THE BIOGEOGRAPHY OF TABLE MOUNTAIN, BONNE BAY, NEWFOUNDLAND. AN INVESTIGATION OF PLANT COMMUNITY COMPOSITION AND DISTRIBUTION ON A SERPENTINE BEDROCK

PHILIP DEARDEN

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Philip Dearden
B.A., University of Birmingham
1973

Submitted to the Department of Geography, Memorial University of Newfoundland, in partial fulfillment of the requirements for the degree of Master of Science

Memorial University of Newfoundland

October - 1975

ABSTRACT

This thesis is a phytogeographical study of Table Mountain, Bonne Bay, Newfoundland (N 49° 28', W 58° 00'). It describes and analyzes the composition and distribution of plant communities on the serpentine bedrock of Table Mountain. Serpentine vegetation is characterized by its discontinuous nature, and stunted and unusual specimens. Research has indicated that four soil properties, low available calcium, and high magnesium, nickel and chromium contents are the dominant limiting factors for plant growth. The thesis postulates that these factors, in conjunction with other environmental variables, may be important in explaining the distribution and composition of plant communities on serpentine.

The vegetation and soils are rigorously sampled, and the vegetation samples analyzed by a three-dimensional indirect ordination. The axis representing the major gradient of compositional change was found to be highly correlated with the amount of available calcium in the soil. The samples with the most diverse species, tallest specimens and most continuous vegetation cover, also had the greatest amounts of available calcium. This would appear to substantiate the theory that low calcium availability is a major factor in serpentine ecology, and furthermore suggest that it is a major factor in determining community composition and distribution on serpentine.

The distribution of characteristic species, groups of species and edaphic properties are graphically presented within a two-dimensional ordination. This facilitates identification of phytosociological and edaphic relationships and permits the delimitation of six abstract phytosociological groups within the ordination. These groups are related to specific topographic situations and locations on Table Mountain, and their composition, edaphic characteristics and interrelationship discussed in detail. The serpentine vegetation is felt to be in dynamic equilibrium with the environment, and the sparsely colonized areas are no less of a climax than the continuous cover of the peatlands.

ACKNOWLEDGEMENTS

The completion of this thesis was facilitated by the assistance of a number of individuals and Departments at Memorial University. I would like to thank the Biology Department for use of the Norris Point Biological Research Station throughout the 1974 field season. The Chemistry Department, particularly Dr. L.K. Thompson provided the facilities and skilled supervision for the soils analyses. I would like to express sincere appreciation to R.J. Rogerson and R.V. Maher, my supervisor, both of the Geography Department, who provided continual encouragement and scholarly advice throughout the study.

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Frontispiece. Table Mountain from Norris Point
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CHAPTER I

INTRODUCTION

This thesis is a biogeographical study of Table Mountain, Bonne Bay (N 49^{0} 28', W 58^{0} 00'), on the west coast of Newfoundland (Figure 1). Biogeography has been defined as the inter-disciplinary field between the biological sciences and geographical sciences (e.g. see Seddon 1971, Tivy 1971 and Cox *et al* 1973), gaining its unique character from the emphasis which is placed on the distribution of biological species on earth. Thus its chief aim is to show how the physical environment of a species, or a group of species, interacts with their biology and evolutionary history to bring about their pattern of distribution.

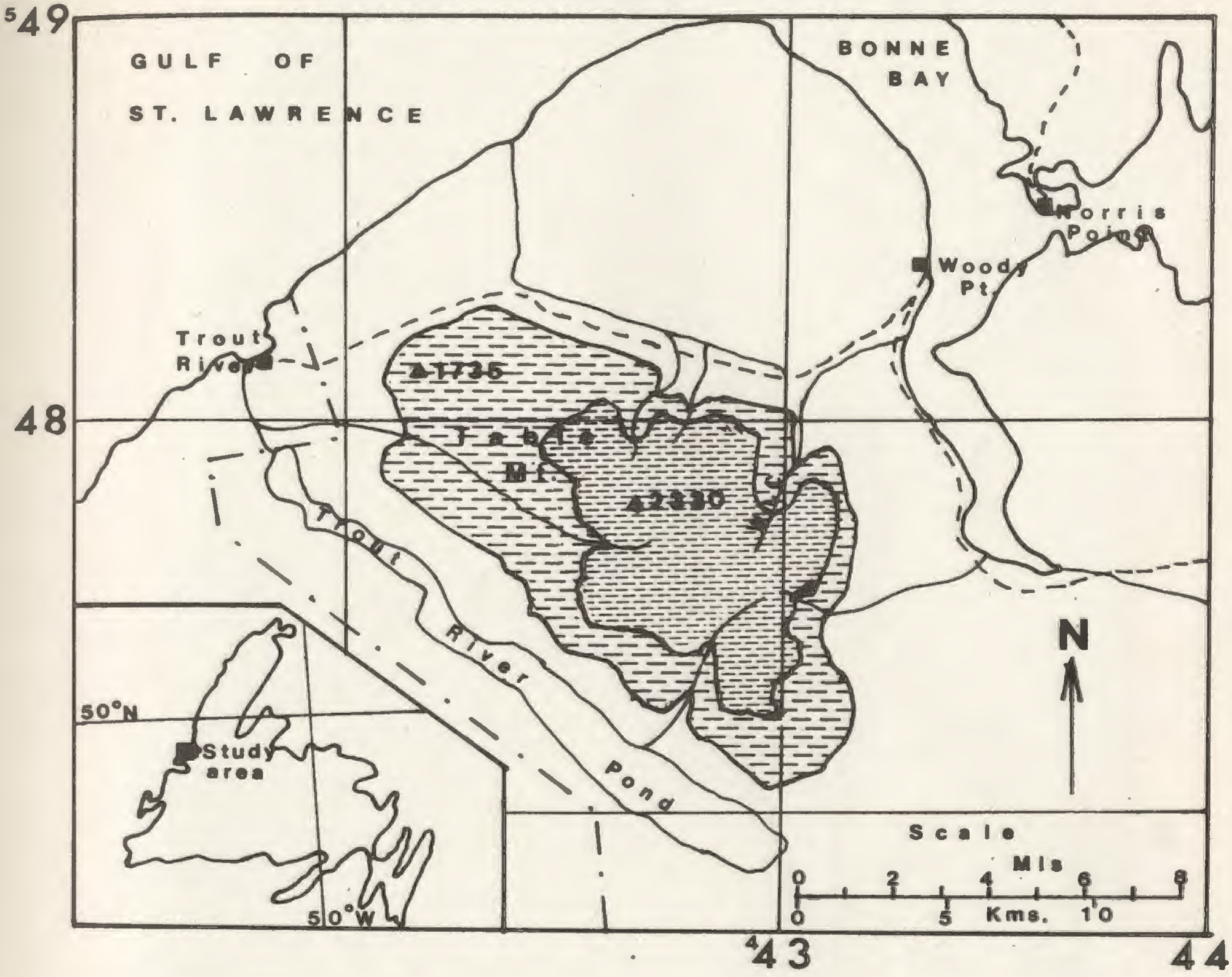
Watts (1971) elaborates:

> "biogeography seeks to establish patterns of order from the apparent chaos of the multiplicity of life forms present upon the surface of the earth, and in its soil, atmosphere and water bodies. In so doing it is concerned with the mechanisms whereby both plants and animals originate, evolve and organize themselves into assemblages which show particular distributions and affinities" (p. 1).

In essence it attempts to document and compare these, 'particular distributions and affinities' in geographic space as relationships between each other, and between the organisms and the environment. The difference between biogeography and ecology is consequently seen to be primarily one of emphasis, ecology being more concerned with environmental-organism relationships *per se*.

1.1 Research Objectives

This study is phytogeographical. Its aim is to describe and analyze the distribution and composition of plant communities on the serpentine of Table Mountain. In so doing it contributes to the understanding of the complex interrelationship of environmental factors sponsoring the distribution of the various species assemblages, and allows an assessment



▤	Land over 1000 ft. (305M)
▦	Land over 2000 ft. (610M)
——	Main rivers
- - - -	Roads
—·—	Gros Morne National Park boundary
Wh.C	Winter House Canyon

Figure 1. Location of study area

of the state of equilibrium existing between the vegetation and environment to be made.

Table Mountain (712 M) is a distinctive steep-sided plateau with a vegetation structure and composition very different from that of the adjacent bedrock. It is characterized by its sparse distribution, stunted growth, lack of species common on surrounding geological formations, and abundance of species found infrequently or totally absent from the surrounding vegetation.

The thesis is significant for three reasons:

1) The distribution of plant communities on serpentine bedrock has received little attention. Most work on serpentine has been autecological and edaphic (see Chapter 2.11, 2.12) in an effort to explain its agricultural infertility. Moreover research has been predominantly in warm-temperate regions and therefore this study will aid to further understanding of serpentine ecology in a mid-boreal locality.

2) The description and analysis of serpentine vegetation constitutes a significant addition to knowledge of the vegetation of Newfoundland. The only published work resulting from botanical research on the Newfoundland serpentine areas is part of a broad scale description of the vegetation of eastern Canada and Newfoundland (Fernald 1911,1926, 1933).

3) The field area lies entirely within the boundaries of the newly established Gros Morne National Park. The resource report for the Park (Strong-Moorhead Sigsby Ltd., 1971) emphasizes the "rare and specialized communities of micro-flora and arctic-alpine species" (p. 85) of Table Mountain, and states that "the wilderness values and interpretive potentials of this area are very high" (p. 87). It is hoped that this dissertation will be a step toward realizing these potentials.

1.2 Thesis Design

The thesis is divided into six chapters after this introduction. Familiarity with previous studies on serpentine ecology is essential before any possible explanation of plant community distributions can be advanced. Consequently Chapter 2 reviews the edaphic, autecological and synecological research to date. This review permits the identification of the various edaphic factors which have been proposed to explain the limited distribution of plant species on serpentine bedrock.

Chapter 3 describes the physical environment, outlining the major geological, physiographic, climatic and vegetational characteristics of the area. This places Table Mountain in a wider geographical context giving a basis for comparison with other serpentine areas in different climatic and vegetation regions. The relationship between physiography and periglacial phenomena is dealt with at length, being of great importance at a later stage in the analysis.

Chapter 4 outlines the methods and analytic techniques used to collect and interpret the data. It comprises two main sections; firstly, the field design, which describes how the sample locations were chosen and the information collected at each; and secondly, the techniques subsequently used to render this data into a coherent and intelligible form. The main analytic method is indirect ordination using a somewhat modified version of the Bray and Curtis (1957) technique. The results, both phytosociological and edaphic are given in Chapter 5, producing the delimitation of six abstract phytosociological areas.

In Chapter 6 these abstract areas are related to reality and specific environmental situations on Table Mountain. Their distribution, floristic composition, relationship to each other and various environmental factors are discussed at length.

The Conclusion identifies the environmental factors thought to be the most important in explaining the distribution and composition of plant communities, and assesses the state of equilibrium existing between the environment and vegetation.

CHAPTER 2

LITERATURE REVIEW

This chapter reviews the major works published on serpentine ecology. Although it is not the principal aim of the thesis to study the plant-environment relationships _per se_, it is necessary to be fully aware of these to gain insight into community distribution. The first section describes the distinctive nature of serpentine vegetation and identifies its major characteristics. The last three sections review the edaphic, autecological and synecological studies on the relationship between serpentine bedrock and plant species. This research is pertinent to community variation on Table Mountain.

2.1 The Serpentine Problem

Serpentine soils are found throughout the world and are everywhere noted for their distinctive vegetation cover. This has been noted in studies from Sweden (Rune 1953), Norway (Bjørlykke 1938), Finland (Kotilainen 1944), Great Britain (Hunter and Vergano 1952; Spence 1957, 1958, 1959, 1970; Proctor 1971a, 1971b) Austria (Lämmermayr 1934), Yugoslavia (Novak 1928), Italy (Pichi-Sermolli 1948), United States (Whittaker 1954) and New Zealand (Lyon _et al_ 1971).

The vegetation of all these widely scattered areas is similar in that it is of marked physiognomic contrast with that on other soils, and possesses an unusual flora characterized by rare isolates and narrow endemic species. Rune (1953) identified six features common to all the serpentine floras of the northern mid-latitudes.

> "1. The serpentine flora is relatively poor in individuals as well as in species.
>
> 2. On serpentine several species are represented by particular races (ecotypes) differing ecologically and sometimes also morphologically from the type races of the species.

> 3. Many plants occur very disjunctively on serpentine.
>
> 4. The serpentine flora contains basicolous as well as acidicolous plants which often grow together.
>
> 5. The serpentine has a relatively xerophytic character.
>
> 6. The serpentine flora is often dominated by a certain family or certain genera, e.g. Caryophyllaceae in North Europe and E. North America" (p. 123).

The causes of this distinct serpentine effect has been the subject of considerable dispute and is still largely unresolved. However, it is essential to be familiar with these edaphic, autecological and synecological studies before any attempt at inter and intra community differentiation on a serpentine massif itself is made.

2.2 Edaphic Studies

Physical Properties

Serpentine typically forms mountainous terrain, the soils in such locations are usually shallow, presumably because the available relief and sparseness of the vegetation encourage continual erosion. They form lithosols or azonal soils where there is considerable clay and organic material included. Under various climatic and soil forming conditions they have been classified as Podzols (Sedletskii 1945; Sasaki et al 1968), Brunisolic (Kanno et al 1965) and utisols (USDA classification system; Nagatsuka 1967). Robinson et al (1935) explained the thin soil mantle on even level areas as a result of an alumina deficiency causing insufficient clay formation for the establishment of a normal soil. From a series of detailed physical analyses they concluded that serpentine soils possess no physical characteristic which would render them particularly unfavourable for plant growth. Rune, working in an arctic-alpine environment, emphasizes the disruptive effect of frost in soil which prevents the formation of closed communities. He does not, however, ascribe these processes a major role in the distinction between serpentine and non-serpentine vegetation. The periglacial features of Table Mountain indicate that it sustains a similar climatic regime as that described by Rune for Norway.

Chemical Properties

The influence of serpentine soil on plant species is usually described in terms of its peculiar chemical composition. A number of different hypotheses have been proposed, regarding soil-plant relationships. Different hypotheses are associated with different climatic regimes. It is probable that at any location several factors are significant. Furthermore the chemical composition of the soil is complex. De Kimpe and Zizka (1973) have indicated that the composition depends on "the degree of serpentinization of the original igneous rocks (dunite, peridotite, pyroxenite, amphibolite), on the nature of the resulting serpentine minerals (chrysolite is more subject to weathering than the platy minerals), and on the degree of leaching in the profiles (Sasaki et al 1968)." (p. 1533)

In brief the outstanding chemical properties of serpentine soils when compared to a "normal" soil are (Table 1):

1. high magnesium content,
2. low calcium content,
3. alkaline pH reaction,
4. low available molybdenum,
5. high nickel and chromium levels,
6. low levels of major nutrient elements,
7. high iron content,
8. low aluminum content

Most of these points have at one time or another been put forward, either alone or in combination to explain the distinct vegetation found on

TABLE 1

Chemical Analyses of Some Typical Serpentine Soils from Different Parts of the World.

Location	Property				
	pH	Available Calcium	Available Magnesium	Total Nickel	% Organic Matter
1. Dublin, Maryland, U.S.A.	5.85	0.16	4.09	0.012	nr
2. Chelan Co., Washington, U.S.A.	6.62	2.03	5.95	nr	nr
3. Lake Co. California, U.S.A.	6.80	2.12	12.1	0.026	nr
4. Meikle Kilrannoch, Scotland	6.2	1.1	13.8	2.50	4.7
5. Meikle Kilrannoch, Scotland	4.9	0.2	2.1	0.500	13.6
6. Unst, Shetland, Scotland	7.1	1.2	4.1	2.500	2.3
7. Unst, Shetland, Scotland	6.7	5.6	16.9	2.500	12.7
8. New Caledonia	5.8	0.6	0.8	0.12	nr

Magnesium, calcium and nickel are expressed as milliequivalents /100 g., nr signifies no reading.

Source

1. Robinson, Edgington & Byers, 1935 (sample no. 4722)
2. Walker, 1954 (sample no. 53)
3. Walker, 1954 (sample no. 30)
4. Proctor & Woodell, 1971a (sample no. 6a - debris soil)
5. Proctor and Woodell, 1971a (sample no. 6a - closed vegetation)
6. Proctor and Woodell, 1971a (sample no. 8a - debris soil)
7. Proctor and Woodell, 1971a (sample no. 8a - closed vegetation)
8. Birrell and Wright, 1945

serpentine soils. For example Gordon and Lipman (1926) noticed the low levels of major nutrient elements nitrate and phosphate in particular, which limited crop species growth in their experiments. However Walker (1954) after citing several such examples, concludes,

> "No doubt deficiencies of major nutrient elements are common in serpentine soils, but there is little evidence that any such deficiencies can serve as a general explanation of poor plant growth on these soils, because in agricultural practice, heavy applications of nitrogen, phosphorus, potassium and sulfur have failed to correct their infertility." (p. 262-263)

Similarly other hypotheses, such as extreme alkalinity (Gordon and Lipman 1926), low available molybdenum (Walker 1948, Johnson, et al. 1952) and high iron content (Novak 1928), although perhaps contributing to the effect are dismissed as not being dominant factors. The major controversy centres around the status of available calcium and magnesium in the soil, and the toxic effects of chromium and nickel.

Robinson, et al. (1935) seem to have been the first to propose and present evidence that the presence of toxic concentrations of heavy metals, such as chromium and nickel, may be responsible for the unfavourable nature of serpentine soils for plant growth. The chromium and nickel contents are generally higher in serpentine soils than in those of other origins (Table 1), and appreciable amounts of these metals may be absorbed by plants.

The chromium occurs partly as highly insoluble chromite and partly as more soluble silicates (Robinson et al. 1935); the latter being more toxic and increasing with increased serpentinization. Similarly nickel occurs partly as a silicate and partly as a sulphide, the latter increasing with degree of serpentinization and having greater effect on plant absorption levels. Therefore the importance of nickel and chromium as the dominant limiting factors may be supported by the observation that the serpentine character of the vegetation increases with degree of serpentinization. Indeed this is the conclusion reached by Rune (1953) one of the foremost researchers of the problem.

However, in a recent paper Proctor (1971) concludes that, "the role of heavy metals in the serpentine soils investigated remains enigmatical. Evidence from plant analyses and tolerance tests suggest that at least nickel is likely to be of importance. Yet experiments in which plants have been grown in the soils yield no evidence of heavy metal toxicity" (p. 840).

Further evidence is required before a definite statement of the importance of heavy metal toxicity in serpentine soils can be made; indeed it is certain that the importance of the heavy metals varies from one serpentine to another.

A comparable degree of controversy centres around the importance of the status of magnesium and calcium available in the soil to the plants. There are three main schools of thought on this, all supported by conflicting experimental results.

1) The low availability of calcium to plants in serpentine soils, that is, essentially an effect of deficiency rather than toxicity (Vlamis and Jenny 1948, Walker 1948, Kruckeberg 1954).

2) The high magnesium content in serpentine soils making them toxic to many plant species (Lammermayer 1928).

3) The balance between available calcium and magnesium. Loew (1901) showed that an excess of magnesium over calcium generally has an injurious effect on plant growth. This is the most popular hypothesis and Proctor (1971) in the most recent published research on the topic concludes that the high magnesium to çalcium ratio is the dominant limiting factor.

The results of this research provide further evidence as to the role of the heavy metals and calcium and magnesium in producing the distinct serpentine effect.

2.3 Autecological Studies

The unusual edaphic properties of serpentine lead to a distinct vegetational response, about which three main problems emerge in the literature.

1) Why are many species excluded from serpentine soils? Cultivation experiments (Vlamis and Jenny 1948, Vlamis 1949, Walker 1948, 1954, Proctor 1971) indicate that many species are excluded simply because they cannot adapt to the serpentine's chemical properties.

2) Why are other species able to grow successfully both on and off serpentine? It is thought that these species are better able to adapt to the low calcium levels (Kruckeberg 1951, 1954, Walker 1954) and resist the large concentrations of magnesium, nickel and chromium (Proctor 1971).

