrate factor, which gives them value as botanical indicators of substrate peculiarities.

CHAPTER V.

INFLUENCES OF THE NON-ESSENTIAL SUBSTRATE ELEMENTS ON PLANTS

A. Consideration of Differential Quantities of the Non-Essential Elements in Soils and Plants.

The relationships of plants to the major nutritional elements have been discussed in Chapter III on the basis of availability to the plants. The assumption was made that if the elements were available in adequate amounts and in the proper proportion they would be absorbed in quantities sufficient for normal nutritional requirements. The writer has shown in Chapter III that arctic and boreal plants are generally oligotropic in regard to these elements.

The normal growth and reproduction of a plant require not only the presence of certain essential elements, but a degree of balance in amounts absorbed, because of the specific functional determinism of these elements. The functions must be in balance to express the growth and reproduction characteristics that have come to be considered "normal" for the species. It is axiomatic that normalcy and adjustment to the particular ecological site are inseparable as a result of the operation of evolutionary adaptation. Individuals that vary too much from this normalcy are eliminated from the population. As an example of a well-known category of nutrient ratio relationships, the following principle is cited. Many species of plants require a rather definite carbohydrate-nitrogen balance to initiate flower bud differentiation. In temperate zones excesses of nitrogen in some common cultivated plants merely delays flowering but does not prevent it. Delay in flowering may not be critical in the reproduction of a plant in a temperate zone, and still less so in a tropical zone; in northern regions this factor is often critical.

Therefore, those species or biotypes that do not maintain a favorable carbohydrate-nitrogen ratio by internal control mechanisms or by their occurrence on a substrate of proper nitrogen supply consonant with environmental conditions controlling carbohydrate accumulation will disappear from the population. It is probable that similar relationships exist between other essential elements or compounds in the metabolism of a species.

This principle in operation tends to make a species homozygous in regard to capability of essential element absorption, especially if it is living in an environment that allows but little variation in morphology and physiology if the plant is to survive. If this is true the amounts of the major elements absorbed by a species is not an accurate indication of its degree of intimacy with the substrate and would not be expected to vary greatly with different substrate contents of the elements. Increased absorption of the essential elements on sites where they are in great supply results in increased growth (within certain limits), therefore the percentage amounts of these elements in the plant tissue tend to remain rather constant. Bard's summaries of her findings (1949, p. 388-389) substantiate the above statements, as follows: "The amount of calcium contained within the leaves and annual stems of the majority of the species appeared to be more dependent upon the inherent capacity of each species to absorb calcium from the soil than on the calcium level of the soil itself. . . The phosphorus content of those species common to all three soil types was found to be highest on the soil type containing the greatest supply of phosphorus but not exhibiting the lowest pH. . . No clear trends were apparent in the potassium contents of most of the species . . . No evident correlation between the total amount of nitrate and ammonia nitrogen in the soil and the nitrogen content within the plant was observed."

The relationships of plants to the non-essential elements are believed by the writer to be quite different. Being non-essential, their amounts and ratios are suggested to be capable of wide variation. The principal limiting factor of this variation is the critical upper toxicity limit, if the element has toxic properties. Their occurrence in large amounts in the substrate does not result in increased growth, therefore plant tissue may show high percentage contents of these elements, which may vary in proportion to their abundance in the substrate. We may consider as an example the wide variation in silicon content, a non-toxic, non-essential (in the metabolic sense) element in plant tissues. The amounts in plant tissue may vary enormously between species, also between individuals of a species. The value of silicon to the plant appears to be largely in the mechanical properties that it contributes.

With those elements having toxic properties the evolutionary process of natural selection favors the individual plants having a wide amplitude in tolerance of these elements, but would not eliminate at once those with a narrow range of tolerance--the latter could still exist as well as the former on sites where these elements were available in non-toxic amounts and would not be eliminated by competition. The operation of these factors eventually becomes expressed as general heterozygosity of a species in respect to absorption of these elements.

Reaction to the minor or "trace" elements is suggested to follow the same principles as outlined above for the non-essential ones, once the specific minimal needs of a plant are satisfied. Some are toxic when in excess (as cited earlier for boron), others seem capable of attaining high levels in plant tissues with no harmful effects on the plant. Analyses of Alaskan soils in the writer's geochemical studies did not indicate that any of the minor elements occurred in such small amounts that plant growth was inhibited. Kellogg and Nygard (1951) suggest, however, that there may be a molybdenum deficiency in the soils of certain areas of Alaska.

In regions having great diversity in element content of the substrate (e.g., in "metallogenic provinces"), the evolutionary trend of the species is also believed by the writer to favor the development of biotypes having high tolerance to certain non-essential or minor elements--this tendency toward high tolerance would be no disadvantage in areas of low supply of these elements, while being of great advantage in areas of anomalous concentrations. The population dynamics would be expected to eventually result in general high tolerance of species to these elements that are encountered under natural conditions in the area of the population. The extent of this development probably depends on inherent amplitude limits that may vary between species. That this actually happens has been proven by Prát (1934) in relation to copper resistance of a flowering plant, Melandrium silvestre. He found that in regions of high copper substrate concentration a copper-resistant biotype had developed. By cultural and transplant experiments he demonstrated the inherited nature of this resistance, and that biotypes of this species from regions of low copper substrate content could not tolerate the substrates on which the adapted biotype throve. Although not reported by Prát, it is probable that the resistant biotype would have thrived as well as the non-resistant biotype if both were growing on a soil of average copper content.

Surface occurrence of mineralization (that is, concentrations of elements designated as "minerals" by geologists) closely corresponds with the occurrence of areas free of glacial deposits because of an obvious reason--glacial deposits ordinarily are not "mineralized" in this sense, and more or less completely isolate the plants from the possible effects of bedrock mineralization. Much of Alaska escaped extensive Pleistocene glaciation, and these parts have been considered refugia of arctic and boreal species during this period. At this time the species were exposed to substrate amounts of mineralization varying from "background" to rich ore veins, and some evolutionary adaptation to this variety of substrates undoubtedly occurred. It is suggested here that this episode in the history of these species, and the variety of substrates subsequently occupied by these species, is expressed as the presently-held characteristic of having a wide tolerance to non-essential element content of the substrate.

Although these hypotheses cannot be proven conclusively by the data assembled during this study, sampling was sufficiently extensive in respect to species and substrates to establish many relevant facts. The capabilities of species to absorb various non-essential or minor elements and the effect of soil content of elements on absorption by these species are presented in the sections which follow. The complete body of biogeochemical data acquired in this study is too voluminous to present in this paper, therefore selections and summaries of data are made which illustrate the concepts presently under consideration.

B. Patterns of Absorption of Metals by Plants, According to Species and Metallic Elements.

1. Presentation and analysis of data. The basic data from which absorption patterns may be determined are presented in Tables V, VI, and VII. These tables are summaries of similar separate tables compiled for each district of study in Alaska, and incorporate all data that was acquired regarding these species and their absorption of copper, lead, and zinc. There is great variation in the number of samples analyzed per species, principally as a result of the greater or lesser frequency of occurrence of the species on sites considered to have significantly low or high element content in the soil. The species of low sampling frequency are included in these tables, although but few and limited deductions can be made from their analyses. For the purposes of this report, those species represented by fifty or more samples are segregated and listed in Table VIII with summaries of their metal content and the ratios of high to low amounts of the metals.

Table V. Copper Content of Selected Alaskan Plant Species

(values in parts per million, based on ash weight)

Plant species sampled	Plant species summaries					
	number of samples	high	low	mean	median	ratios, high to low
Alnus crispa	166	800	40	260	250	20
A. crispa ssp. sinuata	25	1,000	250	580	600	4
Andromeda polifolia	8	600	150	350	300	4
Arctostaphylos uva-ursi	13	600	60	140	80	10
Betula glandulosa	3	400	250	300	250	1.6
B. nana ssp. exilis	211	450	80	270	250	5.6
B. resinifera	116	450	30	290	300	15
Cassiope mertensiana	14	1,200	150	400	300	8
C. tetragona	22	250	40	140	150	6
Chamaecyparis nootkatensis	5	400	100	200	100	4
Cladothamnus pyroliflorus	69	3,000	300	590	600	10
Empetrum nigrum	63	800	100	330	300	8
Fauria crista-galli	73	400	40	100	80	10
Gaultheria shallon	27	200	60	100	80	3.3
Juniperus communis	30	600	20	70	60	30
Ledum palustre ssp. decumbens	201	600	80	240	220	7.5
L. p. ssp. groenlandicum	23	800	150	230	220	5.3
Menziesia ferruginea leaves	61	400	60	140	120	6.7
Menziesia ferruginea stems	76	3,000	150	630	680	20
Phyllodoce glanduliflora	11	400	80	220	250	5

Table V. Copper Content of Selected Alaskan Plant Species (continued)

Plant species sampled	Plant species summaries					
	number of samples	high	low	mean	median	ratios, high to low
Picea glauca	49	450	20	70	40	22.5
P. mariana	73	450	20	110	80	22.5
P. sitchensis	59	800	40	160	150	20
Populus tremuloides	33	450	60	200	220	7.5
Salix commutata	7	1,000	220	400	300	4.6
S. scouleriana	2	80	40	- - -	- - -	2
S. pulchra	32	450	120	290	260	3.8
Sorbus sitchensis	11	600	150	280	250	4
Spiraea beauvardiana	14	300	120	210	220	2.5
Tsuga heterophylla	39	300	60	110	80	5
T. mertensiana	66	800	40	140	100	20
Vaccinium ovalifolium	45	400	100	210	200	4
V. parvifolium	10	300	120	200	200	2.5
V. uliginosum	294	1,200	30	340	300	40
V. vitis-idaea ssp. minus	57	300	40	150	150	7.5
Veratrum eschscholtzii	44	1,000	10	160	100	100

Table VI. Lead Content of Selected Alaskan Plant Species

(values in parts per million, based on ash weight)

Plant species sampled	Plant species summaries					
	number of samples	high	low	mean	median	ratios, high to low
Alnus crispa	166	1,500	20	67	25	75
A. crispa ssp. sinuata	25	3,000	50	220	100	60
Andromeda polifolia	8	50	20	35	35	2.5
Arctostaphylos üva-ursi	13	25	25	25	25	1
Betula glandulosa	3	600	25	233	75	24
B. nana ssp. exilis	211	1,200	25	50	25	48
B. resinifera	116	75	25	30	25	3
Cassiope mertensiana	14	200	20	70	50	10
C. tetragona	22	200	25	72	50	8
Chamaecyparis nootkatensis	5	50	20	30	20	2.5
Cladothamnus pyroliflorus	69	400	20	106	100	20
Empetrum nigrum	63	1,000	20	59	25	50
Fauria crista-galli	73	500	20	59	25	25
Gaultheria shallon	27	1,000	20	80	50	50
Juniperus communis	30	50	25	26	25	2
Ledum palustre ssp. decumbens	201	1,000	25	45	25	40
L. p. ssp. groenlandicum	23	50	25	28	25	2
Menziesia ferruginea leaves	61	200	20	49	25	10
Menziesia ferruginea stems	76	500	20	144	150	25
Phyllodoce glanduliflora	11	75	25	45	25	3

Table VI. Lead Content of Selected Alaskan Plant Species (continued)

Plant species sampled	Plant species summaries					
	number of samples	high	low	mean	median	ratios, high to low
Picea glauca	49	75	25	27	25	3
P. mariana	73	100	25	27	25	4
P. sitchensis	59	500	20	59	25	25
Populus tremuloides	33	50	25	27	25	2
Salix commutata	7	50	25	29	25	2
S. Scouleriana	2	25	25	- - -	- - -	1
S. pulchra	32	150	25	29	25	6
Sorbus sitchensis	11	150	25	57	25	6
Spiraea beauvardiana	14	25	25	25	25	1
Tsuga heterophylla	39	300	25	144	150	12
T. mertensiana	66	300	20	51	25	15
Vaccinium ovalifolium	45	200	20	49	25	10
V. parvifolium	10	80	20	50	50	4
V. uliginosum	294	250	20	41	25	12.5
V. vitis-idaea ssp. minus	57	500	25	48	25	20
Veratrum eschscholtzii	44	250	20	54	25	12.5

Table VII. Zinc Content of Selected Alaskan Plant Species

(values in parts per million, based on ash weight)

Plant species sampled	Plant species summaries					
	number of samples	high	low	mean	median	ratios, high to low
Alnus crispa	166	22,000	300	3,500	3,000	73
A. crispa ssp. sinuata	25	4,000	1,000	3,100	3,000	4
Andromeda polifolia	8	2,000	1,000	1,300	1,000	2
Arctostaphylos uva-ursi	13	4,000	2,000	3,000	3,000	2
Betula glandulosa	3	30,000	10,000	18,300	15,000	3
B. nana ssp. exilis	211	30,000	700	10,300	10,000	43
B. resinifera	116	32,000	1,000	12,500	12,000	32
Cassiope mertensiana	14	2,000	600	900	800	3.3
C. tetragona	22	4,000	1,000	1,400	1,000	4
Chamaecyparis nootkatensis	5	300	200	200	200	1.5
Cladothamnus pyroliflorus	69	3,500	800	1,500	1,500	4.4
Empetrum nigrum	63	3,000	200	1,000	1,000	15
Fauria crista-galli	73	4,000	400	1,100	1,000	10
Gaultheria shallon	27	3,500	500	1,100	1,000	7
Juniperus communis	30	2,500	200	400	400	12.5
Ledum palustre ssp. decumbens	201	6,000	600	1,700	1,500	10
L. p. ssp. groenlandicum	23	2,000	600	1,200	1,000	3.3
Menziesia ferruginea leaves	61	4,000	500	1,500	1,100	8
Menziesia ferruginea stems	76	7,000	800	2,600	2,000	8.7
Phyllodoce glanduliflora	11	1,000	600	800	800	1.7

Table VII. Zinc Content of Selected Alaskan Plant Species (continued)

Plant species sampled	Plant species summaries					
	number of samples	high	low	mean	median	ratios, high to low
Picea glauca	49	4,000	500	1,600	1,500	8
P. mariana	73	3,500	500	1,900	2,000	7
P. sitchensis	59	4,000	800	1,300	1,000	5
Populus tremuloides	33	4,000	1,000	2,600	3,500	4
Salix commutata	7	7,000	2,000	3,900	4,000	3.5
S. scouleriana	2	1,000	1,000	- - -	- - -	1
S. pulchra	32	12,000	2,000	6,000	6,000	6
Sorbus sitchensis	11	4,000	1,000	2,600	3,000	4
Spiraea beauvardiana	14	12,000	5,000	7,600	7,000	2.4
Tsuga heterophylla	39	3,500	400	1,100	1,000	9
T. mertensiana	66	1,500	400	800	800	3.7
Vaccinium ovalifolium	45	4,000	500	1,500	1,000	8
V. parvifolium	10	3,000	500	1,600	1,500	6
V. uliginosum	294	20,000	800	3,100	3,000	25
V. vitis-idaea ssp. minus	57	4,000	500	1,400	1,000	8
Veratrum eschscholtzii	44	3,000	300	720	500	10

It is believed by the writer that the reliability of deductions based on a lesser number of samples is of too low an order to be significant.

Trends in metal absorption by species are presented as expressed by contrasts or similarities of variability between the species. This variability is given for each species as the ratio of the highest amount to the lowest amount of each metal found in the species throughout its total distribution in the areas of study. The ratios of high to low amounts are indications of the ecological amplitudes of species with respect to metal absorption, and may be used for comparing the amplitudes of species. These ratios may also be used for a comparison of the ranges in ratios of the three metals in evaluating ecological amplitudes of all species combined in respect to the separate metals. These ratios are presented for each species and three metals in Table VIII.

On examination of this table it is apparent that there is a great variation in ratios according to the different species and the different metals. In copper, the species with the highest ratio is about four times that of the lowest; in lead, these ratios are 25:1; in zinc, 20:1. We may then conclude that of the three metals, the ecological amplitude of these plant species is greatest in absorption of lead, slightly lower in absorption of zinc, and much lower in absorption of copper. The extent that these variations in absorption reflect the relative toxicity of these elements may be suggested by this comparison, but only autecological experiments on each species would give substantial proof. We may extend the interpretation of

Table VIII. Median metal content, and high to low ratios of metal in plant species represented by fifty or more samples

Plant species	Copper		Lead		Zinc	
	ratios	ppm	ratios	ppm	ratios	ppm
Alnus crispa	20	250	75	25	73	3,000
Betula nana exilis	5.6	250	48	25	43	10,000
Betula resinifera	15	300	3	25	32	12,000
Cladothamnus pyroliflorus	10	600	20	100	4.4	1,500
Empetrum nigrum	8	300	50	25	15	1,000
Fauria crista-galli	10	80	25	25	10	1,000
Ledum palustre decumbens	7.5	220	40	25	10	1,500
Menziesia ferruginea leaves	6.7	120	10	25	8	1,100
M. ferruginea stems	20	680	25	150	8.7	2,000
Picea glauca	22.5	70	3	25	8	1,500
P. mariana	22.5	110	4	25	7	2,000
P. sitchensis	20	160	25	25	5	1,000
Tsuga mertensiana	20	100	15	25	3.7	800
Vaccinium uliginosum	7.5	300	12.5	25	25	3,000
V. vitis-idaea	7.5	100	12.5	25	8	1,000

these data to suggest that excessive amounts of the three elements in the soil would tend to have the inverse order of importance in determining the characteristics of vegetation on a site if the three metals occurred in greatly anomalous amounts.