3) Why are certain species restricted to serpentine soils? Certain authors (Novak 1928, Lammermayr 1928, Morrison 1941) have claimed that such species required some essential substance in the soil. However, there has been no experimental evidence of serpentine endemics being inhibited by the conditions of a non-serpentine soil. Following experimentation on serpentine and non-serpentine soils with a number of endemic and non-endemic species Kruckeberg (1954) concludes, "a serpentine plant occupies a serpentine environment while its potential competitors are excluded by edaphic factors. On the non-serpentine soil, in contrast, the serpentine plant is excluded by the presence of other plants, though very well able to grow on non-serpentine soil in their absence" (p. 273).

2.13 Synecological Studies

Synecological studies of serpentine vegetation have been neglected in comparison to the detailed edaphic and autecological research. The primary emphasis has been the description and cataloguing of the serpentine flora, and comparative research between the vegetation composition of serpentine and non-serpentine areas. There have been many descriptions of serpentine floras throughout the world; here the review is restricted to the research in North America and Europe.

In North America, studies have been concentrated on the serpentine of the Appalachian chain from western Massachusetts through Pennsylvania and Maryland (Harshberger 1903, 1904, Shreve 1910, Pennell 1910, 1913, 1930, Braun 1950), south to Georgia (Radford 1948); or on the more extensive Pacific Coast serpentines (Mason 1946, Kruckeberg 1951, 1954, Walker 1954, Whittaker 1954). These have mainly been in warm temperate regions, concerned with describing the differences between serpentine and non-serpentine tree dominated vegetation structures, and have little relevance to Table Mountain.

The major European studies have been on the serpentine outcrops in Scotland with one major exception, the work of Rune (1953) in northern Sweden. He examines in detail every aspect of serpentine ecology, from problems of an edaphic and genetic nature to large scale regional contrasts. Most of his work was in North Sweden for which he gives a detailed account of every serpentine outcrop, but he also briefly discusses the serpentine vegetation of Norway, Finland, Eastern North America and East Asia.

Although this is a purely descriptive account it is of great value in that it summarizes all serpentine studies up to that date and thus provides a seedbed for hypothesis formulation. His work is of special relevance to Table Mountain because Rune was dealing with essentially the same type of vegetation structure,

> "...the vegetation of at least all these northern serpentine areas shows a superficial similarity. Their barren, rocky character gives the impression of highly arctic or alpine enclaves, sharply contrasting with their vicinity" (p. 45).

Similarly the Scottish studies are dealing with an environment and vegetation structure very akin to that of Table Mountain. However a further complication is involved in many of these studies for the vegetation is subject to far greater biotic interference than are those of northern Sweden or Table Mountain. Proctor and Woodell (1971) when studying the Scottish serpentine heaths comment,

> "Their present state is certainly partly the result of man's influence which includes such destructive agencies as sheep grazing and fire. This influence of man, in maintaining open, unstable habitats appears to be paralleled in Teesdale (Bellamy *et al* 1969), and it is interesting that a few rarities (*e.g.* *Minuartia verna*) are common to some serpentines and Teesdale" (p. 383).

This is an important point and must be borne in mind when seeking replicability between the plagioseres of the Scottish serpentines and the virgin, climax vegetation of Table Mountain.

There are two principal workers on the Scottish serpentines, Spence (1957, 1958. 1959, 1970) and Proctor (1971a, 1971b, 1971c), although Ferreira (1963, 1964) also considers serpentine in his research on the distinctions between calciphilous and basiphilous plants.

Spence's initial work is a survey of Unst in the Shetland Isles in relation to the geology. The species forming the flora of the Unst hill-land are grouped according to their frequency on different bedrocks into serpentine-characteristic, serpentine-indifferent, serpentine-casual, and acid rock characteristic species. In later, more detailed papers he considers the ecological relationships and reaches the conclusion that,

> "It seems established beyond doubt that wind is a master factor in this habitat. It may be said to act directly by stature limitation and indirectly with rain and soil instability, by baring roots. Wind must consequently re-expose debris, with areas re-exposed by rainwash these constitute areas of unassociated debris. Wind and soil instability must also maintain debris as an open habitat by retarding colonization" (Spence 1959, p. 989-999).

Spence appears to be the only worker to attach such importance to the wind as a dominant limiting factor of serpentine.

More recent work by Spence (1970) examined whether four scattered serpentine outcrops shared any unique vegetational feature or whether the vegetation was just locally different. The cool summer climate and winter exposure appeared to emphasize a unity between mountain-top detritus and talus communities of high levels in the eastern Highlands and the corresponding open community found at far lower altitude in exposed sites in the north-west Highlands and Islands. Consequently most of the species typifying examples of the ultrabasic and acid sociations are less clearly restricted, especially in oceanic areas, to debris or talus of one or another chemical type, but they are confined to open habitats. Consequently he concludes that serpentine and other ultrabasic debris vegetation is generally less distinctive than its obvious local differences from surrounding areas would suggest; also that it comprises in part a west Scandinavian sociation of base-rich talus, in part an extension of Icelandic and Faeroese fellfield, and perhaps the most distinctive feature of the serpentine vegetation studies is endemism.

Proctor and Woodell (1971) attempts to relate the serpentine vegetation of England and Wales to serpentine in other parts of the world. They describe eleven sites in terms of vegetation composition and structure, dividing these into debris areas, i.e. those with less than twenty-five percent plant cover, heaths and grasslands. Chemical analyses of soils for each category are given together with those from serpentine outcrops lacking a characteristic vegetation. On this basis they examine the sites with reference to six distinctive characteristics of serpentine vegetation (Rune 1953, p. 123), concluding that,

> "...rock weathering characteristics are largely responsible for the presence of sparsely colonised debris; and that the debris appears to be expanding under the combined influence of exposure and human influences (mainly grazing animals)" (p. 393).

These studies by Spence, and Proctor and Woodell are interesting, for although their aim is synecological and not biogeographical, they both suggest what they consider to be the major spatial limiting factors of certain types of plant community. However, the milder climate, different plant species and damaging biotic interference on the Scottish serpentine are all obstacles to replicability when considering Table Mountain.

Summary

Several major edaphic characteristics have been proposed in the literature to explain the difference between serpentine and non-serpentine vegetation. These factors, high chromium and nickel, low calcium, high magnesium and the ratio of calcium to magnesium may be significant in understanding the community variation and distribution on Table Mountain. Synecological studies in North America and Europe have emphasized the differences between distinct serpentine outcrops and also the differences between the vegetation on serpentine and non-serpentine bedrock. In general, there has been little attention in the literature to community variation on a single serpentine outcrop.

CHAPTER 3

PHYSICAL ENVIRONMENT

This chapter describes the physical background of the study area outlining the major geological, physiographic, climatic and vegetational features of Table Mountain and the surrounding area. Table Mountain is a distinctive ochreous protrusion amongst the greenery of the surrounding hills. Its name describes its general appearance, a flat plateau bounded by steep cliffs on three sides, largely reflecting its geological formation, but also much modified by later glacial action.

3.1 Geology

Table Mountain is one of four separate ophiolite units (Lewis Hills, Blow-Me-Down Mountain and, North Arm being the others), that form the Bay of Islands Complex (Cooper 1936, Smith 1958) (Figure 2). Each unit comprises a number of separate and distinct sub-horizontal slices that were emplaced during Middle Ordovician klippen. The lower structural slices consist of Cambrian and Lower Ordovician chiefly clastic sedimentary rocks, overlain by contrasting igneous assemblages. The uppermost slice is the ophiolite peridotite assemblage and its basic greenschist-amphibolite metamorphic aureole (Figure 2). The assemblages are all in the same structural position and either represent separate transported bodies, or erosional remnants of a once continuous slice (Williams 1971). Stevens (1970) suggests that these peridotite sheets represent a transported oceanic crust and mantle.

Table Mountain is bounded by strike-slip tear faults to the north and south which do not continue westward toward the coast. The nearly vertical dipping Trout River fault on the south side is a continuous transverse fault that has offset Table Mountain from its original position

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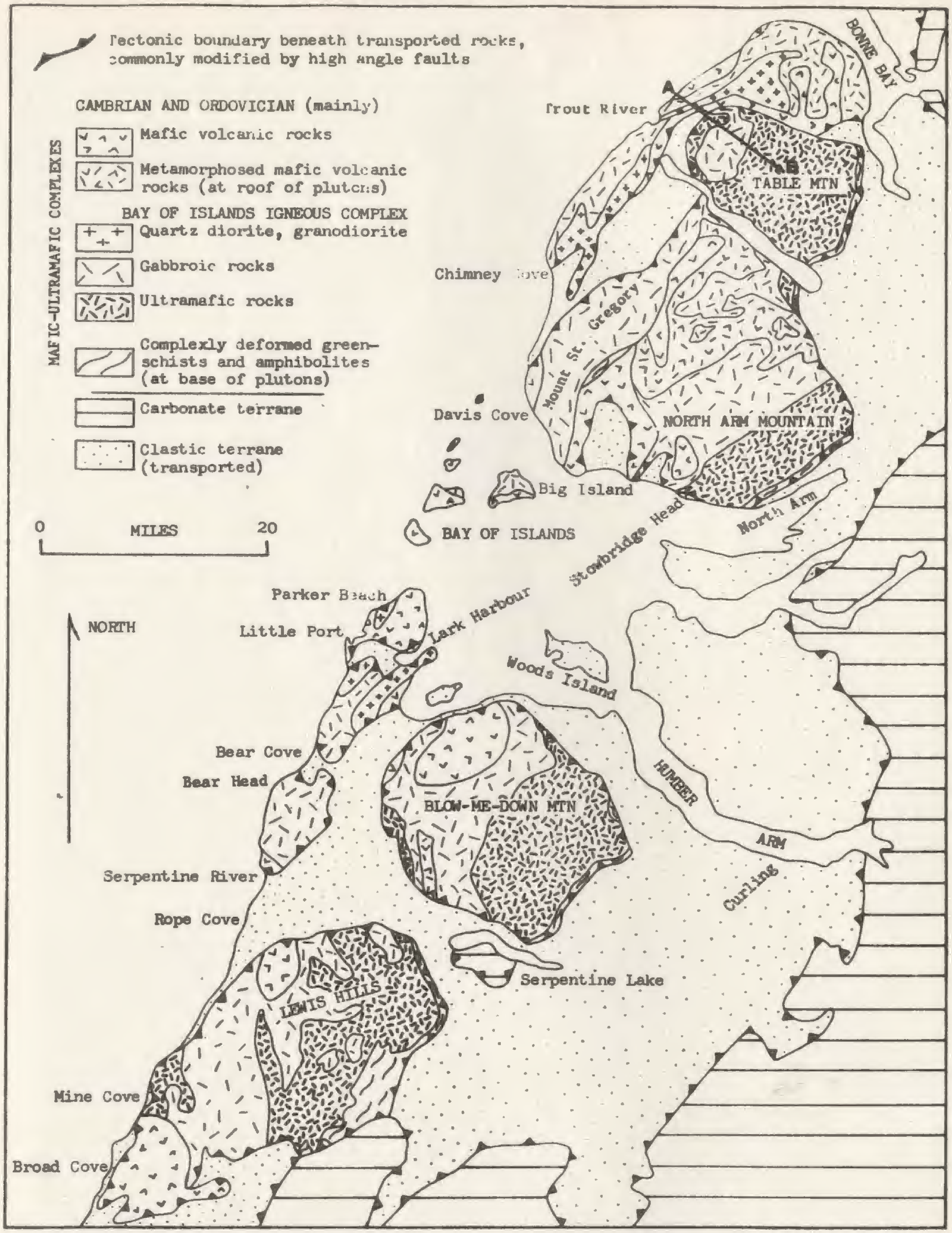
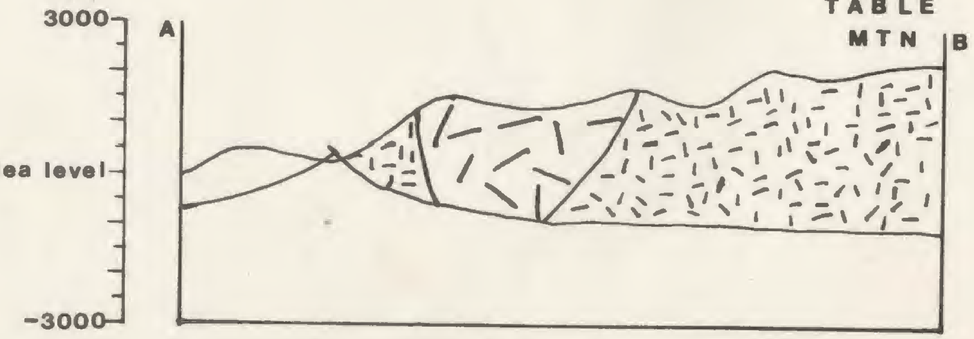
Figure 2. Geological map of the Bay of Islands ultramafic assemblages, and cross section A-B of Table Mountain. (Over)



After Williams (1971)



as a continuation of the North Arm massif.

Table Mountain is composed of ultramafic rocks conformably overlain by layered gabbros. The ultramafics are chiefly dunite, where over ninety percent olivine occurs, and enstatite peridotite where less than ninety percent olivine is present, the remainder being dominantly orthopyroxene (Smith 1958). Chemically there is little difference between the two but dunite weathers to a light yellowish-brown smooth surface, and is found mainly to the eastern end of the Mountain; whereas peridotite weathers to a slightly darker, stucco-like surface caused by resistant enstatite and chromite grains standing in relief, and is found toward the western side of the Mountain. The surface weathering may extend to a depth of two inches, but is commonly less than ½ inch. Below the weathered zone, the fresh dunite has a greyish olive-green to black colour and an aphanitic appearance.

The petrochemical status of the rocks may vary from area to area, but the high silica and magnesium and low magnesium contents are apparent in all examples (see Table 2). There is little significant petrochemical difference between the peridotite and its metamorphosed derivative, serpentine. The serpentine occurs usually as conspicuous greenish veins running through the peridotite, but occasionally covers large areas especially where it has been exposed by differential erosion.

Other minerals such as asbestos and chromite occur on a much reduced scale and have little importance. However, of particular importance as far as vegetation is concerned, are four small seepage zones on the northern flank of the Mountain below which a calcareous tufa deposit has been formed. These seepage zones were not active during the summer field season, but their effect upon the local vegetation is considerable, and will be discussed in greater detail later. (See Appendix I for locations.)

TABLE 2

Petrochemical Comparison Between Serpentine on Table Mountain, Newfoundland and Other Localities in the Northern Hemisphere

	SAMPLE						
Mineral (%)	1	2	3	4	5	6	7
Fe_2O_3	1.8	6.27	5.17	4.03	6.01	12.45	5.0
TiO_2	nr	nr	0.09	0.02	nr	0.10	nr
P_2O_5	nr	nr	nr	0.02	0.02	0.03	nr
SiO_2	38.9	34.39	37.69	41.01	40.49	37.98	40.0
CaO	2.06	0.3	0.6	0.77	0.74	nr	tr
MgO	36.0	40.23	41.5	27.88	37.36	37.68	40.0
Al_2	2.21	0.2	0.4	10.96	1.77	0.78	1.0
FeO	5.4	3.64	2.4	3.90	4.84	nr	5.0
Na_2	0.13	nr	nr	0.22	nr	0.01	tr
H_2O	11.02	12.56	13.09	10.45	nr	nr	nr
MnO	0.11	0.15	0.11	0.03	nr	0.13	tr
K_2O	0.03	0.02	0.02	0.07	0.10	0.06	tr

tr - trace, nr - no reading

Sample	Source
1,2,3	Table Mountain, Bonne Bay, Nfld. - Malpas,J. (unpub.)
4	Tottori Prefecture, Japan - Harada (1953)
5	Scotland - Proctor (1973)
6	Maryland, U.S.A. - Robinson (1935)
7	Sweden - Rune (1953)

3.2 Physiography

Table Mountain is bounded by a steep (40° to 70°) scarp up to 400M high which is fault controlled along its northern and southern flanks. The summit is a relatively flat plateau (maximum elevation 712M) covering approximately 80 sq. kms, that has been identified as part of the Long Range Peneplain by Twenhofel and Mac Clintosh (1940) and assumed to date back to the Cretaceous (Brookes 1964). The existence of this Peneplain is independent of bedrock control, i.e. it continues further north on the granite and gneiss of the Northern Peninsula, but the extraordinary flatness of Table Mountain (see Frontispiece) probably is emphasized by the bedrock.

The area has been greatly modified by glacial action in more recent geological time. The steep glaciated valleys on the northern and southern flanks of the Mountain, the two major troughs cutting back into the plateau, and the well-formed cirques on the mountain sides all evidence this. Whether the area was ever entirely glaciated, and by ice from which direction has been the source of considerable debate. Fernald (1918) saw such upland areas as typically remaining unglaciated throughout the Pleistocene and acting as refugia for various plant species. The presence of roche moutonnes and granite erratics on the plateau would seem however to demonstrate that much or all of it was overridden by ice on at least one occasion. Grant (1969) describes upland areas north of Bonne Bay which were deglaciated several thousand years before the surrounding lowlands, and therefore existed as nunataks for part of the Late Wisconsin. The north eastern flank of Table Mountain with its small tors, altiplanation terraces and felsenmeer may well have been a similar area (Rogerson, *pers comm*).

During final deglaciation, about 10,000 years ago, morainic debris was deposited, especially in the form of lateral moraines along the sides of the glaciated valleys north and south of the Mountain. Coarsely-stratified drift mantles the lower slopes of Winterhouse Canyon and the cirque-like embayments on the Mountain sides.

3.21 Periglacial phenomena

Much of Newfoundland reveals the effect of recent or current periglacial activity in a wide range of landforms. It is particularly evident in poorly vegetated areas such as Table Mountain where, in turn, it has the greatest effect on species distributions. This section deals with the location of different manifestations of periglacial activity in detail as this is of great importance later in discussing the distribution of plant communities.

Bedrock features

The amount of frost shattering (Fr. gélivation) depends upon the strength of the rock and the distribution of water within that rock. The process is at a maximum where the rock is traversed by regular fissures, a few tenths of a millimetre to a few millimetres wide. Two processes are at work; macrogelivation, which exploits the structure of the serpentine, operating along joints and cleavage planes and usually splitting off large pieces; and microgelivation, to a lesser degree, which cuts across the structure of the rock and shatters its constituents, producing silt and finer particles. These processes cause the gradual fragmentation of bedrock outcrops.

On the plateau numerous tors are thus effected leading to the development of large areas of coarse debris (felsenmeer), and continuing exposure of the tors through altiplanation. Cliffs along the steep faulted margins of the Mountain, generally between 100 and 200M in height with angles of 40 to 70°, are subject to similar processes. This material provides sediment to the talus cones and aprons below.

Talus Slopes

Talus slopes occur in various stages of development at the foot of the cliffs and to a more limited extent below the tors. Their size and angle varies considerably depending upon locality.

Different forms of talus slope with different size of debris and varying angles of rest are found around the Mountain. They are most commonly of quite coarse material, (i.e. <20 cms in diameter), much of the finer material having been washed down to the lower slopes.

Solifluction terraces

When the talus slopes become more stable in response to a decrease in supply of sediment, solifluction terraces may form. They vary greatly in size, from two to fifty metres in length and from one to three in height. Whole series of such terraces may occur, rising above each other like giant steps. Generally the coarser the debris then the larger the terrace formed.

Similar terraces have been recognized in many sub-arctic-alpine areas round the world; for example in Jan Mayen Island (Wilson 1952), southern New Zealand (Billings and Mark 1961), the Cairngorm Mountains in Scotland (Watt and Jones 1948), Macquarie Island (Taylor 1955) and in the St. Elias Range in the Yukon (Sharp 1942). A great variety of names have been used, for example Sharp calls them "stone garlands," whereas they are "stone-banked terraces" to Antevs (1932). However in essence they all appear to be basically similar, yarying only in scale and perhaps with slightly different emphases on factors of formation.

There is no general agreement as to their formation, or even the conditions conducive to their formation. For example, Tricart (1969) suggests that they may require steeper slopes than stripes to form, whereas Wilson (1952) maintains that a more gentle gradient is required. Cailleux and Taylor (1954) postulate that terraces form instead of stripes where there is a better vegetation cover. However, most theories focus on the flow of the central fine area, particularly during the spring thaw, which is held in check by the larger stones and dense vegetation cover of the rises.