However, it should be noted that these ratios have nothing to do with relative amounts of each element absorbed. The columns in Table VIII giving median amounts of each element for each species show that there is a greatly different order of magnitude in absorption of the three elements. The highest copper content, in parts per million, is 680; the highest lead content is 150; and the highest zinc content is 12,000. These figures do not indicate upper toxicity limits of these elements--no samples were taken from dead plants--but may be taken as levels of metal content at which no morphological or physiological expressions of toxicity were evident.

The relative variation in amounts (parts per million, based on ash weight) absorbed of the three metals shows an interesting pattern. The absorption of lead shows the least variability, the high to low ratio being 6:1, and the amounts are identical in all but two plant species. Copper is next lowest in variability, with a ratio of 9:1, and zinc is the highest in variability, having a ratio of 12:1.

With these limited data generalizations are not highly reliable regarding plant family tendencies in metal absorption patterns, but the observation may be made that members of the family Pinaceae show uniformly high amplitudes in copper absorption, uniformly low amplitudes in zinc absorption, and an erratic pattern of lead absorption. The species of the family Betulaceae show high amplitudes in zinc absorption, and an erratic pattern in absorption of the other elements. The other families represented appear to show no consistent patterns.

An isolated bit of data is deliberately introduced into Table VIII to illustrate the importance of uniformity in sampling procedures if results are to be compared. Menziesia ferruginea leaves were taken from the stems and analyzed separately. The data show that the leaves contain about one-third as much copper, one-half as much lead, and the same amount of zinc as do the stems. These analyses give some suggestion of the complexities of correlation that are inherent in biogeochemical studies.

It is also of interest to note in Table VIII that the ecological amplitude (again expressed as the ratio of high to low element content) of a species is not similar for all three elements. Thus, Picea glauca has the greatest amplitude in copper absorption, but the lowest in lead, and is quite low in zinc absorption. On the other hand, Betula nana subsp. exilis has next to the greatest amplitude in both lead and zinc absorption, but the lowest in copper. Still another condition of amplitudes exists; Alnus crispa has by far the greatest amplitude in lead and zinc absorption, and next to the greatest in copper absorption--thus it may be characterized as a species of wide adaptation to variations in substrate metal concentration. The importance of this feature in explaining the extensive distribution and ubiquity of this species within its range should not be over-emphasized, for sites of anomalous metal substrate content presumably are not common, yet it is a feature to be considered.

In order to arrive at generalizations concerning the absorption patterns of these northern plant species we may combine the ratios of all three elements, establish ratio classes, and record the number of ratios shown by Table VIII as occurring in each class. This is done in Table IX. In this table, the predominant number of ratio occurrences in Classes 1, 2, and 3 indicate that a generalization can now be made--the ecological amplitude in metal absorption of most of these species is not greater than 29:1; however, at the same time one may state that 62 percent of the ratios have a range greater than 10:1. This is interpreted to indicate that arctic and boreal plant species, if accurately represented by these samples, have in general a wide ecological amplitude in respect to amounts of these three metals that may be absorbed and still show no toxicity symptoms. The writer knows of no similar data available for temperate and tropical plant species that would enable a comparison to be made with these northern species.

2. Summary of data gained from examination of absorption patterns. Tables V, VI, and VII show that none of the species has a constant value for metal content of any of the three metals (i.e., there are no 1:1 ratios of high to low amounts) if the species was adequately sampled. Only those species represented by fifty or more samples are considered for further discussion, although the same tendencies are shown by many species that were sampled less extensively. Table IX shows that more than half (62 percent) of the ratios have a range greater than 10:1. It is concluded that these data demonstrate the general wide ecological amplitude of these species of plants in

Table IX. Species distribution by ratio classes, for all elements combined.

Ratio Class No.	Range in ratios within the class	Number of ratios occurring in a class
1.	1 - 9	17
2.	10 - 19	10
3.	20 - 29	11
4.	30 - 39	1
5.	40 - 49	3
6.	50 - 59	1
7.	60 - 69	0
8.	70 - 79	2

absorption of the minor or non-essential elements that were studied. Additional sampling could only increase rather than diminish the range of these ratios for individual species, therefore these data are held adequate for the above ecological amplitude interpretations.

The causes of these absorption patterns that are characteristic of a species are, however, not proven by these data. The patterns may result from (1) differences in substrate metal content, (2) genetically controlled capabilities of biotypes within a species, (3) physiological responses distinctive of the individual species that are more strongly influenced by other environmental factors, and (4) sampling or analytical error. Causes 2 and 3 above can be but rarely eliminated as possibilities by field studies such as these, but require genetic and physiological experimentation. The possibility of cause 4 being significant must be acknowledged, and the data accepted with the same reservations attending any interpretation based on sampling and laboratory procedures--it can only be stated that all reasonable care was used in securing accuracy (McCarthy, 1956). Cause 1 can be demonstrated as existing, and can, in many cases, be correlated with the metal content of the plant. Herein lies the usefulness of plant tissue analysis in locating anomalous concentrations of elements in the substrate.

C. Relationship of the Metal Content of Plant Tissue to that of the Substrate on which it Grew.

With each plant species sample that was used in obtaining the data shown in Tables V, VI, and VII, as well as in similar tables for other elements not presented in this study, one or more samples of the soil or other substrate on which the plant grew was also collected and analyzed for the same elements that were found in the corresponding plant sample. Ordinarily the soil horizons were sampled separately at each site, if the soil was zonal in nature; however, for purposes of general correlation of soils and plant tissues, the analyses of the lowermost horizon were used. This was ordinarily identifiable as the C horizon, and being the lowest zone of root penetration (except in rare cases), was held to be the source of the geochemical elements that could be put in circulation throughout plant tissues and the upper soil horizons.

It is beyond the scope of this report to give all the relationships that were found in this biogeochemical study, or even to give representative regional data. Instead, the published report of the writer (Shacklette, 1960) on soil and plant sampling at Mahoney Creek, Revillagigedo Island, Alaska will be referred to, and the results briefly discussed as representative of the soil-plant tissue relationships in element content that were found at many sample sites throughout Alaska. This paper is quoted as follows (p. 102-104):

"The Mahoney Creek deposit is a vein of sphalerite and galena in black slate. The vein and country rock are covered with talus, soil, and vegetation, but the vein is exposed at the surface in a number of exploration pits. A base line was established along and parallel to the vein, and five traverse lines were laid out to cross the base line at or near the exploration pits. Sample sites on the traverse were spaced 30 to 40 feet apart; soil and plant samples were collected at each site and analyzed for lead and zinc content. . . .

"For the purpose of making comparisons the samples were divided into three groups: (a) those collected on or near the base line, which approximated the vein suboutcrop, designated "vein" samples; (b) those collected at sites on either side of the vein samples, designated "halo" samples; and (c) those collected from sites more remote from the vein than the "halo" samples, designated "background" samples. Mean percentages of lead and zinc with their standard deviation and standard error were computed for each plant species in each of the three sample groups. . . . Table 48.2 presents a comparison of mean lead and zinc percentages in all plant species sampled and all soil samples in the Mahoney Creek area.

"Table 48.2.--Comparison of mean lead and zinc percentages in soils and plants sampled at Mahoney Creek, Revillagigedo Island, Alaska.

(D. R. Marx, analyst)

	Lead			Zinc		
	Background	Halo	Vein	Bkgrnd.	Halo	Vein
Mean percentage in ash of all plant species sampled - - -	.0090±.001	.011±.002	.016±.002	.14±.01	.21±.02	.27±.03
Mean percentage of all soil samples - - -	.002±.001	.011±.004	.130±.069	.003±.001	.008±.003	.087±.046

"It is apparent that a close correlation exists between the relative 'background,' 'halo,' and 'vein' values of corresponding plant and soil samples, and that both classes of samples accurately reflect the known location of the mineral vein."

Although the element content of plants and their supporting soils corresponded very closely in this Mahoney Creek study, there were many study sites where the correspondence was not so close, and at certain sites there were apparently non-correlable relationships. The interpretation of values obtained from such sites as the latter requires a consideration of other environmental factors that may influence the response of the plant to its substrate, and the use of interpretative techniques that are presented elsewhere by the writer to deal with these relationships ("Problems of interpreting element content of plants in relation to underlying deposits, " Proceedings, Symposium on "Detection of Underground Objects, Materials, and Properties," Fort Belvoir, Virginia, 19-20 March 1962, in press).

D. Patterns of Absorption of Metals in Plants According to Geographic Areas.

A comparison of absorption of metals by species as related to their geographical areas of occurrence is rendered difficult by the small number of species that occurs in all areas of the study. This is due primarily to the wide range of climatic factors found in Alaska because of its great north-south extent, its varied topography, and its long and varied coastline. Only four species of vascular plants suitable for chemical analysis in this biogeochemical survey were found in all areas of study--*Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, and *Andromeda polifolia*. Of these species, only *Vaccinium uliginosum* occurred with suitable regularity and in sufficient abundance to be sampled in all areas, therefore only limited area-to-area comparisons can be made of species capabilities for metal uptake in the various areas.

In determining statistical values (ratios, highs, lows, medians, and means) for the plants included in the biogeochemical study separate computations were made by locality and by regions. This is not shown in the data presented in Tables V, VI, and VII, and is too extensive to tabulate in this report. However, from this regional data the median values for Vaccinium uliginosum are extracted, and are presented in Table X. This table shows a striking difference in the values for each of the three metals in this species in Southeastern and South Coastal Alaska when they are compared to the almost uniform values for the other three regions of Alaska. Studies of substrate metal content in these regions do not lead to the conclusion that these values are due to a response to regional substrate variation of metal content. The differences are so great that they at once suggest we are dealing with a "different" plant in this region. Sampling of this species was sufficiently thorough to make these analyses statistically significant, for the median values in this table are based on 882 separate analyses of this species. The distinctiveness of the climate of this region, and the region's ecological isolation and relative geographic discontinuity from the other regions studied support the assumption that a genetically distinct variant of this species has become established here. It is therefore concluded that a regional comparison of metal content of the plant tissue has revealed that Vaccinium uliginosum is represented in Southeastern and South Coastal

"Table X.--Median values in metal absorption of Vaccinium uliginosum in four geographical regions of Alaska (amounts expressed in parts per million, based on ash weight).

Element	Southeastern & South Coastal Alaska	Southwestern Alaska	Alaska Range	Yukon-Tanana Uplands
Copper	500	300	300	300
Lead	65	25	37.5	25
Zinc	1,250	2,500	2,750	2,500

Alaska by a physiologically-distinct biotype. A sufficient series of herbarium specimens was not collected during this study to determine if this regional variant is also distinct morphologically--no differences were noted in field observations that suggested more than ecotype variation. There is no reason to assume that a physiological biotype must also be distinct morphologically; however, the same speciation processes leading to physiological distinctiveness could also be suspected of causing morphological changes to become established at the same time.

Because of the limited number of species common to the different regions of Alaska, regional patterns of metal accumulation by plants must be determined statistically by comparing mean values of all plant species analyses collectively. When this is done definite regional patterns become apparent that are believed to have significance in several fields of biological as well as mineralogical investigations. This comparison has been made by the writer (Shacklette, 1962), from which the following is quoted:

"Approximately 17,100 separate chemical analyses of plant parts were made by the U. S. Geological Survey, using colorimetric procedures. The copper, lead, and zinc content of the plant tissues was determined for each plant sample, and some samples were analyzed for nickel, iron, molybdenum, and other elements (Chapman and Shacklette, 1960). Average values were then determined according to the metal, the species of plant, and the geographical region. From these data Table I is derived.

"Table I. Averages of the mean values of metal content of all plant species sampled in 4 regions of Alaska (All values expressed as percentages of plant ash weight, in grams)

	Number of plant species	Copper	Lead	Zinc	Nickel
Southeastern and South Coastal Alaska .	19	.030	.0082	.14	.044
Southwestern Alaska	8	.028	.0028	.66	- - -
Alaska Range . .	14	.026	.0073	.40	- - -
Yukon-Tanana Upland	13	.016	.0030	.25	.022

"There was no indication that these average concentrations caused morphological or physiological aberrations in the vegetation. . . . However, the regional variation in metal content of vegetation may be a factor to consider in the study of animal ecology and geography."

The above table shows the vegetation of the Yukon-Tanana Upland to be lowest in copper, and quite low in lead and zinc. The Southeastern and South Coastal Alaska region is notably high in copper and lead, but the lowest in zinc in the vegetation, and nickel is shown to be twice as high here as in the former region. If there is a general correspondence in the amount of metals in plants and the amount in their underlying soils, as was stated to be true in the preceding discussion, and if plants are especially efficient in the sampling of soils on which they are growing, these data may have value in characterizing the general geochemical properties of these regions of Alaska.

E. Ecological Significance of Varying Absorption Capabilities of Plants.

The discussion which follows is limited to a consideration of the minor and "non-essential" elements because there was no indication in this study that varying abilities in absorption of the major essential elements was a feature of ecological significance, except possibly with calcicolous and nitrophilous species. Here the differences between species, if any, were in the physiological necessity for large amounts of these elements or for other conditions associated with calcium and nitrogen concentrations, rather than in differential abilities of plant species to absorb these elements.

The wide variation in absorption of the metallic elements has been demonstrated in preceding paragraphs, and various interpretations were made of this phenomenon. However, no positive evidence was found that these varying abilities, which had characteristic species patterns, influence the occurrence of a plant species at a particular site, or enter into the determination of plant community composition. The occurrence of certain species on sites of very high concentrations of toxic elements, to the exclusion of other species, was not demonstrated to be due to differences in absorption abilities, but was most probably because of toxicity resistance of an undetermined nature.

These geochemical studies have established the intimate relationships of plants and the chemical composition of their supporting substrates, in that the species by their tissue content of metals ordinarily reflect the metal content of the soils. A general "passive" absorption up to certain limits is suggested by the writer for all the non-metabolic elements and within this range the amount in the substrate appears to be the controlling factor. Beyond these limits, which may be different in different species, biotic processes may control further intake, which appears to be largely physiologically regulated within the species, but may also relate, in the highest levels attained, to the total substrate content. Unless levels of accumulation in the tissues reach toxic amounts (which was not observed to occur at other than mineral vein sites or ore mills), it is not clear how the differential absorption capabilities of species could affect their geographic or site distribution. Analysis of soils shows a wide variation in element content, often at contiguous sites; plant communities often also vary greatly on adjacent sites--but no evidence is at hand to establish causal relationships between the two events. Again we are forced to the same conclusions reached earlier in this report--other environmental factors, not the chemical nature of the substrate, are ordinarily the predominant determiners of species occurrence. The phytoecological value of data derived from biogeochemical studies is to conclusively demonstrate the wide ecological amplitude of the boreal and arctic plant species with respect to tolerance of the non-metabolic elements in their supporting substrate, and that this inherent amplitude augments other adaptive features which make the existence of these plants possible in this generally hostile environment.

CHAPTER VI.

SUMMARY

A. Methods, Scope, and Results of this Study.

This study was made of plant communities and the soils or other substrates that support them to determine and explain some of their unique relationships in high latitudes. This work is based on four summer field seasons (1948, 1957, 1958, and 1960) spent in arctic and boreal regions of Alaska and Canada. Particular emphasis was placed on vascular plants and bryophytes. The field studies were done in conjunction with geochemical and biogeochemical investigations made concurrently in which the amounts of certain elements in the plant tissues and in associated substrates were thought to be indicative of the degree of intimate relationship between plants and soils.