Patterned Ground

Patterned ground is a common feature of Table Mountain and has been recognized in many arctic-alpine environments (e.g. Huxley and Odell 1924; Polunin 1934; Taber 1943; Bellair 1969). Two main types, stone polygons and stone stripes, occur on Table Mountain.

Stone polygons (Figure 5), also called nets, are quite extensive and well-developed, occurring on level ground, (0-5°) particularly on the platforms in between the solifluction terraces. They vary considerably in diameter and in the size of materials composing them, but are all characterized by a polygonal arrangement of large stones around an area of finer material. These interlock to cover large areas and may be internally subdivided by even smaller polygons.

Stone stripes are narrow stony stripes, from 10 cms to a meter wide, separated by earthy bands two to four times broader and extending parallel to the slope. On slopes over 2.5° polygons lose their regularity and become elongated in the direction of slope. They become longer and narrower as the angle increases and by 7.5° polygons are usually transferred into open-ended stripes. The size and spacing of the stripes is

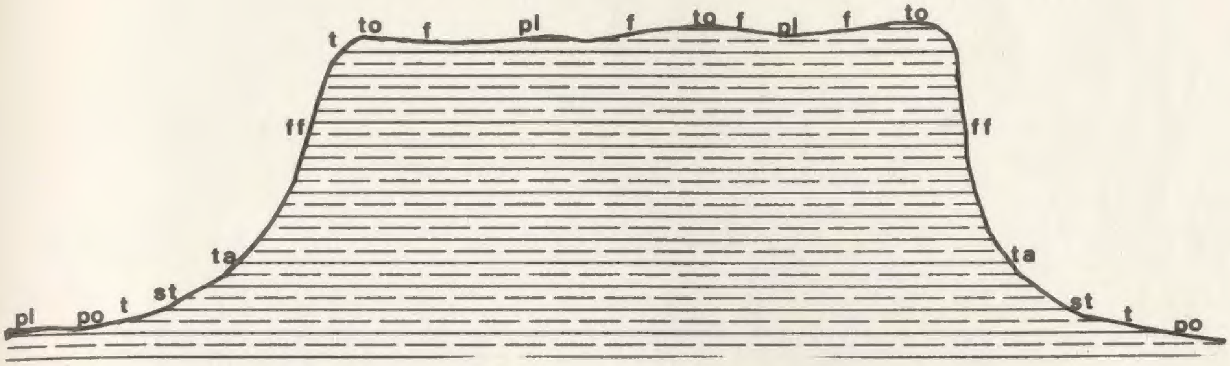


Figure 3. Schematic cross-section of Table Mountain indicating the relationship between periglacial phenomena and physiography

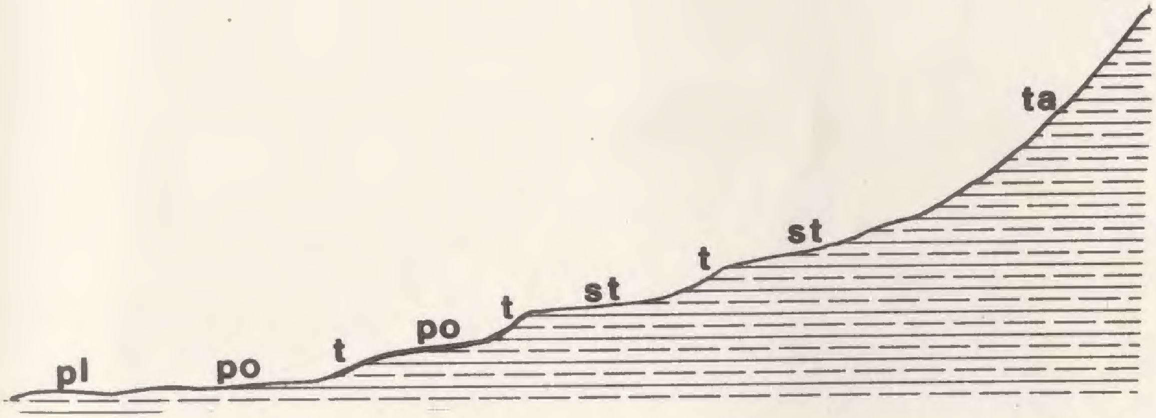


Figure 4. Schematic cross section of the lower slopes, indicating the relative location of peatlands, stone polygons, solifluction terraces, stone stripes and talus slopes.

Key: pl - peatland, po - stone polygon, t - solifluction terrace, st - stone stripe, ta - talus, ff - free face, to - tor, f - felsenmeer

Photo: Rogerson

Figure 5. Stone polygons at the mouth of Winterhouse Canyon. Large areas of Table Mountain display similar periglacial phenomena.

dependent on, among other things, the degree of slope and size of fragments. Broader stripes are formed by larger fragments with closer spacing on steeper slopes.

3.3 Climate

Woody Point (Figure 6) is the nearest climatological station to Table Mountain. It is located at sea level two miles north of the Mountain on the sheltered South Arm of Bonne Bay, and has been in operation for three years. Forty miles inland, the station at Deer Lake has a longer period of observations but is an unsuitable index of the climate of Table Mountain in view of the Mountain's predominantly marine exposure. The readings for Woody Point indicate the major climatic characteristics of the local region. By extrapolation it is possible to suggest the nature of the weather processes on Table Mountain.

From Figure 6 it can be observed that there is possibly a very wide monthly range of temperature, particularly in Spring. This is very unusual for such a maritime situation, but it reflects one of the major environmental features of the area, sea ice. Ice usually begins to form in late December, early January and may persist until April or May before it beings to break up to any degree. This has quite a profound effect on the climate, for the ice, once consolidated, may cool the air above it almost as much as a continental land surface. Thus the coldest weather of winter often occurs in the clear and strong currents of continental polar air that sweep across this sea ice in the wake of cyclones moving into the Atlantic. It is this effect which is largely responsible for the extremely low temperatures recorded in March, when the ice is most extensive. However, these storms may also bring very mild weather if their course lies north of

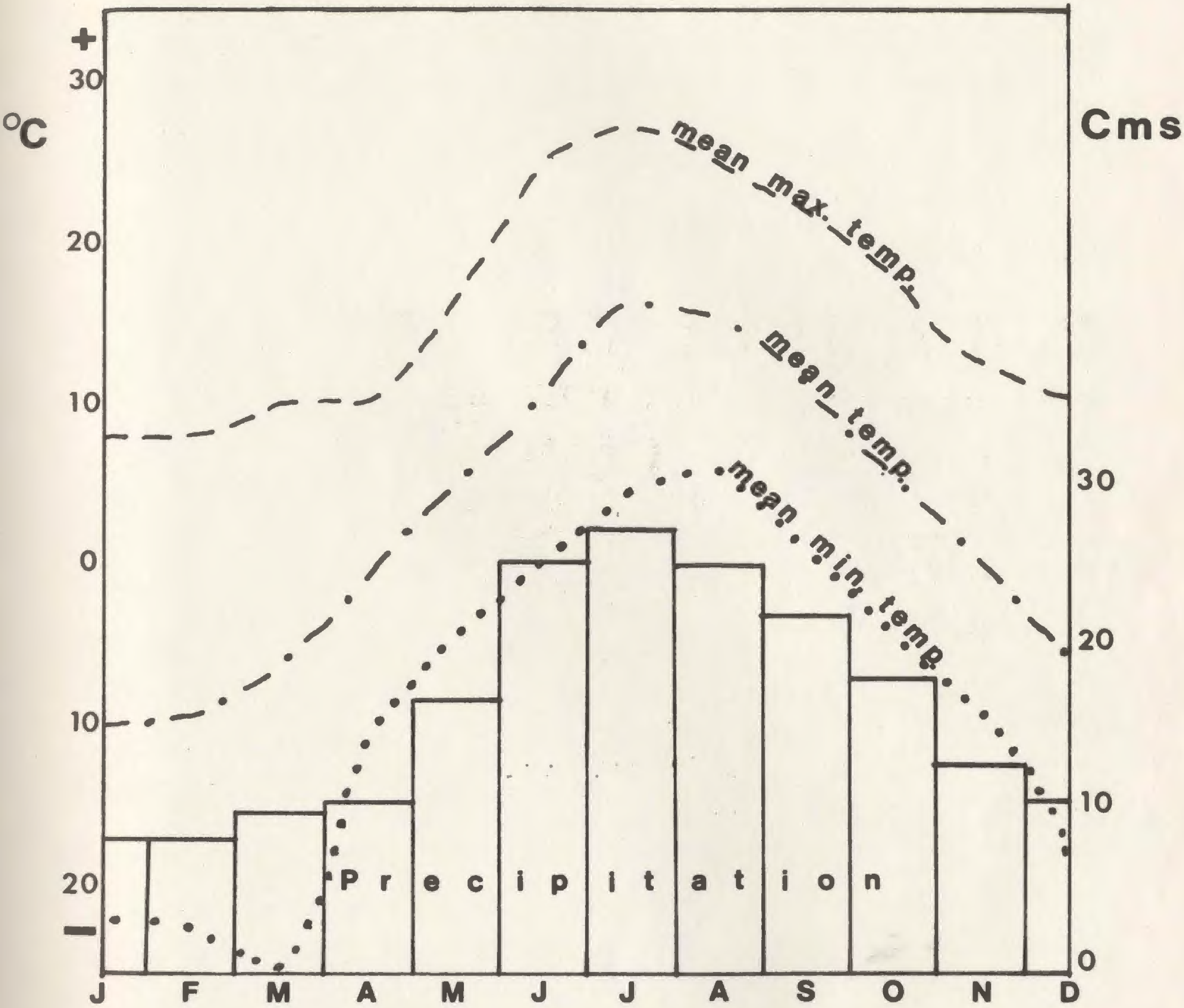


Figure 6. Temperature and precipitation means, Woody Point, Bonne Bay

Newfoundland and southwesterly air streams may bring thawing temperatures to the whole of the island.

The presence of the late sea ice effectively delays all seasons somewhat. The spring is particularly late for the warm air streams approaching the island are chilled at low levels. The start of the vegetative season, conventionally taken to be temperatures above 5.6° C is thus considerably delayed, usually not commencing until early May. However because of the delay of all the seasons it is relatively long and may go on until October.

Precipitation is abundant and evenly distributed throughout the year, falling mainly during the passage of numerous cyclones from the west. The locally high relief no doubt gives an orographic emphasis to the precipitation levels and is partly responsible for the relatively high annual mean of 165.21 cms. The varied belief in the area can also lead to peculiar local effects of precipitation such that one side of the Mountain may be in sunshine all day whereas the other is enveloped in a thick but localized cloud formation.

In relating these figures to Table Mountain it is essential to take into account the sheltered position of Woody Point, and their difference in elevation. These differences may be indeed sufficient to allow the doubling of the precipitation values at Woody Point for Table Mountain. The difference in wind exposure between the localities must also be a very significant factor, although there is no quantitative data to substantiate this claim. In addition the lack of a well developed vegetation structure on Table Moutain, as compared to Woody Point, would serve to amplify climate extremes.

The wind is, however, known to be of great importance during the winter months mainly because of its effect on redistribution of snowfall. During February 1974 snow hydrology studies were undertaken to ascertain the relationship between snow depth, density, physiography and vegetation.

It was observed that the wind effectively redistributes the snow such that certain exposed areas often those with the greatest patterned ground development, were blown practically clear of snow, whilst other areas, particularly those at the scarp foot and the banks of terraces, accumulated quite a deep (>2m) snow pack. This is of great importance in explaining vegetation patterns, and will be discussed more fully later (Chapter 6.0).

Snow typically begins to melt in late March or early April, but considerable areas may still be under snow as late as early July in exceptional years, such as was experienced in the field season of 1974. In these years, and indeed in most years, a few snowpatches in sheltered north facing gullies survive the summer and are reinforced by the next winter's snowfall.

3.4 Vegetation

The long growing season, varied geology and undulating physiography give the Bonne Bay area a particularly well developed and diverse vegetation cover, except for the serpentine of Table Mountain. A marked altitudinal progression of vegetation types can be distinguished. On the coastal plain a mosaic of raised bogs, *Alnus rugosa* swamps and *Picea mariana* scrub dominates, depending upon local conditions. The lower foothills have a second growth forest of *Abies balsamea*, with associated species *Picea glauca* and *Betula papyrifera* and occasionally *Picea mariana*. The latter becomes increasingly dominant with altitude as do the Ericaceae, particularly *Kalmia angustifolia*. Increased exposure at this altitude stunts growth to as little as 50 cms, with shrubs such as *Vaccinium angustifolium*, *Ledum groenlandicum and Rhododendron canadense* beginning to dominate large areas. This is typically the most widespread community on the Long Range Plateau with occasional bare rocky knolls protruding through.

On the serpentine of Table Mountain, however, the vegetation on the adjacent diorite and gabbroic bedrocks terminates abruptly at the geological boundary, (figure 7) as if, "the waves of new climaxes following climatic changes, (c.f. Clements 1916, 1934), have never been able to wash over the serpentine areas to any noteworthy extent" (Rune 1953, p. 80). There is little in common between the vegetation structure and composition of Table Mountain and that of the adjacent bedrocks.

The serpentine massifs of Newfoundland have received little ecological attention. Fernald (1907, 1911, 1918a, 1918b, 1925, 1926, 1933) in his botanical expeditions to Newfoundland, and in support of his hypotheses of the origin of the Newfoundland flora, does mention a few of the more unusual species found mainly on the Bay of Islands serpentines (see figure 2). He notes of the 1932 expedition,

> "the arduous climb over arid blocks of serpentine seemed to have few rewards, for nowhere did they find continuous carpets of vegetation, merely scattered plants of a few inconspicuous species" (Fernald 1933, p. 9-10).

These 'inconspicuous species' include notables such as Adiantum pedatum var aleuticum, Danthonia intermedia, Salix anglorum var kophophylla, Salix cordifolia var Macounii, Arenaria marcescens, Arenaria cylindrocarpa, Cerastium terrae-novae, Lychnis alpina, Statice labradorica, Conioselinum pumilum and Solidago hispida var tonsa.

In other papers of a more general nature, Fernald (1907) makes more extensive reference to the serpentine areas to be found in the Shickshock Mountains on the Gaspe Peninsula, and in particular of Mt. Albert. He quotes Low (1884) on the general appearance of Mt. Albert, which could be equally applicable to Table Mountain.

Figure 7. The geological boundary between the serpentine and gabbroic bedrocks along the stream channel, is dramatically reflected in the contrasting vegetation cover.

> "The top of Mt. Albert is nearly flat, and is rent by a deep gorge on the east side, which, near its head, splits into several smaller ones. The sides of these gorges are quite destitute of vegetation, and the bare serpentine rocks are weathered to a light buff colour. On the top of the mountain blocks of serpentine are scattered around, covered by a thick growth of mosses, (chiefly *Rhacomitrium lanuginosum*) and lichens. Sheltered places are occupied by a stunted growth of black spruce (*Picea mariana*), which rarely attains a height of ten feet. The branches interface near the ground and form an impenetrable thicket. The whole surface has a dead appearance, and reminds one of the pictures of the moon" (p. 173).

Fernald was impressed by the arctic-alpine species he found on Mt. Albert, which he failed to find on the more southerly but much higher Mt. Washington. He mentions by name such species as *Adiantum pedatum* var *aleuticum*, *Festuca altaica*, *Salix desertorum*, *Arenaria arctica*, *Statice sibirica*, *Solidago decumbens*, *Artemisia borealis*, and many other plants, unknown south of the St. Lawrence. He concludes,

> "The great tableland and canon-walls of Mt. Albert, although exposing many square miles of alpine region, have a comparatively meagre flora; but the few species which there abound are of the greatest interest to the eastern botanist, for with but a few exceptions they are quite unknown upon any other mountain or cliffs in eastern North America" (p. 167).

However, the species found on serpentine on the mainland, even as near as Mt. Albert, can not necessarily be expected on the Newfoundland serpentines. The results of researchers such as Fernald (1918a, 1924), Marie - Victorin (1938), Raup (1941), Deevey (1949), Danserau (1950), Damman (1964) and Drury (1966) all confirm the lack of basis for assuming replicability between mainland and Newfoundland vegetation.

CHAPTER 4

METHODS AND ANALYSES

The study of community variation on Table Mountain requires field collection on edaphic and other environmental variables and sampling of the vegetation cover. This chapter has been divided into two sections: field design and analytical procedures. Field design describes the location of the samples and the sampling method. The analytical procedures refer to the ordination of plant species data and also the laboratory soils analyses.

4.1 Field Design

The vegetation cover of Table Mountain is discontinuous and includes several different growth forms. These characteristics create a number of sampling problems. It is important that the variation in vegetation of the entire serpentine area be described, and yet be sufficiently rigorous to allow the use of certain quantitative techniques. The following design meets both these requirements.

Certain areas (see Appendix I for locations) were selected from aerial photographs and field observation, that were representative of the variation in plant communities on the Mountain. Transects were oriented along the long axis of each of the selected areas, and quadrats located systematically along the transects. Tidmarsh and Havanga (1955) conclude that such systematic sampling, provided the spacing does not correspond with a repetitive pattern in the vegetation, can be treated as if the data was obtained from the same number of random points.

The spacing between the quadrats was constant for each area, but varied between areas depending upon their size. Optimally the sampling fraction should be varied in proportion to the standard deviation of the data in each area (Gregory 1963). However, it was impossible to calculate the standard deviation before sampling and therefore a rough estimate was made and applied to standardize the distance between the quadrats in any one area. In all, one hundred eighteen quadrats were thus obtained.

In selecting the size of the quadrat, factors such as the variation in growth form of the vegetation, and the information sought, have to be taken into consideration. Ultimately a two metre square quadrat was selected as being the most appropriate.

Within each quadrat the local frequency of each species was determined. The frequency of a species is the chance of finding that species in the quadrat in any one trial, and is determined by recording the species present in each quadrat. For local frequency, instead of a simple quadrat in which presence or absence is recorded, the quadrat is divided into a number of smaller squares and each of those is assessed for species presence and absence. The location of these subunits is determined by use of random coordinate tables. Local frequency has an advantage over simple frequency in that, "the value obtained,... can be localized to an area considerably smaller than any within which random placing of quadrats would be practicable"(Greig-Smith 1964, p. 10). This facilitates correlation with habitat factors which vary over small areas.

Presence of species in each quadrat was by shoot rather than root presence. This is the more practical alternative because of the difficulty in tracing the roots of many species. Frequency is an efficient quality to assess, for not only is assessment rapid, but frequency is dependent partly on density and partly on pattern and does to some extent integrate these two important aspects of the vegetation, thus the information content of this quality is high.

Soil samples were taken from the central sub-quadrat of each quadrat. They were taken from the rooting medium, the depth of which varied from sample to sample. Occasionally several samples were taken from different horizons of the same soil. Upon collection each sample was sealed in a labelled polythene bag for subsequent laboratory analysis.

Detailed field notes were kept for each area, sample and subsample in an effort to provide a comprehensive background for later ecological interpretation. The location of each sample was noted by grid-reference on the map, on the aerial photographs, and many were also photographed and/or sketched to show local topography and aspect. The altitude of each sample was taken by altimeter readings and the mean degree of slope by use of a hand level. Besides recording presence and absence of species, other vegetational characteristics, such as those species in the quadrat but not the sub-quadrat, different stratas, and any indications of succession or colonization were noted. The percentage of the quadrat covered in vegetation, bedrock, stones or fine soil was estimated and finally the date on which each quadrat was sampled, giving an indication as to different species phenologies on different parts of the Mountain.

4.2 Analytical Procedures

4.21 Phytosociological Ordination

<u>The Method</u>

It is now necessary to order this data so that the phytosociological affinities between samples becomes apparent. This is achieved by indirect ordination (Bray and Curtis 1957) whereby the graphical distance between samples is proportional to their compositional similarity. Different areas of the graph can then be characterized by species composition and related to specific environmental conditions and locations on Table Mountain.