The several substrate factors were studied separately in their effects on plant growth and plant community development. A relatively small portion of the area studied had surface exposures of bedrock; the soil most commonly is derived from parent materials that have been transported and now exist as glacial, fluvial, and aeolian deposits. Soil stability, soil texture, and water relationships are physical properties influenced directly by this parent material. Representative plant communities are described that are strongly affected by each of these factors. The development of soil chemical properties under the influence of the far northern environment is considered relative to the major elements in plant nutrition. The plant species are found to be, in general, oligotropic in their response; however, there are certain compensating factors found in the environment that contribute to the adequacy of these elements for plant growth. Nitrogen is probably the most commonly deficient element that directly inhibits plant growth. Nitrophilous species are few, and are peculiarly adapted to obtain their nitrogen requirement. Warm-blooded animals are thought to be particularly important in the nitrogen economy of these regions; on the other hand, leguminous plants with their associated symbiotic nitrogen-fixing microorganisms are of lesser importance here than in temperate or tropical regions.

Particular attention was paid to the development of acidity or alkalinity in the substrate and the subsequent effects on the plant communities. The accumulation of acid humus, favored by the climate, tends to make all substrates acid; only in the presence of basic rocks or by soil processes that concentrate calcium in the solum, are they neutral or basic. Field studies of the writer and reports from the literature when carefully evalutated support the conclusion that only three to four percent of arctic and boreal species are definitely calciphilic. However, adapted biotypes may be present that show regional variation in alkaline requirements.

Bryophytes were studied in detail in their substrate requirements and tolerances, as well as their response to other environmental factors, because of the generally-held concepts of their environmental specificity. They were found, in general, to have a rather narrow range of ecological amplitude when compared to that of vascular plants; however, individual species were found to be remarkably resistant to extremes of water supply, temperature, and concentrations of certain metallic elements. Substrate factors were statistically shown to be of less importance to bryophytes as a whole than were the other factors, taken collectively, of the environment.

Having studied individual factors of the substrate in their effects on plant growth, these factors taken together as represented by specific soil types (Great Soil Groups) were evaluated in their relationship to the plant communities developed thereon. The occurrence of a soil type showed no constancy with the occurrence of a particular type of parent material. Soil type development was most often related to moisture content (as determined by slope, exposure, tempera ture, and amount of humus) and the plant community thereon that was adapted to the water supply. There is no uniform degree of homogeneity in properties of different soils found in the several Great Soil Groups, consequently there was no uniformity in degree of association of a specific plant community and a single Great Soil Group. Plant communities on Podzol, Subarctic Brown Forest, and Tundra soils have more similarity within their associated soil group than do plant communities on Bog, Half-Bog, Regosol and Lithosol soils. It is thought that of the two influences on soil type development, parent materials and plants, the latter are ordinarily predominant; however, both factors are overshadowed by the effects of climate (particularly temperature and degree of wetness) in that it basically controls plant growth.

Biogeochemical studies made concurrently with this investigation in which the relationship of certain non-essential elements found in the soils and in the plants supported thereon support the conclusion that the plants of these regions have wide ecological amplitude in their adaptation to substrate element content. The amounts of these elements in plant tissue, as determined by chemical analysis, is related to (a) the inherent ability of the species to accumulate these elements, and (b) the amount of the elements in the soil solution. There is great variation between species and between individual plants of a species in their accumulation ability; this ability in the latter instance may be genetically controlled and expressed as physiological biotypes. The general wide ecological amplitude of arctic and boreal species in element absorption and element toxicity tolerance is considered to be an evolutionary adaptation to these regions.

In the final analysis, low temperature is the predominating environmental factor influencing plant growth in these regions. It operates directly on plants by limiting their growing season, reducing the rate of physiological processes, and inhibiting or terminating growth by freezing. Indirectly the effects are even more diverse. The rate of rock weathering is reduced, soil-forming processes are attenuated, the supply of nutrient elements is severely limited, water relationships tend toward extremes, and the substrate of the vegetation is often rendered unstable. Yet in an environment so unfavorable to most plant species areas of land surface below an altitudinal limit of 3,500 to 4,000 feet generally are vegetated with an almost continuous plant cover.

There are in these species morphological and physiological adaptations to environments of this nature that are of fundamental importance in fitting these plants to survive and prosper here. If the species is to exist, for every rigor of the environment imposed on it by the physical nature of these regions there must be an adaptive biotic adjustment of the species, or a compensating mechanism in the ecosystem. This is to say that there must be certain compensating factors for each inhibitor. The compensation may be expressed as a complete cancellation of the effects of one factor by those of another, as a reduction of these effects, or perhaps more frequently as an interaction of factors producing a synergistic result. The object of this presentation has been the identification of these processes within the concept of a holocenotic environment.

Inhibitors and their compensating factors of plant growth and vegetational development of northern regions as contrasted to those in more temperate regions are presented in outline form as follows:

1. Inhibitor -- Low supply of the major essential elements.

    a. General compensations -

        (1) Limited vegetational productivity due to absolute environmental control (light, temperature).

        (2) Reduced loss of soluble nutrients, due to low temperature.

        (3) Species adaptation to low supply.

        (4) Formation of organic colloids and clays having great surface area.

    b. Specific compensations -

        (1) Low phosphorus supply is compensated by biologically-developed soil acidity that promotes the formation of the most readily available form of phosphorus (H_2PO_4).

(2) Low potassium supply is compensated by

(a) the direct action of vegetation in increasing solubility of potassium compounds,

(b) many species of the region are those low in the evolutionary scale, and may have a greater extractive power in removing potassium from the rocks than do higher plants.

(3) Low nitrogen supply is compensated by

(a) release of substrate nitrogen store by burning,

(b) displacement of soils by frost and animal action, thus increasing aeration and promoting growth of soil microorganisms.

(c) the contribution to the total available nitrogen made by animals, in that their digestive tracts provide a year-round warm environment for bacterial decomposition of organic compounds, releasing available nitrogen in dung and urine,

(d) the production of numerous wind-borne diaspores by obligate nitrophilous species.

(e) Reduced azofication is compensated by

(i) reduced volatilization in the cold climate,

(ii) local calcium concentrations,

(iii) aeration by frost action.

(f) Reduced nitrogen fixation. (No adequate compensation; legumes do not contribute much nitrogen to other plants, or to following generations; nitrogen accumulates and remains in undecomposed tissues.)

(g) Reduced and incomplete decay and ammonification is compensated by

(i) use of amino-compounds (especially ammonium carbonate) by higher plants,

(ii) production of ammonium carbonate from animal excreta,

(iii) utilization of NH_4 ions by plants of bogs and tundras.

(h) Reduced nitrification has been said to be compensated by increased amount of light during the growing season.

2. Inhibitor -- Reduced total insolation.

a. General compensations -

(1) Long days during the growing season.

(2) Increased prevalence of one-layer vegetation northward, thus the species that are permitted to grow by other environmental factors do not find the light supply to be limiting.

(3) Sciophytes, as defined for more temperate zones, are regionally expressed as heliophytes.

3. Inhibitor -- Low annual precipitation.

a. General compensations -

(1) Low rate of evapotranspiration, as a consequence of lower temperature.

(2) Smaller percolation loss, because of widespread permafrost and impervious clays.

(3) Reduction of runoff by the longer season of frozen ground.

(4) Water is released from the frozen state only during the growing season, when it can be used effectively by plants.

(5) The low precipitation provides for variety of habitats, including xeric, mesic, as well as hydric sites; if high precipitation values obtained, all sites would be hydric owing to reduced percolation, evaporation, and evapotranspiration.

4. Inhibitor -- Low rate of chemical weathering of rocks.

a. General compensations --

(1) Adaptation of many species to lithosols and regosols; these plants may be benefitted by the increased ambient temperature of their microclimates, thus may be more active metabolically.

(2) Increased physical weathering, due to temperature extremes, providing for more effective operation of such chemical weathering as does take place.

(3) Congeliturbation, which results in repeated exposures of soil parent material to maximum physical weathering.

(4) The abundance of organic colloids compensates for the reduction in inorganic colloids.

5. Inhibitor -- Low temperature (direct effect).

a. General compensations -

(1) Physiological and morphological adaptations by species as a result of evolutionary processes.

(2) Phenological adaptations.

(3) Snow cover.

6. Inhibitor -- Widespread occurrence of acid substrates.

a. General compensations -

(1) Indifference of most species to substrate pH.

(2) The higher acidity reduces decay of organic matter, resulting often in deep organic soils even on relatively unweathered parent materials.

7. Inhibitor -- Unstable soil surfaces, with special reference to frost action.

a. General compensations -

(1) Increased aeration of the soil, which increases development of microflora.

(2) Exposed mineral soil is more favorable to the establishment of some seedlings, and surface algae.