Goodall (1954) outlines the basic assumption:

> "It is the high correlation between different environmental factors that often suggests a deceptively simple relationship between plant distribution and the environment. There is much to be said for the view that the complexes of environmental factors determining plant distributions can be indicated and measured better indirectly, through the plants themselves, than by direct physical measurements..." (p. 306)

Gause's principle (Gause 1934), states that no two species in a stable community can occupy the same niche, thus species evolve toward avoidance of competition by differentiation of niche, such that each species has an optimal distribution in a different part of the compositional hyperspace. This is simply illustrated along a single hypothetical gradient in figure 8 . Species have peak frequency where total environmental conditions are optimal for their growth. Along a single gradient, as illustrated, binomial distributions of continuously overlapping species populations occur. Thus species A is most frequent at the xeric end of the moisture gradient, whereas species D is most frequent at the mesic, but the compositional gradient reflects the environmental gradient. The compositional hyperspace is an 'n' dimensional abstract space wherein species and groups of species (samples) may be represented with compositional gradients as axes, for example xy, xz and yz in figure 9.

In figure 8 the compositional gradient is related to one environmental gradient, moisture. However, an environmental hyperspace can also be abstracted from the landscape pattern, its axes being the 'n' complex environmental gradients recognized in the landscape. This can be envisaged as the same space as the compositional hyperspace, although axes may, or may not correspond to the compositional axes (figure 9).

This is a useful abstraction wherein numerous plant species with population centres distributed along environmental gradients, each with

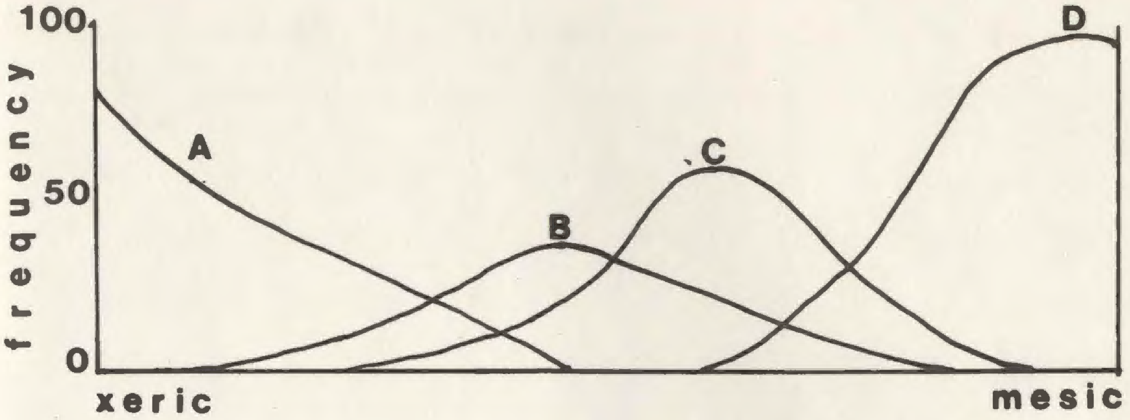


Figure 8. Hypothetical niche differentiation of species A to D along a single environmental gradient

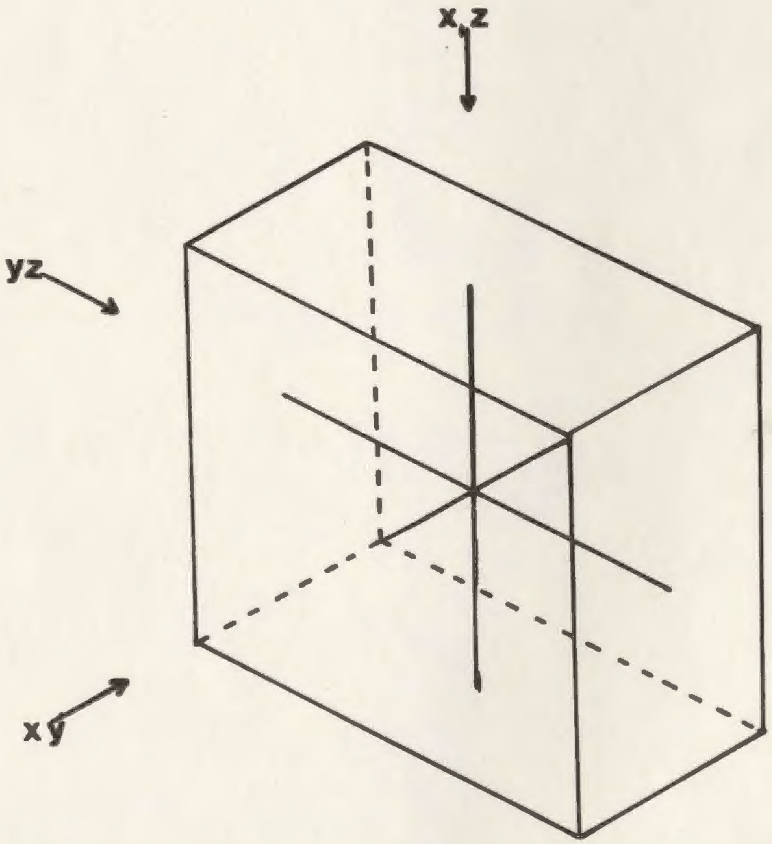


Figure 9. Compositional hyperspace with compositional gradients xy, xz, yz

binomial distributions overlapping those of other species, combine into intergrading communities. Indirect ordination uses the degree of phytosociologic relationship between samples to indicate the distance by which they should be separated within an abstract spatial ordination. "The ordination can thus relate to one another environmental factors, species populations and community trends, in an intergrading pattern of community types as recognized by the investigator" (Whittaker 1973, p. 206-207). The following section details the step by step procedure used in the ordination. (see figure 10).

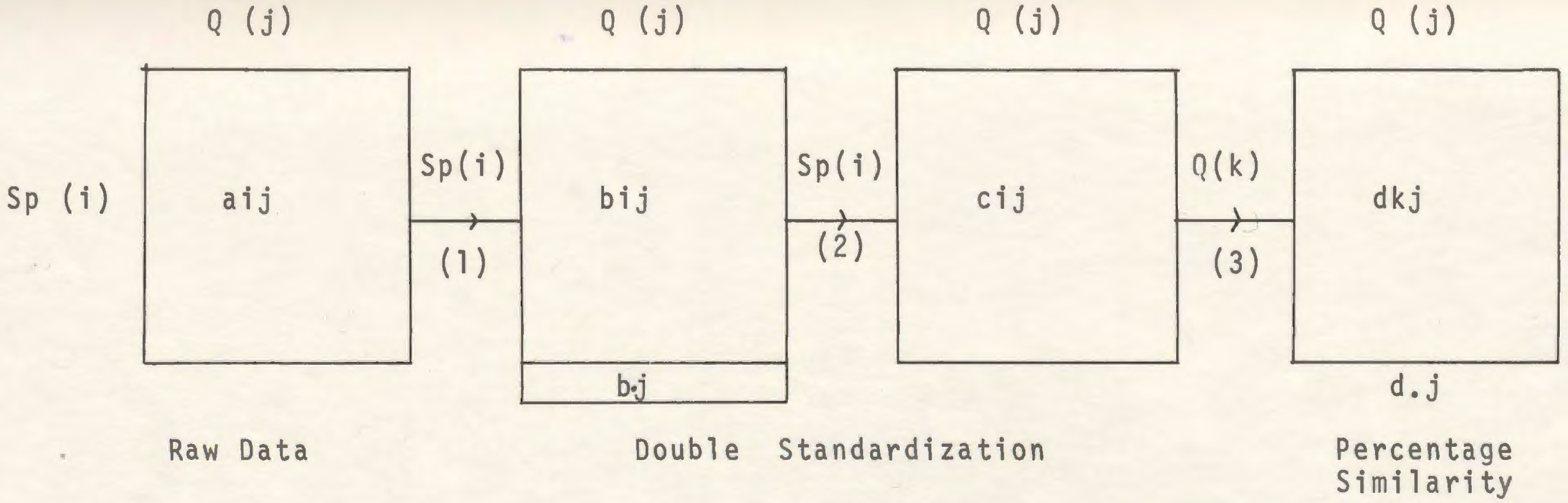
The Analysis

(i) The primary input is a data matrix of the species occuring in each quadrat. This is the raw data matrix in figure 10.

(ii) Previous researchers using indirect ordination methods (e.g. see Whittaker 1973, p. 200), have observed that double standardization of the primary matrix leads to greater clarity in the final ordination. Consequently the second step was to doubly standardize the primary matrix.

The frequency values of each species were converted into percentages of the maximum value in the row for that species (bij in figure 10). The standardized percentages were then summed in each column (b.j), and converted to percentages of the total for that column (cij). Thus each sample was represented by a column of relative importance values totalling 100%.

(iii) The second step is to compute a sample similarity matrix (step 3, figure 10), showing the similarity of each sample with every other sample. There has been considerable debate as to the best indicator of sample similarity. Alternatives suggested have been the simple coefficient of community, percentage similarity applied to raw or doubly



(1) $b_{ij} = \frac{a_{ij}}{\mathrm{Max}\ (a_{ij})} \times 100$

$b_{.j} = \sum_{i=1}^{m} b_{ij}$

(2) $c_{ij} = \frac{b_{ij}}{b_{.j}} \times 100$

(3) $d_{kj} = \sum_{i=1}^{m} \min(c_{ik}/c_{ij})$

$d_{.j} = \frac{\sum_{j=1}^{n} d_{kj}}{n-1}$

$i = 1$ to m
$j = 1$ to n
$k = 1$ to n

Figure 10. Procedural steps in Indirect Ordination

standardized data and Euclidean distance. Detailed examinations of the relative performance of these measures exist, (Orloci 1966, Austin and Orloci 1966, McIntosh 1967, Whittaker 1967, Bannister 1968, Swan 1970, Gauch 1972, Beals 1973, Goodall 1973), the more recent papers favouring the use of percentage similarity of doubly standardized data (dkj). The formula

$$dkj = \sum_{i=(1)}^{m} \min (cik/cij) \qquad (1)$$

where min (cik/cij) is the smaller of the two values for a given species in samples k and j, was thus applied to all values in the doubly standardized matrix.

(iv) The sample with the lowest mean similarity (d.j) was chosen as one end of the first axis, the other end being the sample with the lowest similarity with that sample. However, it has been found that if there is too wide a range of community diversities there is a very good chance that a few samples will have zero similarities with the end points and cannot be effectively ordinated by comparison with them. This is a frequently encountered problem when using ordination. Bray and Curtis (1957) recommend that, "a stand pair with a 0 co-efficient of community be used as a reference pair only if each member of the pair shows a value greater than 0 with all stands which are not members of reference pairs" (p. 332).

Swan (1970) attempted to take zero values into account by proposing use of a "degree of absence" value. However, Whittaker (1973) suggests three possible steps.

(a) Reduction of number of samples, either by random selection or systematic selection of samples representing the different community types in the set.

(b) Classification of samples in composite samples, and then ordinate the composite samples.

(c) Division of the data set into a few large subsets and ordinate within the subsets.

The first step appeared to be the most appropriate and consistent with the aims of the study, and thus after systematic selection, eight samples were discarded.

Sample 9 had the lowest mean similarity with all other samples (12.7) and sample 77 had the lowest similarity (0.5) with sample 9. After checking to ensure that these were ecologically viable end points they were used as end points for the first axis.

(v) All other samples were then ordered along an axis between these points using the formula:

$$\mathrm{Dg} = \frac{(\mathrm{dag} + \mathrm{dbg})(\mathrm{dag} - \mathrm{dbg})}{(2)\mathrm{dab}} \qquad (2)$$

where dag is the distance between stand g and reference stand a, dbg that between g and reference stand b, dab that between the reference stands (Maarel 1969). The distance of each stand along the first (X) axis is given in Appendix II.

(vi) The first axis having been established, the next step is to select end points for a second axis. The basic prerequisites for the end points are that they have low similarity values both with themselves and the end points of the first axis, and that they be in the central part of the X axis and yet be the furthest apart of the possible pairs.

The procedure was as follows:

(a) The values of dag + dbg and dag - dbg were noted as calculated in formula (2).

(b) Those stands with high sum and low difference values were selected and for possible pairs e and f the values of:

$$(dae + dbe + daf + dbf) \quad - \quad (dae - dbe -(daf - dbf)) \qquad (3)$$

were calculated.

Those pairs with the highest value for (3) and appearing to be ecologically suitable (Whittaker (1973) suggests that second axis end points may be chosen solely on the basis of ecological knowledge), were tried as possible end points.

Thus formula (3) was applied to every sample for several different combinations of end points and the results plotted against the X axis. Visual inspection indicated that samples 57 and 23 would provide the clearest, most compact ordination, in that there were no extreme values along either axis. The distance of each sample along the Y axis with end points 57 and 23 is given in Appendix II.

(vii) A third axis, Z, was extracted using the same procedure. A number of different end points were plotted before 37 and 28 were selected as being the most meaningful. The distance of each sample along the Z axis is given in Appendix II.

Whittaker (1973) aptly summarizes the value of this procedure:

> "Ordinations thus provide useful graphical summaries of vegetational variation. A large amount of information can be conveyed in forms representing coherently and at a glance the interrelations of species, communities, and environments. An ordination may be colloquially referred to as a "coat-rack for ideas" about vegetation, or a conceptual "skeleton" by which the complex relationships in the field can be held together and given recognizable form. Once the ordination is prepared, the vegetation can be described by referring to segments or areas within the vegetational hyperspace, without the necessity for classification. On the other hand the vegetational hyperspace can be divided to give a classification that is based on the relationships revealed by ordination, or an ordination of samples that have been classified into units can reveal the relations of these units to one another and environment" (p. 209).

In the next chapter (5.0) the results obtained through this ordination are presented in graphical form, and these used as the basis for the subsequent description (Chapter 6.0) of community composition and variation on Table Mountain.

4.22 Soils Analysis

It was not feasible to analyze the soil for every vegetation sample for a large number of physical and chemical properties, and a restricted number of samples had to be tested for the more important chemical properties. The samples to be analyzed were chosen from the complete set so as to include a similar number of samples associated with certain floristic and physiographic locations. These samples were analyzed for what were thought to be the major properties in relationship to intercommunity variation and distribution based on the edaphic, autecological and synecological research reviewed in Chapter Two. The properties were available calcium and magnesium, total nickel and chromium, pH, percentage organic matter and water retention capability. The laboratory techniques used for each are briefly described below, and the results given in Table 3.

The samples were air dried and sieved either through a 10 or 60 mesh sieve depending on the proposed test. The following methods were based on those outlined in Jackson (1958) and Hesse (1971).

1. pH - Thin paste method

Distilled water was added to 40 gms of the soil until the "liquid limit" was reached. After standing for 10 minutes the pH was measured using a pH meter.

2. Percent moisture content - Oven drying method

A known weight of soil (mineral 25 gm, humus 5 gm) was dried overnight in an oven at 105° C, reweighed, and the percent moisture content calculated.

3. Available calcium and magnesium - Atomic absorption spectroscopy

Ammonium acetate solution (1 M) was added to the weighed sample, which was shaken and allowed to stand before being filtered. The filtrate was collected, made up to volume and analyzed for each element using atomic absorption spectroscopy. Elemental concentrations were determined by comparison with standard calibration plots.

4. Total nickel and chromium - Atomic absorption spectroscopy

Weighed samples (60 mesh) were digested with concentrated nitric acid, followed by ternary solution (conc. HNO_3, H_2SO_4, $HClO_4$ in 10:1:4 ratio). The extracts were diluted with water, filtered, made up to volume and analyzed for each element using an atomic absorption spectrophotometer. Elemental concentrations were determined by comparison with standard calibration plots.

5. Organic matter content - Walkley - Black method

Standard potassium dichromate and concentrated sulphuric acid were added to a weighed sample of 10 mesh soil, and the excess dichromate back titrated against standard Ferrous ammonium sulphate. The percent oxidiseable organic carbon calculated from the titration data was multiplied by a factor of 2 to obtain percent organic matter content.

CHAPTER 5

RESULTS

5.1 Phytosociological

Using the values obtained in the ordination (Appendix II), each of the 108 samples was located on a two-dimensional graph. These can be envisaged as three views of the compositional hyperspace (Figure 9) within which each point is located at the intersection of lines projected from each axis. Thus they are points within a compositional hyperspace wherein the proximity of the points in the ordination is directly proportional to the compositional similarity of the stands.

These axes can be used to plot the frequency distributions of individual species, and groups of species (Bray and Curtis 1957, Ayyad and Dix 1964, Gittins 1965). This has been done with 10 important species (Figures 11 to 24) to show their relative locations within the ordination. Most of these two dimensional views are plotted on the X Z, axis, for this was found to give a greater clarification of phytosociological relationships than the other two axes combinations. However, species such as *Myrica gale*, which is shown on all three axes (Figures 11, 12, 13) is relatively clustered on them all, whereas *Juniperus communis* (Figures 14, 15, 16) shows very little clustering on X,Z, but a much clearer view on YZ. Other species, in particular very common ones, such as *Scirpus cespitosus* and *Andromeda glaucophylla* prove to be so frequent that such a representation on the ordination is practically meaningless.

Most of the species plotted, however, have a clustered position of high frequencies in certain areas of the ordination, but others show no such concentration. High frequency clusters of species represent the location where conditions are optimal for that species, and is therefore a graphical expression of the concept of ecological amplitude. Away from this centre frequency values diminish, although not always equally in all directions, as conditions become less optimal.

Species such as *Vaccinium uliginosum* var *alpinum* (figure 17) and *Larix laricina* (figure 18) show quite marked centres of optimal occurrence indicating perhaps a more limited ecological amplitude than other species like *Potentilla fruticosa* (figure 19) and *Solidago multiradiata* (figure 20).

Certain species such as *Myrica gale* (figure 11) and *Sanguisorba canadensis* (figure 21) can be seen to occur in the same area of the ordination indicating optimal response of both species to the same combinations of environmental factors. Groups of such species with similar ecological amplitudes and distributions can be plotted together to build up a more complete phytosociological picture. Hence the arctic-alpine species *Armeria labradorica* var *submutica*, *Lychnis alpina*, *Silene acaulis*, *Cerastium arvense* var *villosissimum*, *Sagina nodusa*, *Arenaria humifusa*, *Rhododendron lapponicum* and *Salix* when all plotted on one graph (figure 24) show a marked high frequency area in the lower left corner of the X,Z ordination. This restriction contrasts to other distributions such as *Betula pumila*, the most abundant tree species, which has an area of high concentration yet occurs throughout the ordination. (Figure 22).

If the dominant species and species groups are mapped at the 50% frequency level on the same graph phytosociological relationships become more obvious. This can be seen in figures 25 and 26 in which eight important and characteristic species distributions are shown. It is but a small step on from such phytosociological groupings to divide the ordination into different areas in order to facilitate the spatial distribution of community types. Although it follows from the existence of the species continuum previously described that classification must be a somewhat

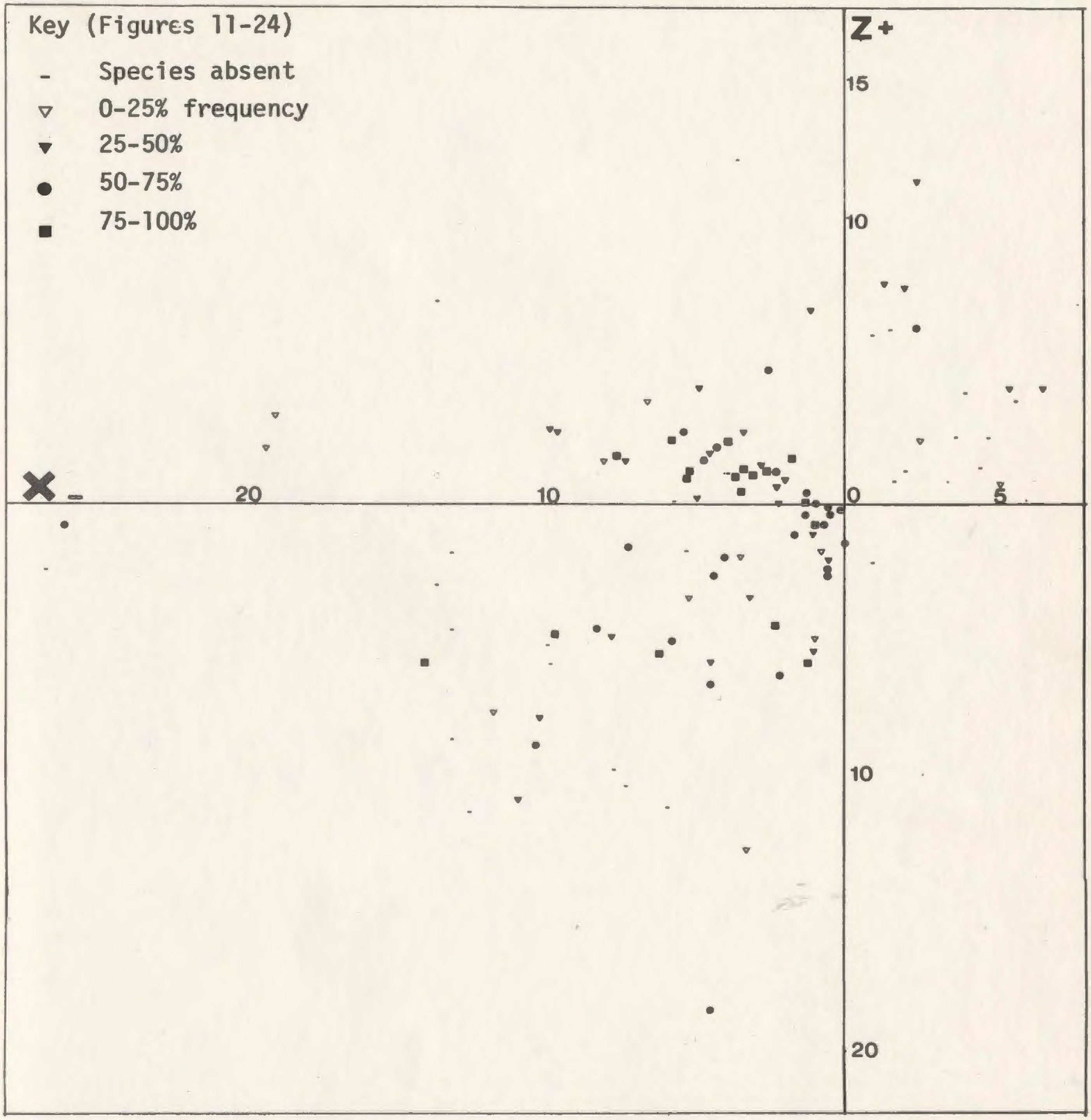


Figure 11. Distribution of Myrica gale within the XZ ordination

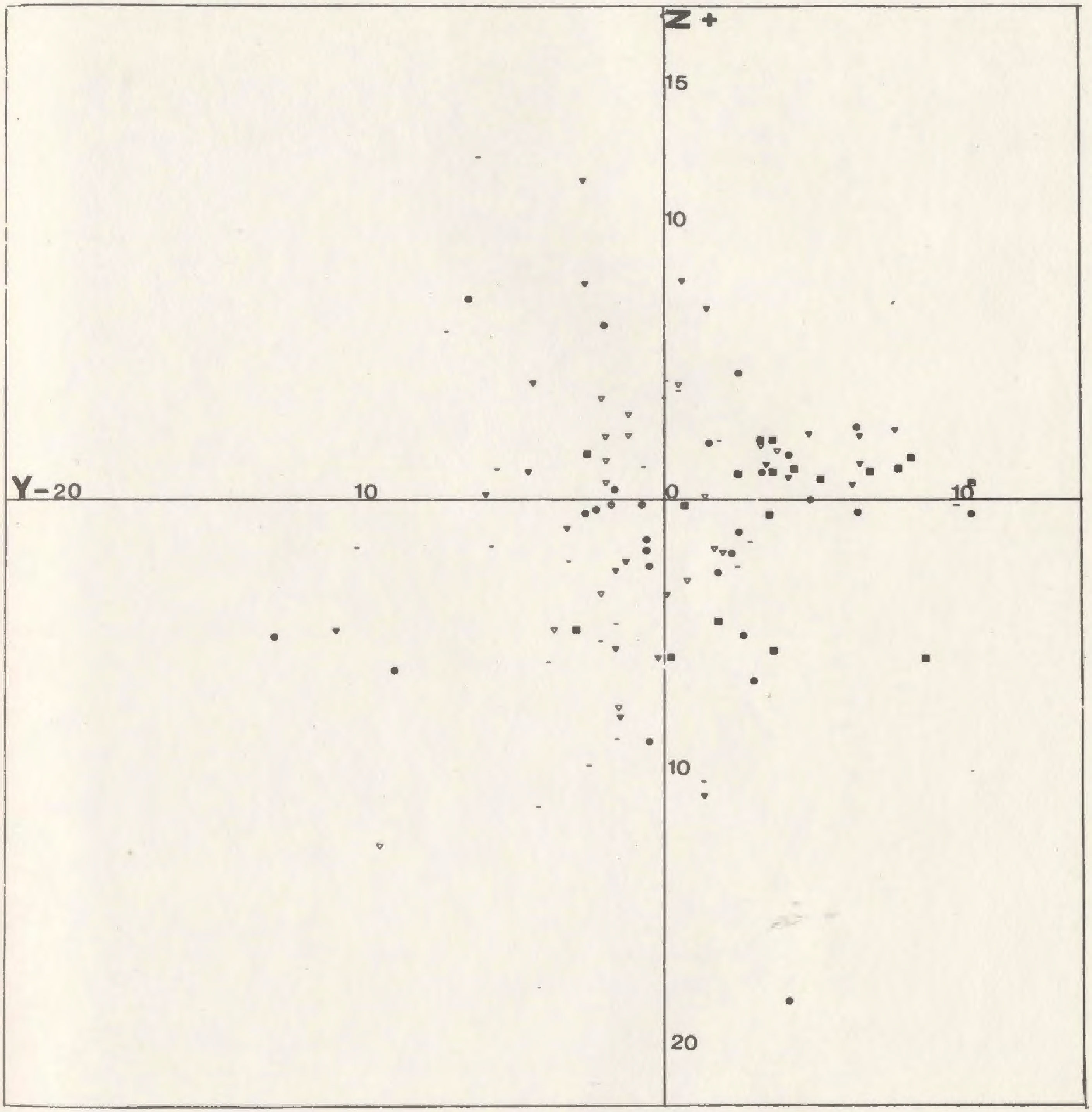


Figure 12. Distribution of Myrica gale within the YZ ordination

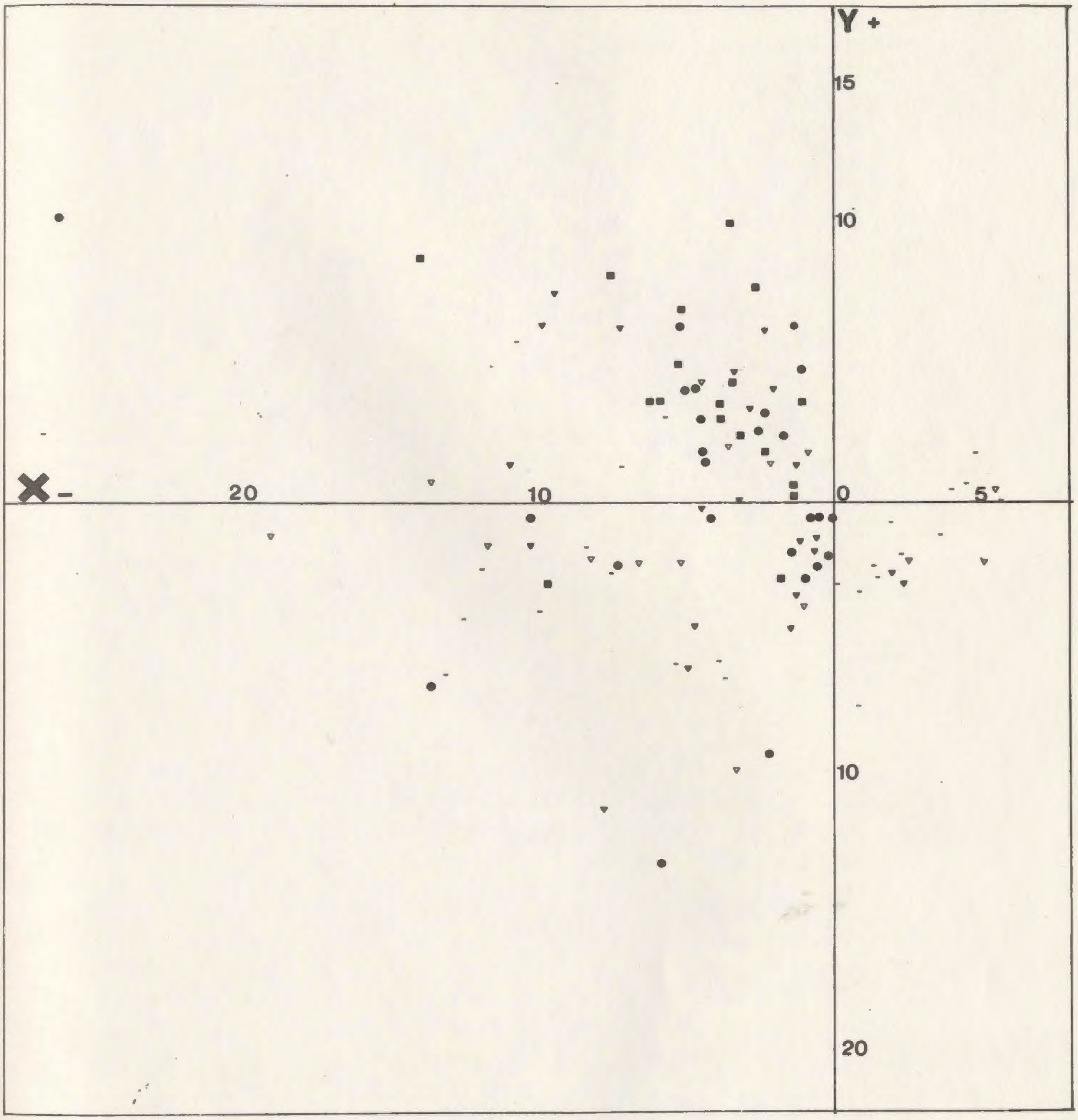


Figure 13. Distribution of Myrica gale within the XY ordination

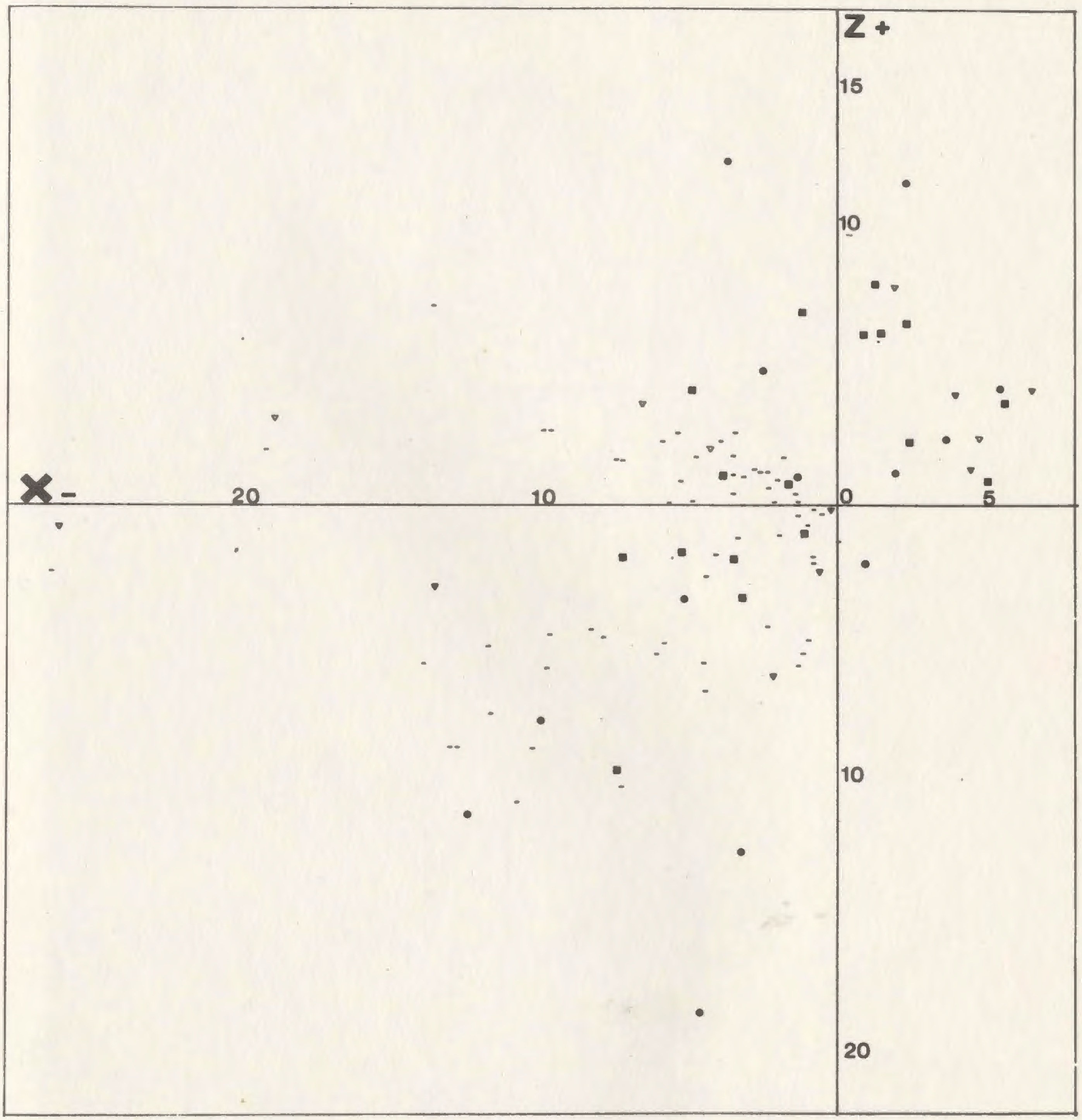


Figure 14. Distribution of Juniperus communis within the XZ ordination

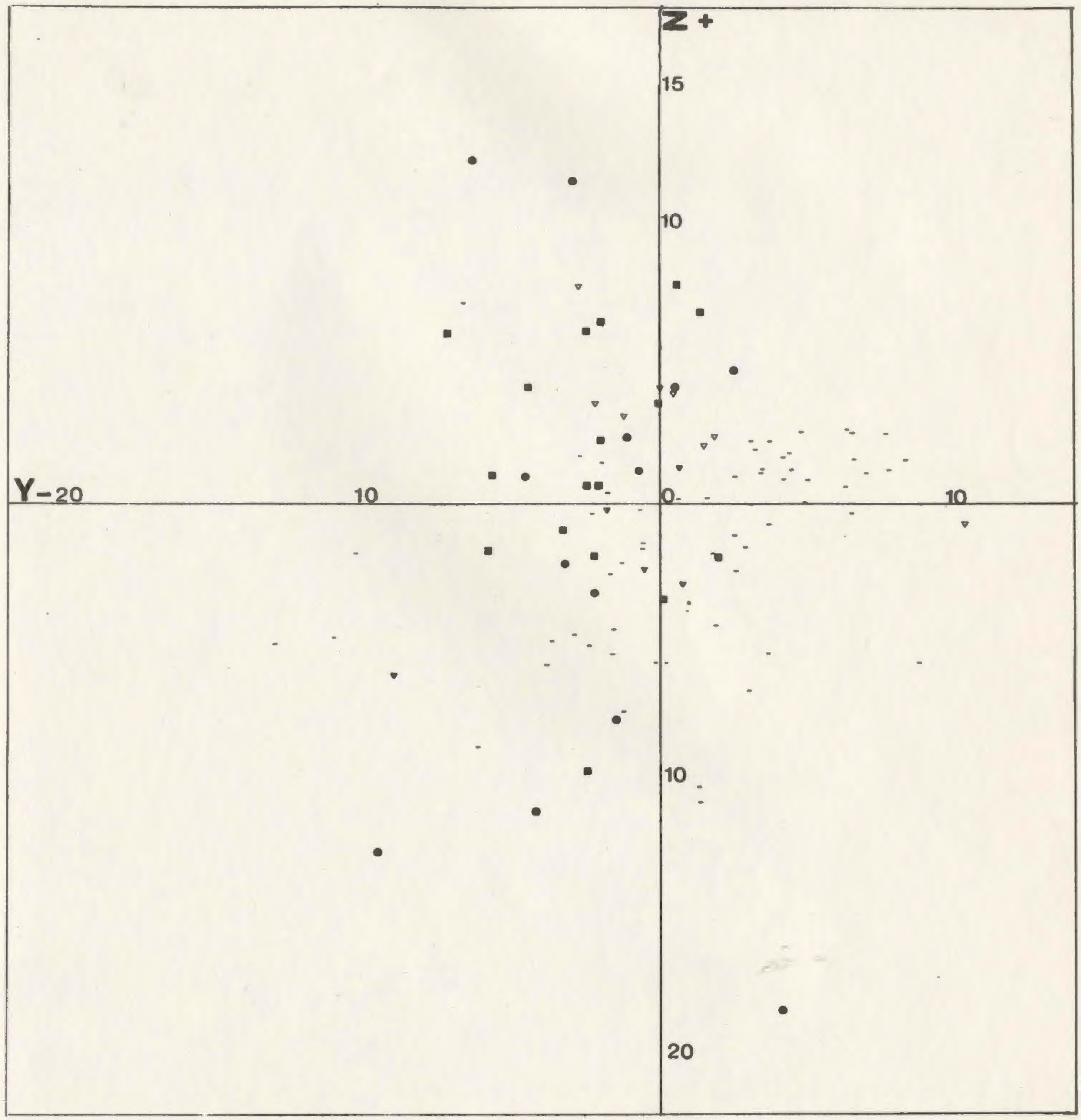


Figure 15. Distribution of <u>Juniperus</u> <u>communis</u> within the YZ ordination