(3) Coarser grained mineral soil warms earlier in the growing season because of greater thermal conductivity.

(4) Increased prevalence of perennial species northward, especially of those capable of extensive vegetative propagation, thus demanding less frequent invasion of new plants to maintain a community.

8. Inhibitor -- Occurrence of substrate elements in toxic quantities.

a. General compensations -

(1) Deep surficial deposits, or ground ice, often isolate plants from bedrock sources.

(2) Ectohydric plants, very prevalent in northern regions, have but little dependence on soil solutions.

(3) Limited absorption of these elements by certain species.

(4) Genetically-controlled toxicity thresholds higher than maximum toxic element intake, in certain species.

(5) Synergistic relationships of certain toxic and non-toxic elements in the substrate.[1]

1. Work in progress by the writer on serpentine areas near Eagle, Alaska indicates a relationship of calcium concentrations and toxicity of certain metallic elements.

CHAPTER VII.

CONCLUSIONS

A. Soil Factors as Determiners of Species Occurrence and Community Species Composition.

The great variety of plants, each with its own genetic pattern of responses and modifications that are continuously capable of evolutionary adaptations, and the infinitely complex interplay of the environmental factors mentioned in the preceding discussion interact to form an almost endless variety of plant species combinations on the multitude of available sites. The result is a complex mosiac of plant communities, often in close association. These communities may be taxonomically or systematically grouped at the discretion of the student to reflect a degree of similarity or unity in genesis, physiognomy, floristics, proportionate composition, or in habitat similarities. They are not without pattern, nor are they largely random assemblages, but are the products of definite processes. These processes are the interactions of environmental properties with biotic capabilities.

Soil properties are but one set of factors constituting the complex, and as such, would not be expected to dominate the total number of relationships. At the same time, we cannot divorce the plant species or the plant community from the soil that supports it. This specific relationship has been stressed throughout this report. Certain types of soils do regularly support a rather discrete plant community--but the exact causal nature of the association is often difficult to determine. It may be a cause external to both the soil and the plant community, but to which both respond in unison. It may be that, chemically and physically, both are so intimately related that primacy is indeterminable. Or it may be that one is the primary provider of a factor necessary to the development of the other; plants as a source of organic matter to the soil, and the latter supplying the plants with a source of essential elements.

However, if we consider soils from the taxonomic standpoint as Great Soil Groups presumed to be established on a genetic basis, the relationship of recognizable plant communities and these soil categories becomes vague, erratic, and confusing. It has been suggested that this is due in part to the difference in allowable ranges of variation that are inherent in the two sets of categories. The conclusion must be that these soil units, as now defined, have no consistent relationships to specific plant communities.

We may summarize, for these arctic and boreal regions, the characteristics of the fundament in its various manifestations as finally relating to the vegetation that it supports as follows:

1. There is often no correspondence of bedrock type and surface parent material.
2. There is ordinarily little relationship between the nature of surficial parent material and the zonal Soil Group that develops.
3. There is no consistent relationship between the Soil Group and the specific plant community that it supports. One problem here is that of definitions and terminology.
4. There is usually little effect of differential amounts of the essential elements and the pH of the soil on the plant community. The species are in general oligotropic.

5. The content of "geochemical" elements in the soil ordinarily has little or no effect on species occurrence and plant community composition. The plants of these regions are characterized by their wide ecological amplitude. However, bryophytes are in general more closely restricted to a specific substrate than are vascular plants.
6. Plant-soil actions and reactions are closely interdependent. Plants commonly are more effective in determining final soil type that is formed than are soils (excluding effect of water content) in determining the final vegetation type, but both are controlled by the effects of the low temperature. They are, in the final analysis, expressions of a holocenotic environment whose pattern is set by the regional climate.
7. The data assembled in this report support the generalization that in arctic and boreal regions the environmental factors of temperature, exposure, frost action, and water relationships are of more importance in determining plant species occurrence and community composition than are the chemical properties of the soil or other substrate.

APPENDIX

REFERENCE LIST OF TAXA

(Underscored page numbers indicate that the name appears in a Figure caption)

LIST OF REFERENCES

Ahlgren, I. F., and Ahlgren, C. E., 1960, Ecological effects of forest fires: The Bot. Rev., v. 26, p. 483-533.

Allen, A. E., 1929, Influence of Cladonia ground cover on the establishment of seedlings: Ecology, v. 10, no. 3, p. 254-255.

Allison, F. E., 1931, Forms of nitrogen assimilated by plants: Quart. Rev. Biology, v. 6, p. 313-321.

Anderson, J. P., 1959, Flora of Alaska and adjacent parts of Canada: Ames, Iowa State Univ. Press, 543 p.

Baldanzi, Giampiero, 1960, Burning and soil fertility, in Trans. 7th Internat. Cong. Soil Sci., Madison, Wisc., U.S.A., v. 2: Gronigen, Dykstra's Drukkerij, p. 523-530.

Bard, G. E., 1949, Mineral nutrient content of the annual parts of herbaceous species growing on three New York soil types varying in limestone content: Ecology, v. 30, no. 3, p. 384-389.

Benninghoff, W. S., 1952, Interaction of vegetation and soil frost phenomena: Arctic, v. 5, no. 1, p. 34-44.

_________, 1953, Use of aerial photographs for terrain interpretation based on field mapping: Photogrammetric Engineering, June, 1953, p. 487-490.

Bliss, L. C., 1956, A comparison of plant development in microenvironments of arctic and alpine tundra: Ecol. Mon., v. 26, no. 4, p. 303-337.

Bloom, Harold, 1955, A field method for the determination of ammonium citrate-soluble heavy metals in soils and alluvium: Econ. Geol., v. 50, no. 5, p. 533-541.

Brown, Jerry, 1962, A pedological investigation of the soils from the Northeastern Brooks Range, Alaska: Ph. D. Thesis, Dept. of Soils, Rutgers University.

_________, and Tedrow, J. C. F., 1958, Characteristics of two tundra soils from the Arctic Slope of Alaska, in Science in Alaska, Proc. Ninth Alaskan Sco. Conf., College: p. 2.

Braun-Blanquet, J., 1932, Plant sociology: New York, McGraw-Hill, 439 p.

Burd, J. S., 1948, Chemistry of the phosphate ion in soil systems: Soil Sci., v. 63, p. 227-247.

Byers, H. G., Kellogg, C. E., Anderson, M. S., and Thorp, J., 1938, Formation of soil, in Soils and Man, Yearbook of Agriculture, 1938: U. S. Dept. Agr., p. 948-978.

Canney, F. C., and Hawkins, D. B., 1958, Cold acid extraction of copper from soils and sediments - a proposed field method: Econ. Geol., v. 53, p. 877-886.

________, Myers, A. T., and Ward, F. N., 1957, A truck-mounted spectrographic laboratory for use in geochemical exploration: Econ. Geol., v. 52, no. 3, p. 289-306.

Cannon, H. L., 1952, The effect of uranium-vanadium deposits on the vegetation of the Colorado Plateau: Am. Jour. Sci., v. 250, p. 735-770.

________, 1957, Description of indicator plants and methods of botanical prospecting for uranium deposits on the Colorado Plateau: U. S. Geol. Survey Bull. 1030-M, p. 399-516.

Carlisle, Donald, and Cleveland, G. B., 1958, Plants as a guide to mineralization: Special Report No. 50, State of California Dept. of Natural Resources, Division of Mines, San Francisco, 31 p.

Chapman, R. M., and Shacklette, H. T., 1960, Geochemical exploration in Alaska, in Short Papers in the Geological Sciences: U. S. Geol. Survey Prof. Paper 400-B, p. B104-B107.

Cuyler, R. H., 1931, Vegetation as an indicator of geologic formations: Amer. Assoc. Petroleum Geol., v. 15, no. 1, p. 67-78.

Dachnowski-Stokes, A. P., 1941a, Peat deposits in United States of America: their characteristic profiles and classification: Handbuch der Moorkunde, v. 7, Berlin, Borntraeger, 140 p.

________, 1941b, Peat resources in Alaska: U. S. Dept. Agr. Tech. Bull. 769, 84 p.

Douglas, L. A., and Tedrow, J. C. F., 1960, Tundra soils of arctic Alaska, in Trans. 7th Intern. Cong. of Soil Sci., Madison, Wisc., U. S. A., v. 4: p. 291-304.

Drury, W. H. Jr., 1956, Bog flats and physiographic processes in the upper Kuskokwim River region, Alaska: Contr. Gray Herbarium Harvard Univ. no. CLXXVIII, 130 p.