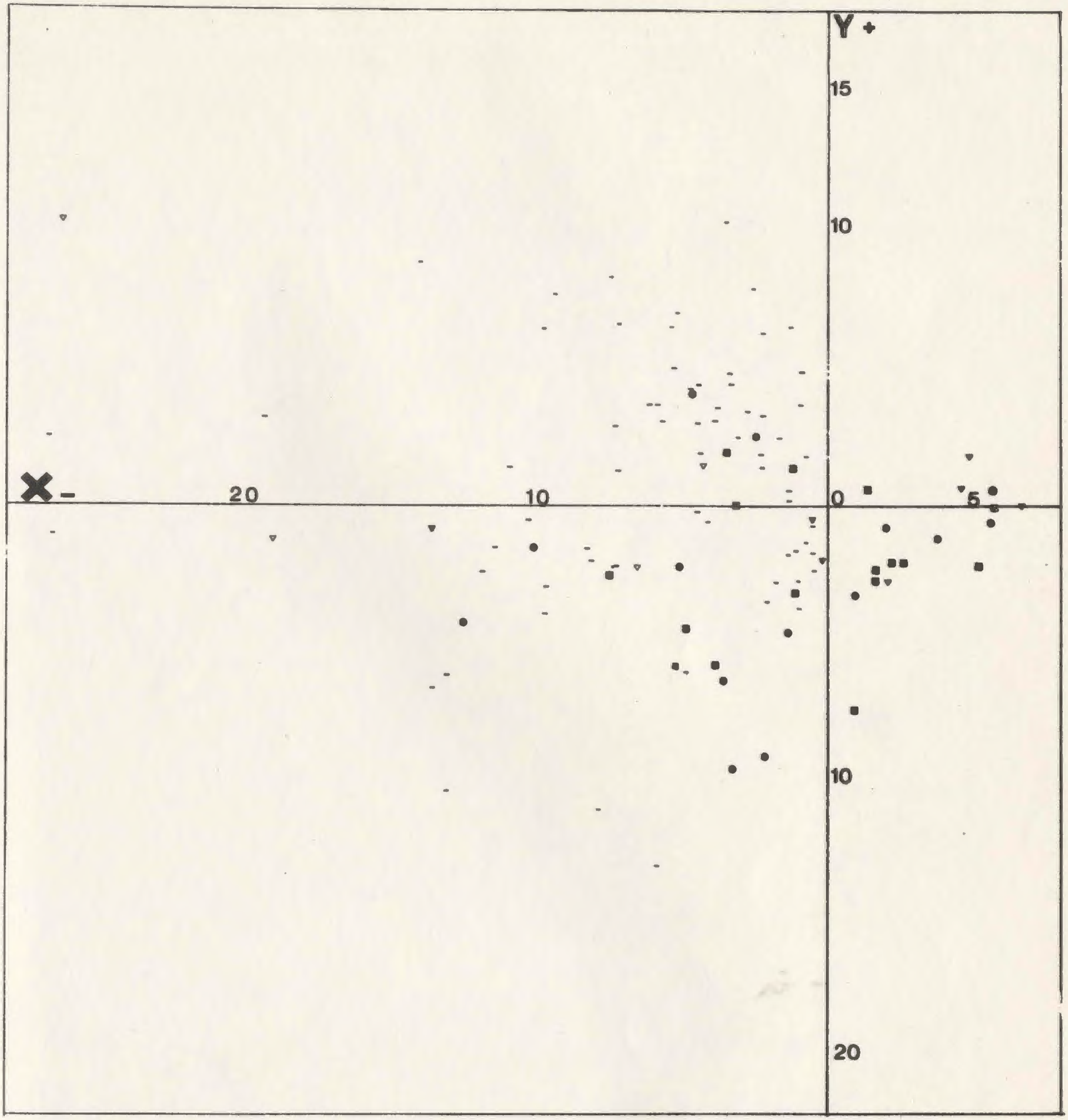


Figure 16. Distribution of Juniperus communis within the XY ordination

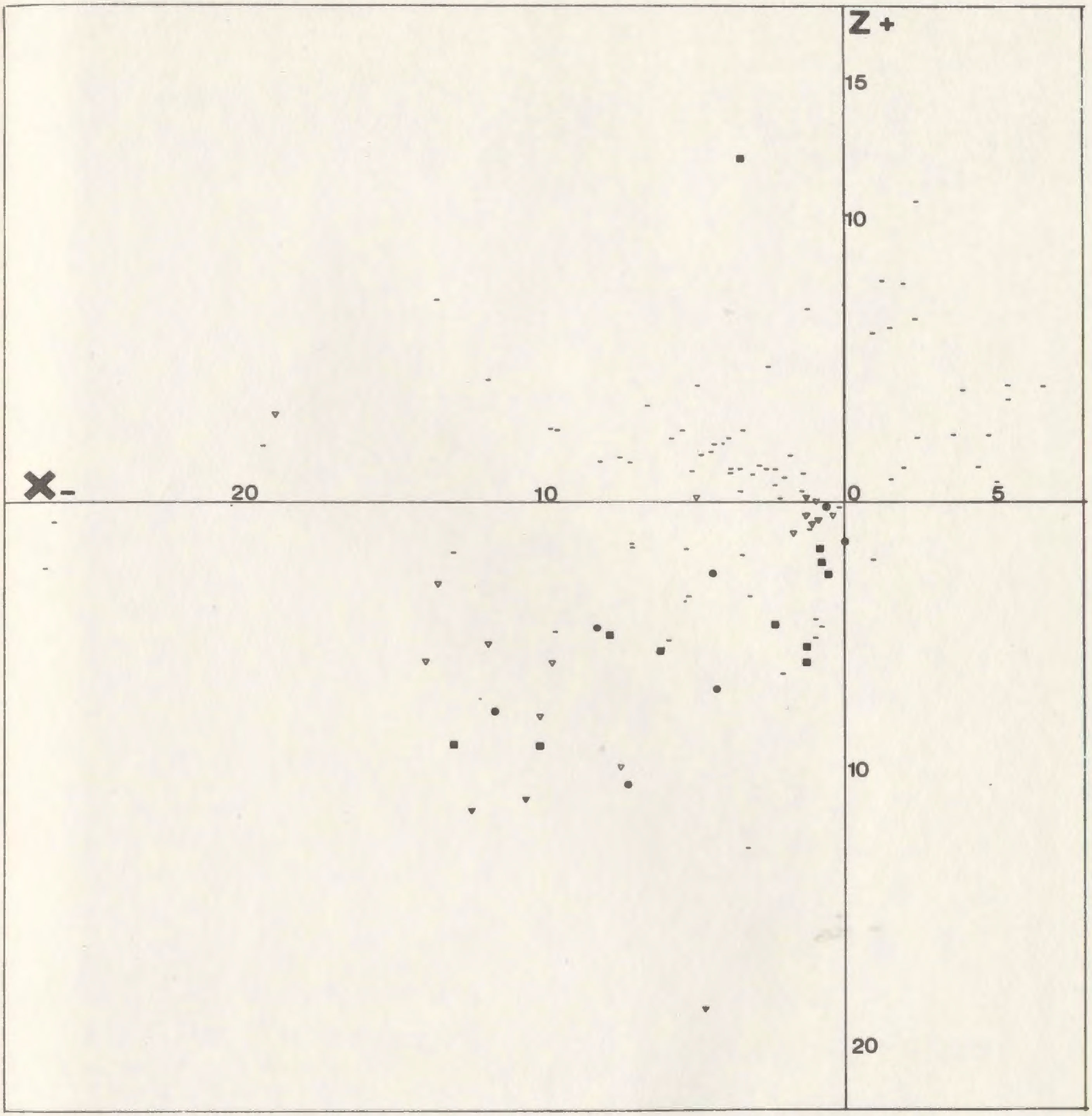


Figure 17. Distribution of Vaccinium ulinginosum var alpinum within the XZ ordination

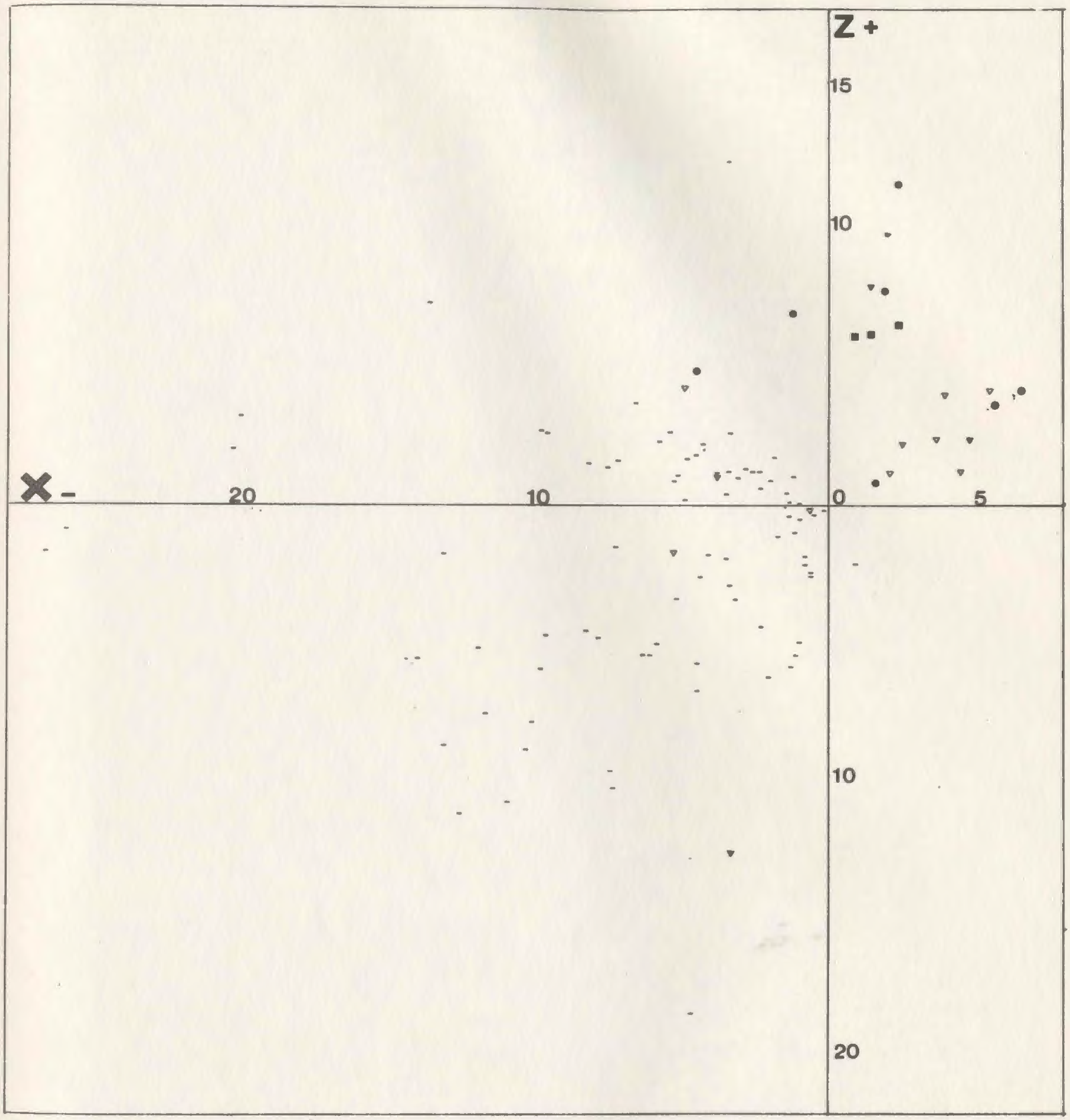


Figure 18. Distribution of Larix laricina within the XZ ordination

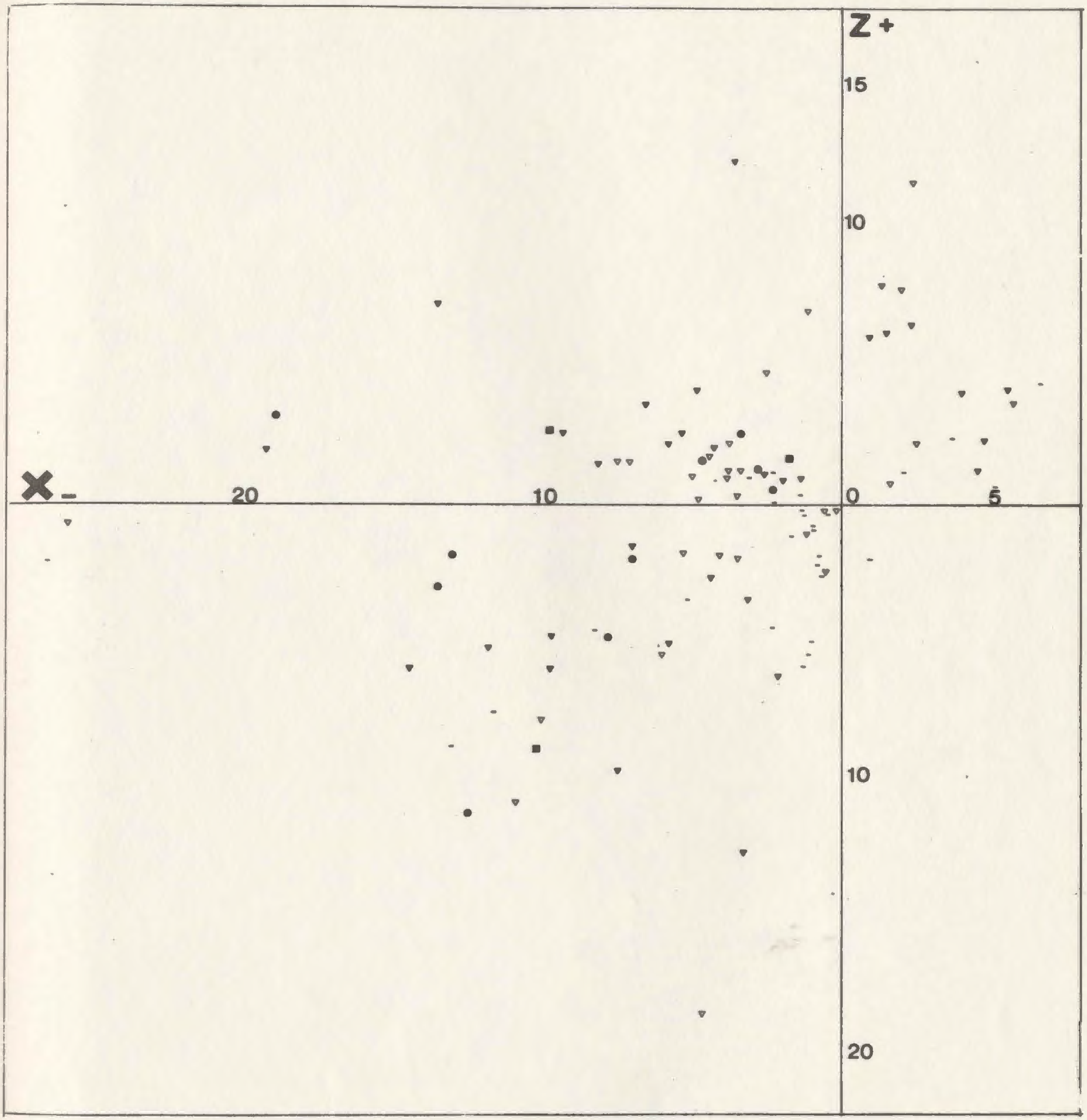


Figure 19. Distribution of Potentilla fruticosa within the XZ ordination

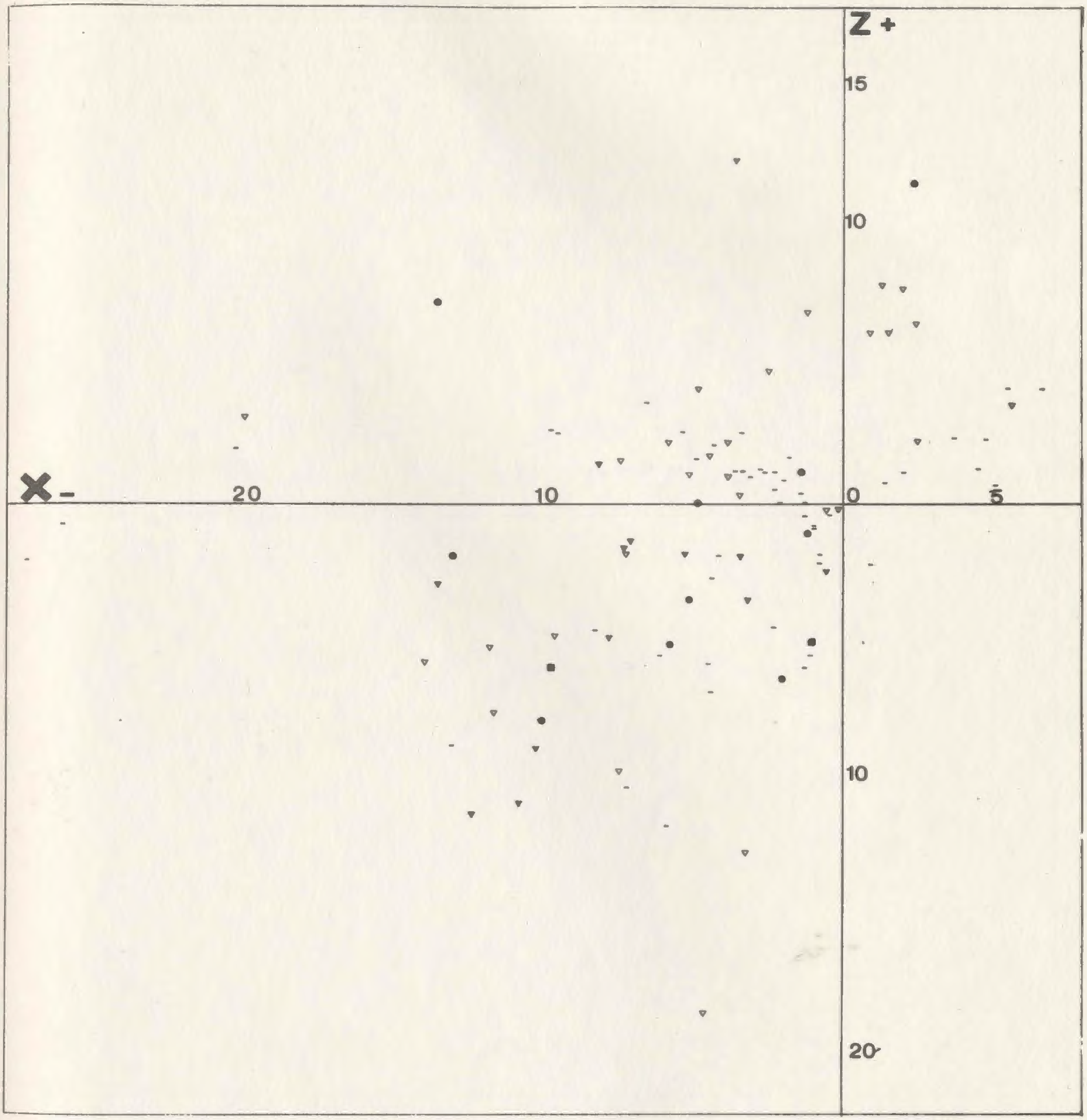


Figure 20. Distribution of Solidago multiradiata within the XZ ordination

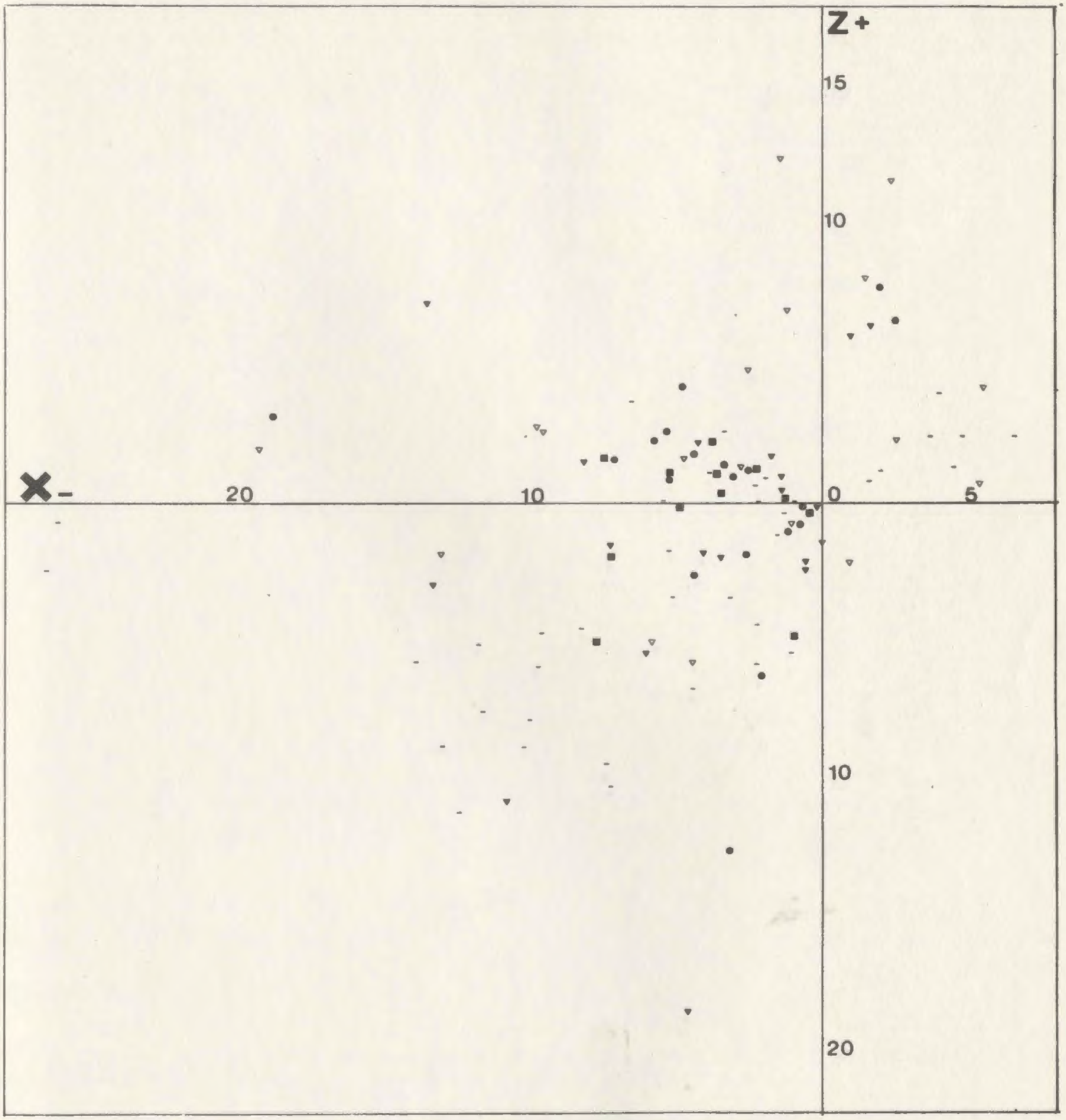


Figure 21. Distribution of Sanguisorba canadensis within the XZ ordination

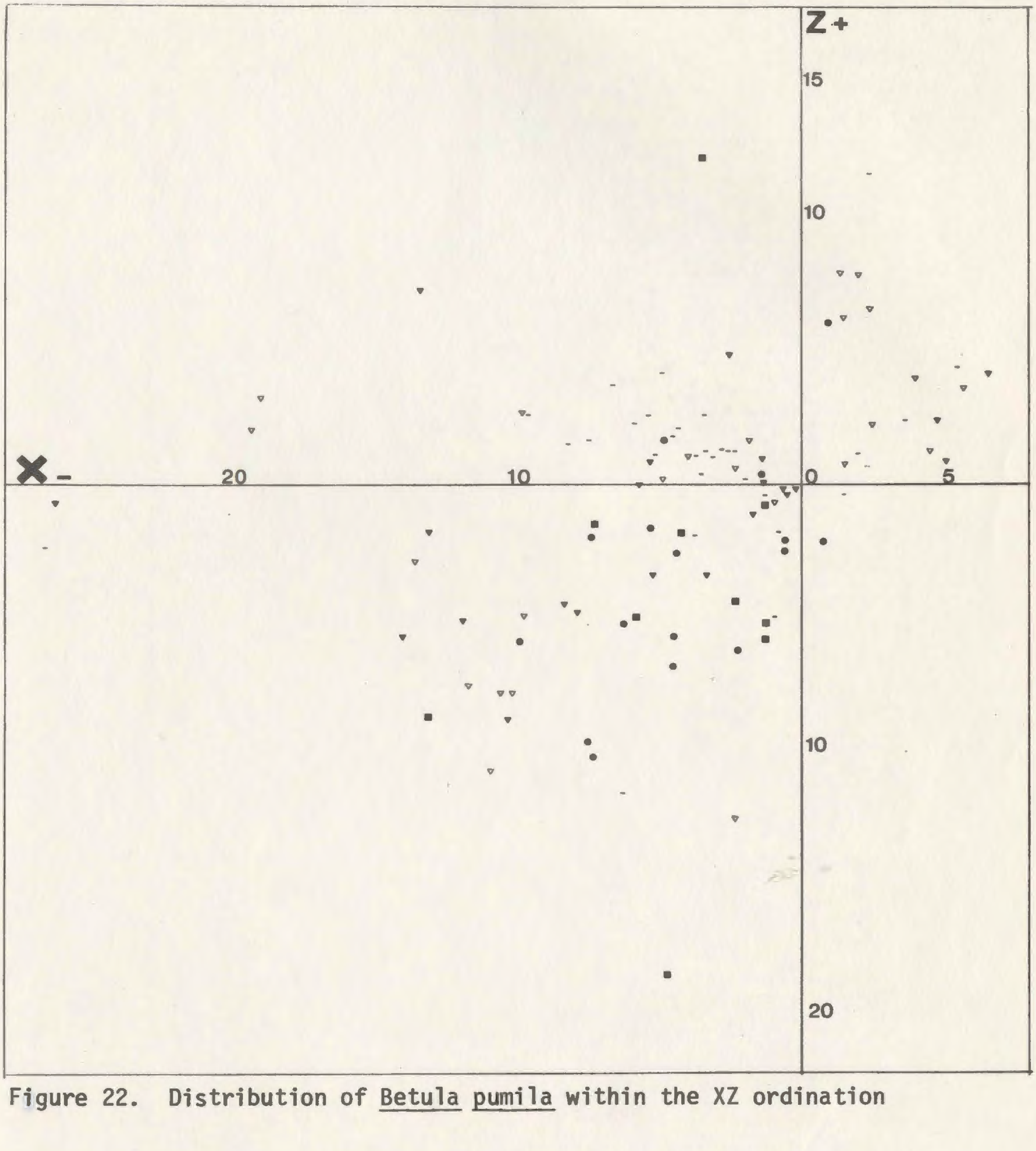


Figure 22. Distribution of Betula pumila within the XZ ordination

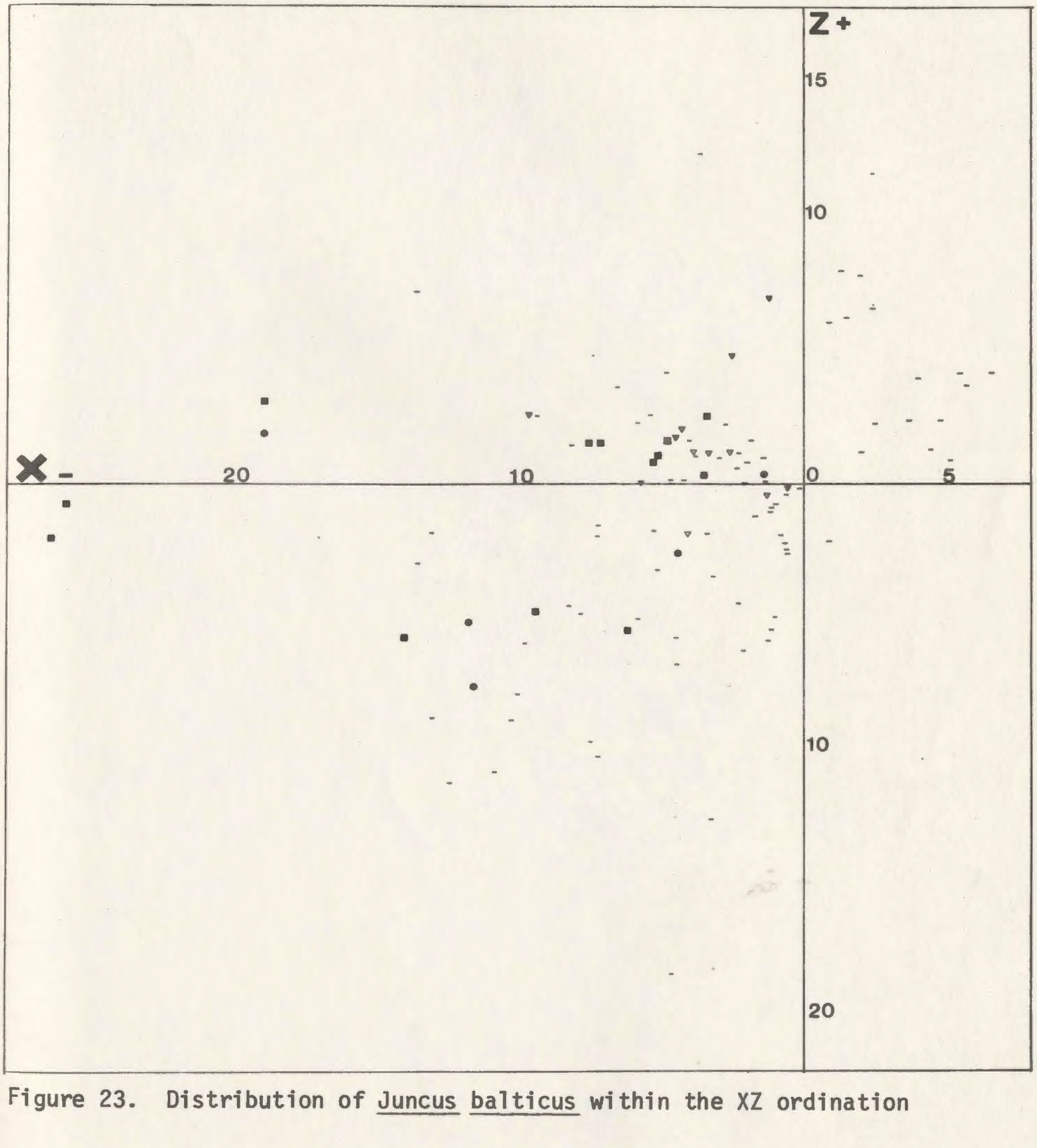


Figure 23. Distribution of Juncus balticus within the XZ ordination

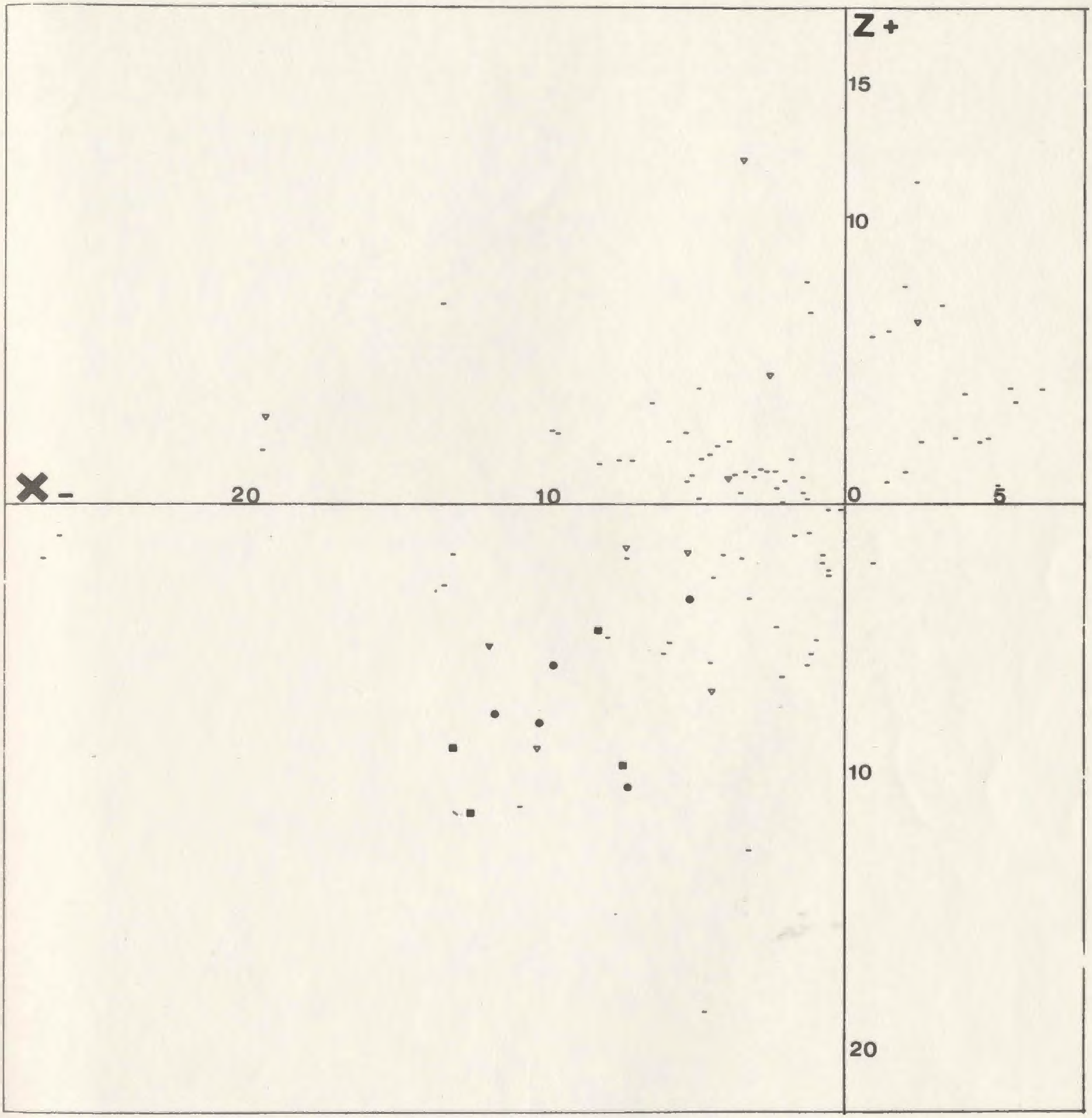


Figure 24. Distribution of the arctic-alpine species, Lychnis alpina, Silene acaulis, Cerastium arvense var villosissimum, Sagina nodusa, Arenaria humifusa, Armeria labradorica var submutica, Rhododendron lapponicum and Salix, within the XZ ordination

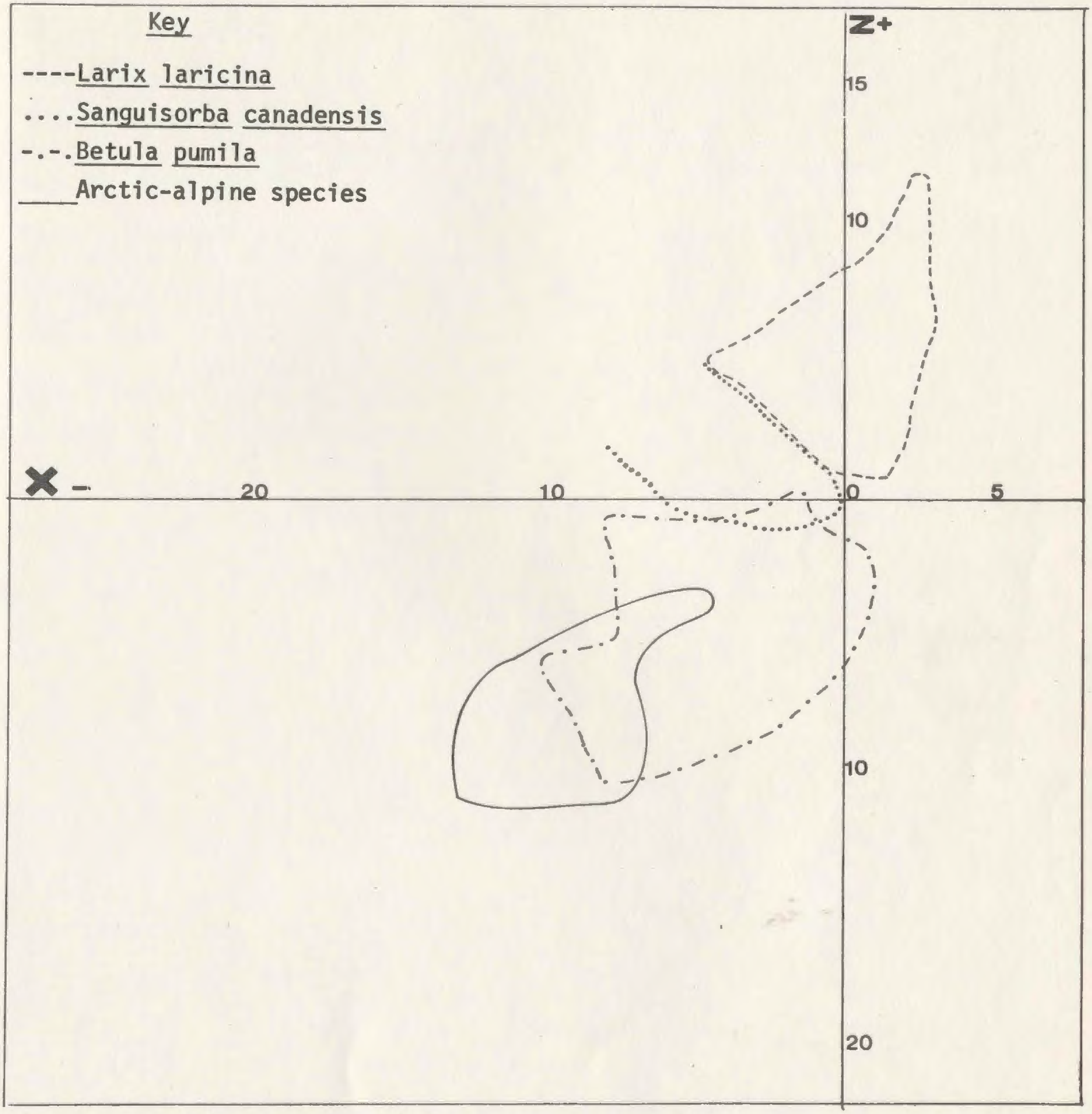


Figure 25. Distribution of Larix laricina, Betula pumila, Sanguisorba canadensis, and eight arctic alpine species at the 50% frequency level on the XZ ordination

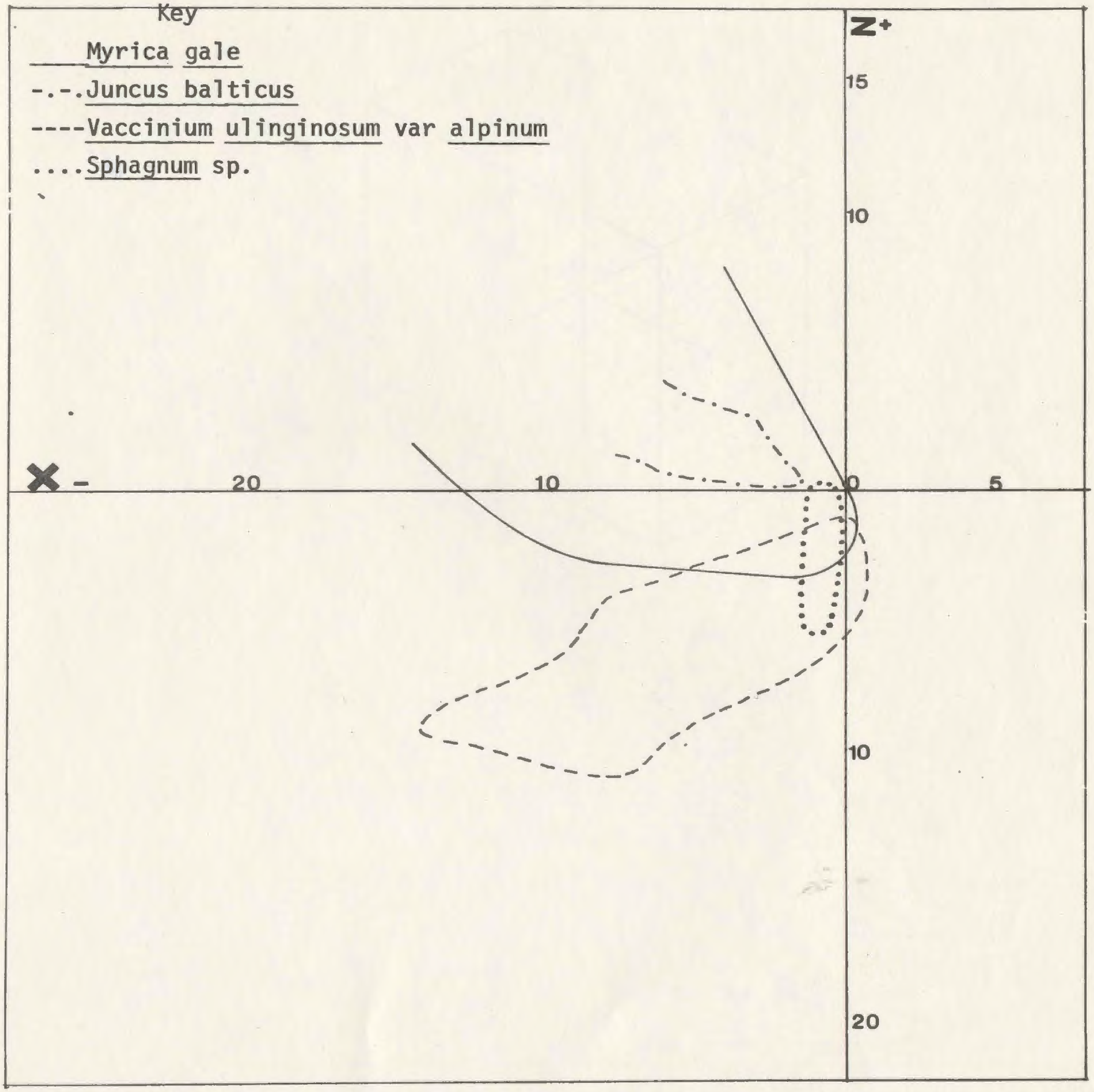


Figure 26. Distribution of Vaccinium ulinginosum var alpinum, Myrica gale, Juncus balticus and Sphagnum species at the 50% frequency level on the XZ ordination