Dutro, J. T., and Payne, T. G., 1957, Geologic map of Alaska: U. S. Geol. Survey, 1:2,500,000.

Duvigneaud, Paul, 1958, La végétation du Katanga et de ses sols metalliferes: Bull. Soc. Royale de Bot. de Belgique, v. 90, p. 127-286.

Fernald, M. L., 1918, American variations of Epilobium section Chamaenerion: Rhodora, v. 44, p. 238-246.

_________, 1942, Misinterpretation of Atlantic Coastal Plain species: Rhodora, v. 44, p. 238-246.

Fraser, D. C., 1961, Syngenetic copper deposit of recent age: Econ. Geol., v. 56, p. 951-962.

Gjaerevoll, Olav, 1958, Botanical investigations in Central Alaska, especially in the White Mountains, Part I, Pteridophytes and Monocotyledones: Det Kgl. Norske Vidensk. Selsk. Skr. no. 5, Trondheim, 74 p.

Gleason, H. A., 1917, The structure and development of the plant association: Bull. Torrey Bot. Club, v. 43, p. 463-481.

Godman, R. M., 1953, Moss retards regeneration in Southeast Alaska: Tech. Notes no. 18, Alaska Forest Research Center, U. S. Dept. Agr. Forest Service, Juneau, 1 p.

Goldman, C. R., 1961, The contribution of alder trees (Alnus tenuifolia) to the primary productivity of Castle Lake, California: Ecology, v. 42, p. 282-288.

Greenland, D. J., and Nye, P. H., 1960, Does straw induce nitrogen deficiency in tropical soils?, in Trans. 7th Intern. Cong. Soil Sci., Madison, Wisc., U.S.A., v. 2: Gronigen, Dykstra's Drukkerij, p. 523-530.

Grout, A. J., 1938, Moss flora of North America north of Mexico: v. 1, pt. 3, Newfane, Vermont, Grout, p. 137-192.

Hawkes, H. E., 1957, Principles of geochemical prospecting: U. S. Geol. Survey Bull. 1000-F, p. 225-355.

Hopkins, D. M., 1959, Some characteristics of the climate in forest and tundra regions in Alaska: Arctic, v. 12, p. 214-220.

_________, Macneill, F. S., and Leopold, E. B., 1960, The coastal plain at Nome, Alaska: A late Cenozoic type section for the Bering Strait Region, in Rept. of the Intern. Geol. Cong., XXI Session, Pt. IV., Chronology and Climatology of the Quaternary: Copenhagen, Norden, p. 46-57.

________, and Sigafoos, R. S., 1951, Frost action and vegetation patterns on Seward Peninsula Alaska: U. S. Geol. Survey Bull. 974-C, p. 51-101.

Hultén, Eric, 1941-50, Flora of Alaska and Yukon: Lunds Univ. Arsskrift, new ser., sec. 2 in 10 parts, 1941, 37: 1-28; 1942, 38: 129-412; 1943, 39: 413-568; 1944, 40: 569-769; 1945, 41: 897-978; 1946, 42: 979-1066; 1947, 43: 1067-1200; 1948, 44: 1201-1342; 1949, 45: 1343-1482; 1950, 46: 1483-1902.

Hunt, E. C., North, A. A., and Wells, R. A., 1955, The application of paper chromotographic methods of analysis to geochemical prospecting: The Analyst, Jour. Soc. Analytical Chemistry, v. 80, no. 948, p. 172-194.

Karlstrom, Thor N. V., 1960, Surficial deposits of Alaska, in Short Papers in the Geological Sciences: U. S. Geol. Survey Prof. Paper 400-B, p. 333-335.

Keller, W. D., 1955, The principles of chemical weathering: Lucas Bros., Columbia, Mo. 88 p.

Kellogg, C. E., and Nygard, I. J., 1951, Exploratory study of the principal soil groups of Alaska: U. S. Dept. Agr. Mon. 7, 138 p.

Krause, H. H., Rieger, S., and Wilde, S. A., 1959, Soils and forest growth on different aspects in the Tanana watershed of Interior Alaska: Ecology, v. 40, p. 492-495.

Lakin, H. W., Almond, Hy, and Ward, F. N., 1952, Compilation of field methods used in geochemical prospecting by the U. S. Geological Survey: U. S. Geol. Survey Circ. 161, 34 p.

Laughlin, W. M., 1958, Biometric procedures for estimating Alaska's soil productivity, in Science in Alaska, Proc. Ninth Alaskan Sci. Conf., College: p. 24-25.

Lewis, C. C., and Eisenmenger, W. S., 1948, Relationship of plant development to the capacity to utilize potassium in orthoclase feldspar: Soil Sci., v. 63, p. 495-500.

Lid, Johannes, 1944, Norsk Flora: Oslo, Det Norske Samlaget, 637 p.

Löve, A., and Löve, D., 1957, Arctic polyploidy: Proc. Genetics Soc. Canada, v. 2, p. 23-27.

Lutz, H. J., 1956, Ecological effects of forest fires in the interior of Alaska: U. S. Dept. Agr. Tech. Bull. 1133, 121 p.

Lyon, T. L., and Buckman, H. O., 1937, The nature and properties of soils: New York, Macmillan, 392 p.

Marshall, Robert, and Averill, Clarence, 1928, Soil alkalinity on recent burns: Ecology, v. 9, p. 533.

Mayr, Ernst, 1961, Cause and effect in biology: Science, v. 134, p. 1501-1506.

McCarthy, J. H., Jr., 1956, Accuracy and precision of field methods of trace analyses used in geochemical exploration by the U. S. Geological Survey, in Resumenes de los Trabajos Presentados, XX Congreso Geologico Internacional, Mexico: p. 370-371.

McInteer, B. B., 1941, Distribution of the woody plants of Kentucky in relation to geologic regions: Kentucky Dept. Mines Minerals Geol. Div. Bull. 6, Series VIII, 20 p.

________, 1947, Soil preferences of some plants as seen in Kentucky: Castanea, v. 12, p. 1-8.

Meijer, W., 1960, Bryologische Brief uit Noord-Borneo: Buxbaumia, v. 14, p. 15-18.

Mertie, J. B., Jr., 1930, Geology of the Eagle-Circle district, Alaska: U. S. Geol. Survey Bull. 816, 168 p.

Meyer, B. S., Anderson, D. B., and Böhning, R. H., 1960, Introduction to plant physiology: Princeton, Van Nostrand, 444 p.

Nasvetailova, N. G., 1955, Geobotanical investigations in prospecting for ore deposits, in Trans. All Union Geol. Trust, Ministry of Geol. and Nat. Resources No. I: Moscow.

Oda, Uteana, Myers, A. T., and Cooley, E. F., 1959, A field method of spectrographic analysis for use in geochemical exploration work: U. S. Geol. Survey, open-file report.

Oosting, H. J., 1956, The study of plant communities: San Francisco, W. H. Freeman and Co., 440 p.

Persson, Herman, 1956, Studies in "copper mosses": Jour. Hattori Bot. Lab. No. 17, 18 p.

________, and Gjaerevoll, Olav, 1957, Bryophytes from the interior of Alaska: Det. Kgl. Norske Vidensk. Selsk. Skr. No. 5, Trondheim, 74 p.

________, and Shacklette, H. T., 1959, Drepanocladus trichophyllus found in North America: The Bryologist, v. 62, p. 251-254.

_________, and Weber, W. A., 1958, The bryophyte flora of Mt. McKinley National Park, Alaska: The Bryologist, v. 61, no. 3, p. 214-242.

Polunin, Nicholas, 1940, Botany of the Canadian Eastern Arctic, Part I: Nat. Mus. Canada Bull. 92 (Biol. ser. no. 24), Ottawa, 408 p.

_________, 1948, Botany of the Canadian Eastern Arctic, Part III., Vegetation and ecology: Nat. Mus. Canada Bull. 104 (Biol. ser. no. 32), Ottawa, 304 p.

Porsild, A. E., 1955, The vascular plants of the western Canadian Arctic Archipelago: Nat. Mus. Canada Bull. 133, Ottawa, 226 p.

_________, 1957, Illustrated flora of the Canadian Arctic Archipelago: Nat. Mus. Canada Bull. 146, Ottawa, 209 p.

Prát, S., 1934, Die Erblichkeit der Resistenz gegen Kupfer: Ber. Deutsch. Bot. Ges., v. 52, p. 65-67.

Raymond, M., 1950, Esquisse phytogéographique du Québec: Mem. Montreal Bot. Garden No. 5, Montreal, 147 p.

Reynaud-Beauverie, M. A., 1936, Le milieu et la vie en commun des plantes, in Encyclopédie Biologique, v. 14: Paris, Paul Lechevalier, 237 p.

Richards, P. W., 1932, Ecology, in Manual of Bryology, ed. by Fr. Verdoorn: The Hague, Martinus Nijhoff, p. 366-396.

Robinson, W. O., 1951, The minor or trace elements in soils, plants, and animals: U. S. Dept. Agr. Leaflet (unnumbered).

Ross, C. S., and Hendricks, S. B., 1946, Minerals of the montmorillonite group: U. S. Geol. Survey Prof. Paper 205, p. 23-79.

Rübel, Eduard, 1935, The replaceability of ecological factors and the Law of the Minimum: Ecology, v. 16, no. 3, p. 336-341.

Scarseth, G. D., 1960, Temperature influences upon vegetation and soil properties, in Trans. 7th Intern. Cong. Soil Sci., Madison, Wisc., U.S.A., v. 3: Gronigen, Dykstra's Drukkerij, p. 7-11.

Schreiner, Oswald, and Brown, B. E., 1938, Soil nitrogen, in Soils and Man, U. S. Dept. Agr. Yearbook, 1938: p. 361-376.

Scoggan, H. J., 1957, Flora of Manitoba: Nat. Mus. Canada Bull. 140 (Biol. ser. no. 47), Ottawa, 619 p.

Senstius, M. V., 1925, The formation of soils in equatorial regions, with special reference to Java: American Soil Survey Assoc. Rep. Bull. v. 6, p. 149-161.

Shacklette, H. T., 1958, Biogeochemical sampling in Alaska: Bull. Geol. Soc. America, v. 69, no. 12, pt. 2, p. 1756.

________, 1960, Soil and plant sampling at the Mahoney Creek lead-zinc deposit, Revillagigedo Island, Southeastern Alaska, in Short Papers in the Geological Sciences: U. S. Geol. Survey Prof. Paper 400-B, p. B102-B104.

________, 1961a, Substrate relationships of some bryophyte communities on Latouche Island, Alaska: The Bryologist, v. 64, no. 1, p. 1-16.

________, 1961b, Physiographic processes of sedge meadow pool formation on Latouche Island, Alaska, in Short Papers in the Geologic and Hydrologic Sciences: U. S. Geol. Survey Prof. Paper 424-D, p. D197-D198.

________, 1962, Biotic implications of Alaskan biogeochemical distribution patterns: Ecology, v. 43, no. 1, p. 138-139.

Shtina, E. A., 1960, Zonality in the distribution of soil algae communities, in Trans. 7th Internat. Cong. Soil Sci., Madison, Wisc., U.S.A., v. 2: Gronigen, Dykstra's Drukkerij, p. 630-634.

Sigafoos, R. S., 1958, Vegetation of northwestern North America, as an aid in interpretation of geologic data: U. S. Geol. Survey Bull. 1061-E, p. 165-185.

Sjörs, Hugo, 1959, Bogs and fens in the Hudson Bay Lowlands: Arctic, v. 12, p. 2-19.

Skinner, C. E., and Nygard, I. J., 1930, The presence of Azotobacter and absence of Thiobacillus thiooxidans in peat soils: Ecology, v. 11, p. 558-560.

Spetzman, L. A., 1959, Vegetation of the Arctic Slope of Alaska, in Exploration of Naval Petroleum Reserve #4 and adjacent areas, northern Alaska, 1944-1953, pt. 2: U. S. Geol. Survey Prof. Paper 302B, p. 19-58.

Steere, W. C., 1947, The cryptogamic flora of the Arctic: V. Bryophytes: Bot. Rev., v. 20, p. 6-7.

________, 1961, Biological problems in arctic America: The American Biol. Teacher, v. 23, p. 263-272.

Sweetman, W. J., and Brundage, A. L., 1960, Better forage for Alaska's dairy industry: Univ. Alaska Agr. Expt. Station Bull. 30, 9 p.

Tedrow, J. C. F., and Cantlon, J. E., 1958, Concepts of soil formation and classification in Arctic regions: Arctic, v. 11, no. 3, p. 156-179.

________, Drew, J. V., Hill, D. E., and Douglas, L. A., 1958, Major genetic soils of the Arctic Slope of Alaska: Jour. Soil Sci., v. 9, no. 1, p. 33-45.

________, and Hill, D. E., 1955, Arctic Brown soil: Soil Sci., v. 80, p. 265-275.

Url, W., 1956, Ueber Schwermetall-, zumal Kupferresistenz einiger Moose: Protoplasma, v. 46, p. 768-793.

(U. S.) Soil Survey Staff, 1960, Soil classification, a comprehensive system. Seventh approximation: Soil Conservation Service, U. S. Dept. Agr., Washington, U. S. Govt. Printing Office, 265 p.

U. S. Weather Bureau, 1943, Climatic Atlas for Alaska: Rpt. no. 444, Washington, U. S. Govt. Printing Office.

Viktorov, S. V., 1955, The use of the geobotanical method in geological and hydrogeological investigations: Acad. Sci. Press of the U.S.S.R., Moscow, 199 p. (in Russian)

Walker, R. B., 1954, The ecology of serpentine soils II. Factors affecting plant growth on serpentine soils: Ecology, v. 35, p. 259-266.

Ward, F. N., and Lakin, H. W., 1954, Determination of antimony in soils and rocks: Analytical Chemistry, v. 26, p. 1168.

Warren, H. V., Delavault, R. E., and Fortescue, J. A. C., 1955, Sampling in biogeochemistry: Geol. Soc. America Bull., v. 66, p. 229-238

________, and Matheson, C. R., 1949, Some relationships between geology and forest growth: Western Miner, June issue, p. 52-54.

Washburn, A. L., 1961, Instrumental observations of mass wasting in a permafrost environment, in Geol. Soc. Am. Program 74th Ann. Meeting, Cincinnati, Ohio, 1961: p. 168A.

Webley, D. M., 1960, Evaluation of the plate technique in use for studying phosphate-dissolving micro-organisms, in Trans. 7th Internat. Cong. Soil Sci., Madison, Wisc., U.S.A., v. 2: Gronigen, Dykstra's Drukkerij, p. 657-663.

White, M. G., and Tolbert, G. E., 1954, Miller House-Circle Hot Springs Area, in Reconnaissance for radioactive deposits in East-Central Alaska, 1949: U. S. Geol. Survey Circ. 335, p. 4-6.

Wiggins, I. L., 1951, The distribution of vascular plants on polygonal ground near Point Barrow, Alaska: Stanford Univ. Dudley Herbarium Contr., v. 4, p. 41-56.

Zach, L. W., 1950a, Effect of rainfall on stream flow in Southeastern Alaska: Tech. Notes No. 4, Alaska Forest Research Center, U. S. Dept. Agr. Forest Service, Juneau.

__________, 1950b, A northern climax, forest or muskeg?: Ecology, v. 31, p. 304-306.

UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
Washington, D. C.

For release DECEMBER 21, 1962

The Geological Survey is releasing in open files the following reports. Copies are available for consultation in Room 1033, GSA Building, Washington, D. C., and in other offices as listed:

1. Preliminary geologic map of the NE 1/4 Mount Union quadrangle, Yavapai County, Arizona, by C. A. Anderson and P. M. Blacet. 1 map. Bldg. 25, Federal Center, Denver, Colo.; 345 Middlefield Rd., Menlo Park, Calif.; Arizona Bureau of Mines, College of Mines, University of Arizona, Tucson, Ariz. Copies from which reproductions can be made at private expense are available in the Geological Survey Library, Room 1033, GSA Bldg., Washington, D. C.

2. Influences of the soil on boreal and arctic plant communities, by Hansford T. Shacklette. 345 p., 47 figs., 10 tables. 345 Middlefield Rd., Menlo Park, Calif.; 503 Cordova Bldg., Anchorage, Alaska.

3. Geology of the Straight Creek tunnel site, Clear Creek and Summit Counties, Colorado, and its predicted effect on tunnel construction, by C. S. Robinson and F. T. Lee. 41 p., 5 figs., 1 table. Bldg. 25, Federal Center, Denver, Colo.; Colorado Department of Highways, 4201 East Arkansas Ave., Denver, Colo.

* * * * *