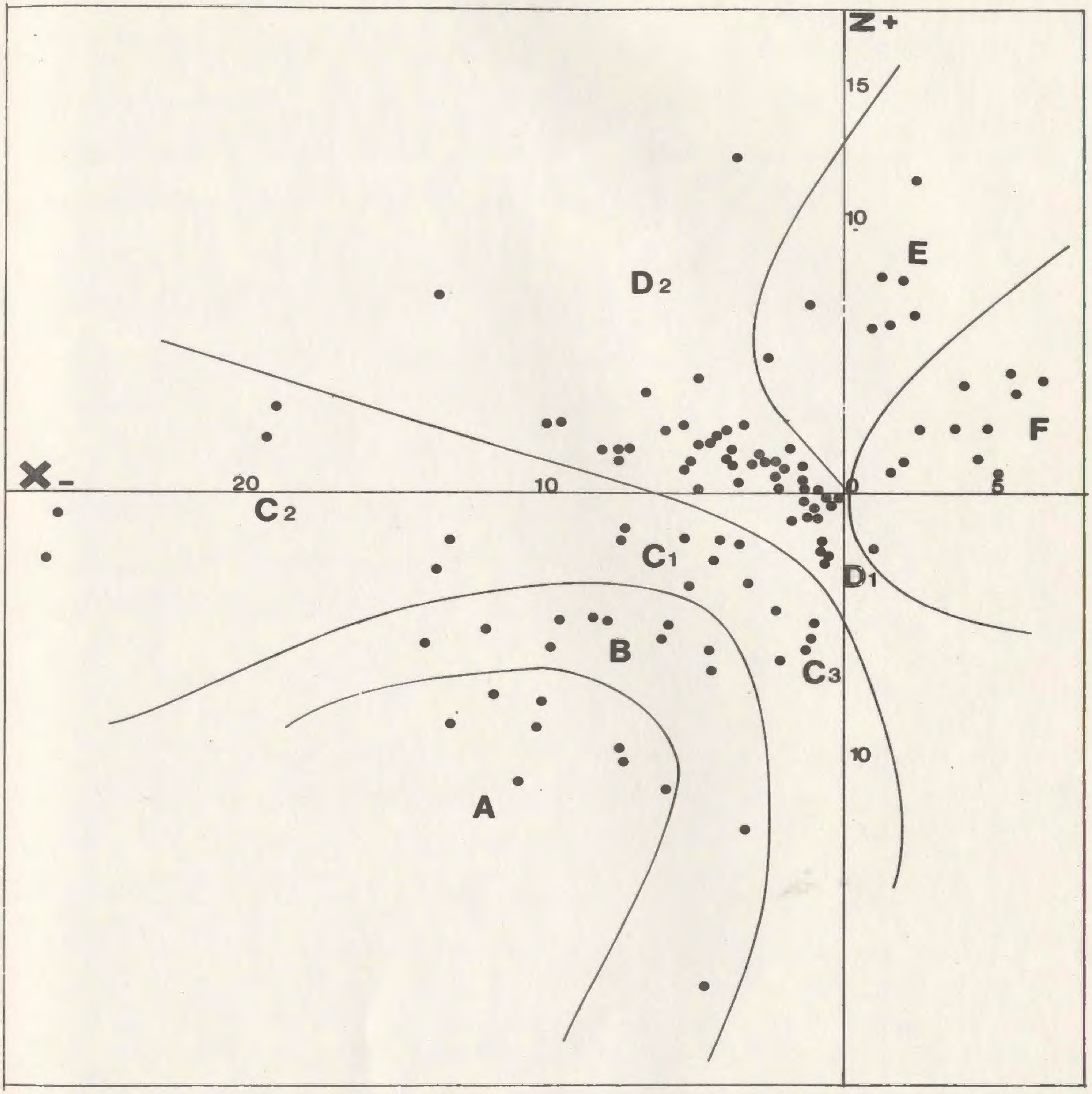


Figure 27. Delimitation of phytosociological groups A to F within the XZ ordination

arbitrary process, the slight tendency for stands to be clustered in the ordination provides the basis for establishing a classification which can be justified on practical grounds (Gittins 1965).

The positions of the community-type boundaries (Figure 27) follow the lines of least similarity between the samples, giving a certain degree of homogeneity within each boundary. This slight tendency for stand aggregation indicates that the vegetation is modified by the commoner occurrence of certain combinations of species than of others, which may be interpreted in one of two ways. It can either reflect the more frequent occurrence of certain kinds of site, or alternatively, where different sites are more or less equally represented, it may imply the stability of certain species combinations. The area boundaries are at right angles to the main lower left to upper right trend of the ordination. Within the areas (particularly Areas C and D) variation of less magnitude occurs from lower right to top left.

5.2 Edaphic Results

The aim of such an ordination is not to correlate environmental factors with phytosociological groups, for,

> "The overwhelming probability that all the measured environmental factors plus numerous non-measured factors are interacting with each other and with biotic forces, and that plants are responding to the interaction rather than to single factors indicates that attempts to pinpoint the axes too closely are doomed to failure" (Bray and Curtis 1957, p. 345).

In spite of these limitations, certain patterns and trends are suggested between phytosociological and edaphic distributions when the edaphic properties (Table 3) are plotted on the ordination (Figures 28-33).

Since the majority of species frequency distributions were plotted on the XZ axis, the edaphic quantities were plotted on the same axis so

TABLE 3

Chemical and Physical Properties of Table Mountain Soil Samples

Organic content and moisture retention capabilities are percentages. Available calcium, magnesium and total nickel are mg/gm. Group is the phytosociological grouping as defined in Chapter 5.1; nr signifies no reading.

Sample	Group	pH	Organic Content	Moisture Retention	Available Calcium	Available Magnesium	Total Nickel
27	A	6.87	3.25	2.68	0.128	3.25	0.00128
44	A	6.61	4.99	8.29	0.0948	2.66	0.00692
51	A	6.50	2.82	2.63	0.128	2.16	0.00423
31	B	6.83	3.40	4.21	0.107	2.94	0.00645
47	B	6.97	0.56	3.59	0.0685	1.66	0.00420
87	B	6.72	8.03	4.60	0.169	4.48	0.00537
91	B	6.52	0.78	1.76	0.0499	1.29	0.00249
24	C	6.74	2.14	2.59	0.160	2.90	0.00380
30	C	6.97	1.56	2.79	0.112	2.42	0.00485
41	C	6.67	4.36	4.75	0.208	3.26	0.00623
51	C	6.84	3.20	5.17	0.129	2.87	0.0126
68	C	4.66	1.71	10.83	0.0403	0.302	0.00433
76	C	5.73	12.31	6.89	0.0786	2.75	0.0113
58	D_1	4.59	38.08	11.57	0.665	5.63	0.0757
61	D_1	5.40	43.04	9.58	0.294	7.84	0.0152
80	D_1	5.27	32.03	9.06	0.678	7.05	0.0191
82	D_1	4.94	41.39	9.78	0.678	5.74	0.0104
96	D_1	5.48	49.47	11.57	0.458	8.15	0.134
3	D_2	6.58	5.98	5.11	0.177	3.73	0.00894
7	D_2	5.61	6.34	10.99	0.787	2.88	0.0460
16	D_2	6.36	4.4	3.68	0.0953	2.88	0.0125

19	D_2	6.78	6.3	4.12	0.163	3.16	0.0055
20	D_2	6.52	17.52	7.85	0.470	7.41	0.0020
33	D_2	6.10	10.68	9.11	0.214	4.99	0.0144
23	E	6.43	7.7	3.89	0.0287	2.77	0.00411
90	E	7.18	5.96	4.12	0.0872	2.71	0.0356
94	E	6.23	4.15	4.82	0.0409	3.79	0.00698
101	E	5.31	3.17	2.87	0.100	2.31	0.0139
8	F	6.70	3.11	2.91	0.768	1.90	0.00216
9	F	7.94	3.71	1.87	1.15	0.247	0.000748
10	F	7.83	7.17	3.03	1.83	0.696	nr
12	F	8.06	2.99	1.95	1.09	0.290	nr

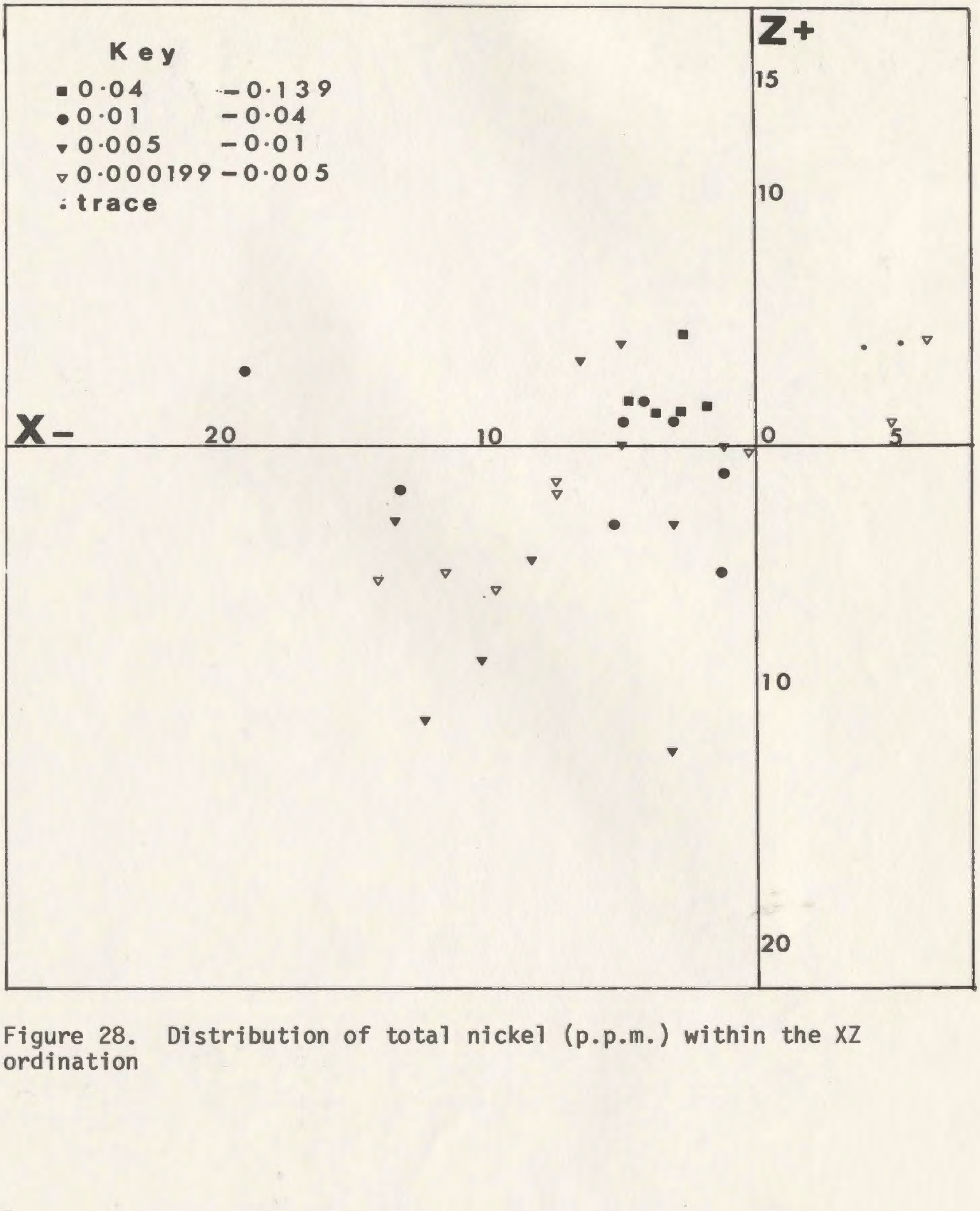


Figure 28. Distribution of total nickel (p.p.m.) within the XZ ordination

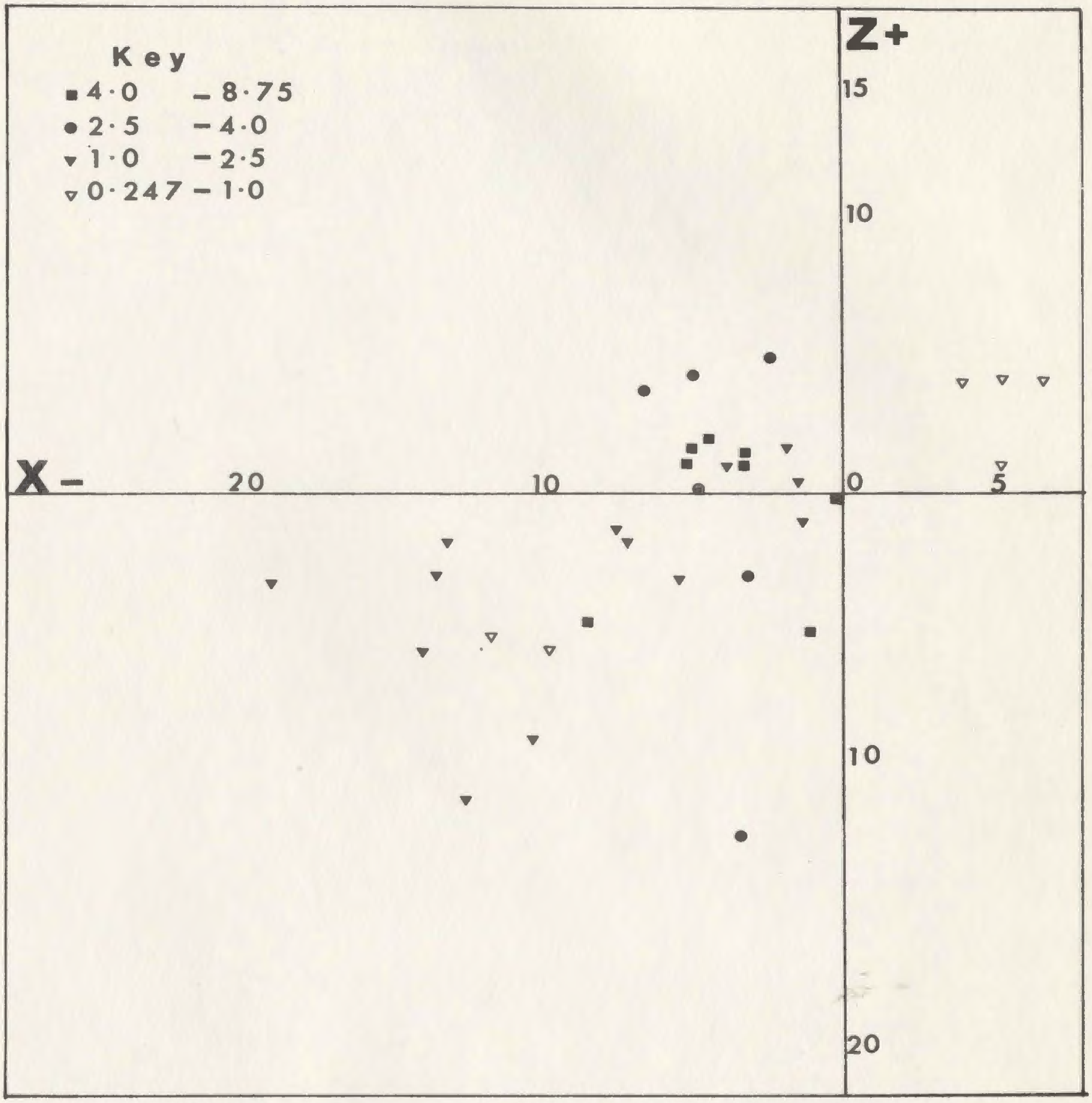


Figure 29. Distribution of available magnesium (p.p.m.) within the XZ ordination

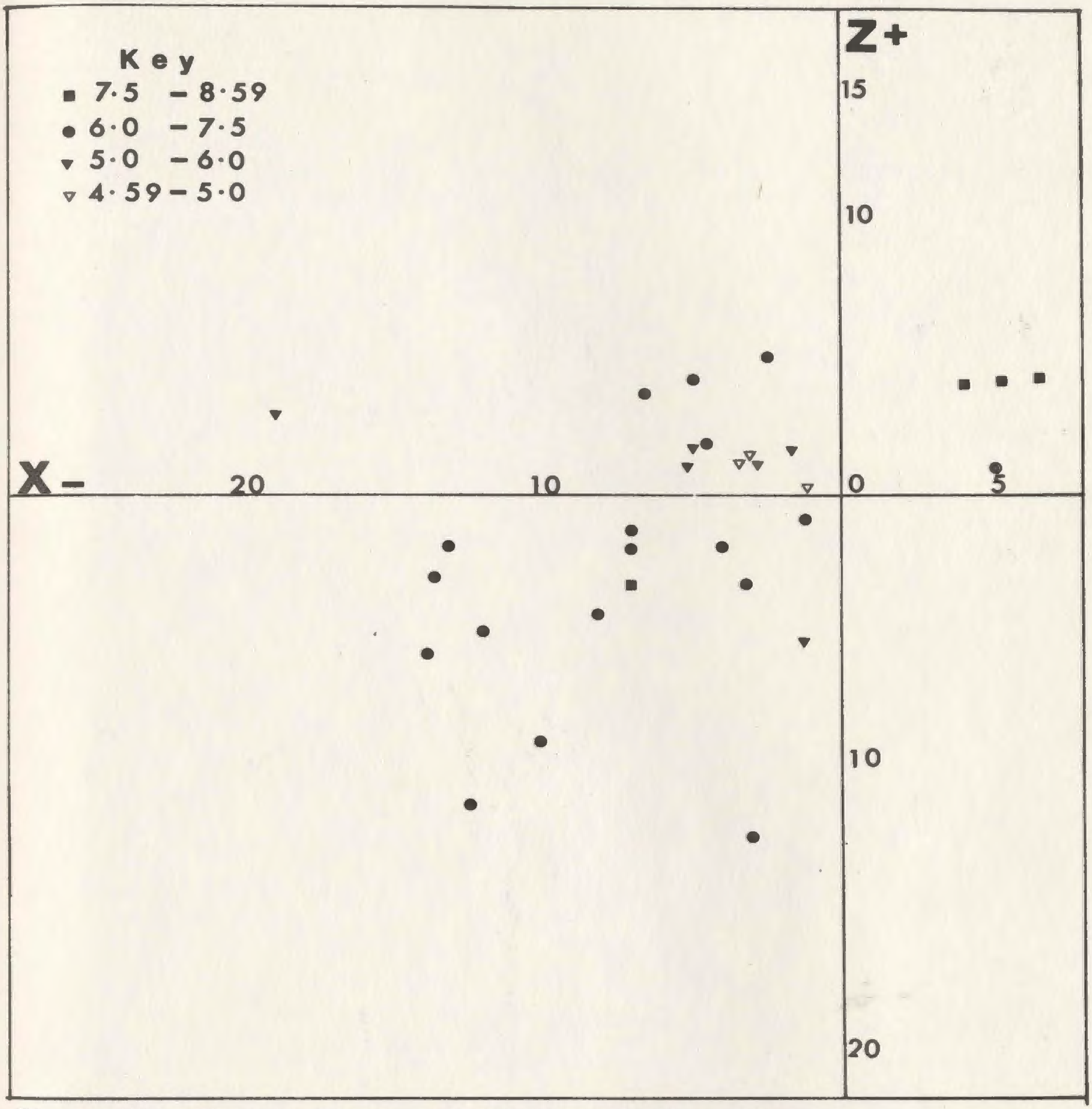


Figure 30. Distribution of pH within the XZ ordination

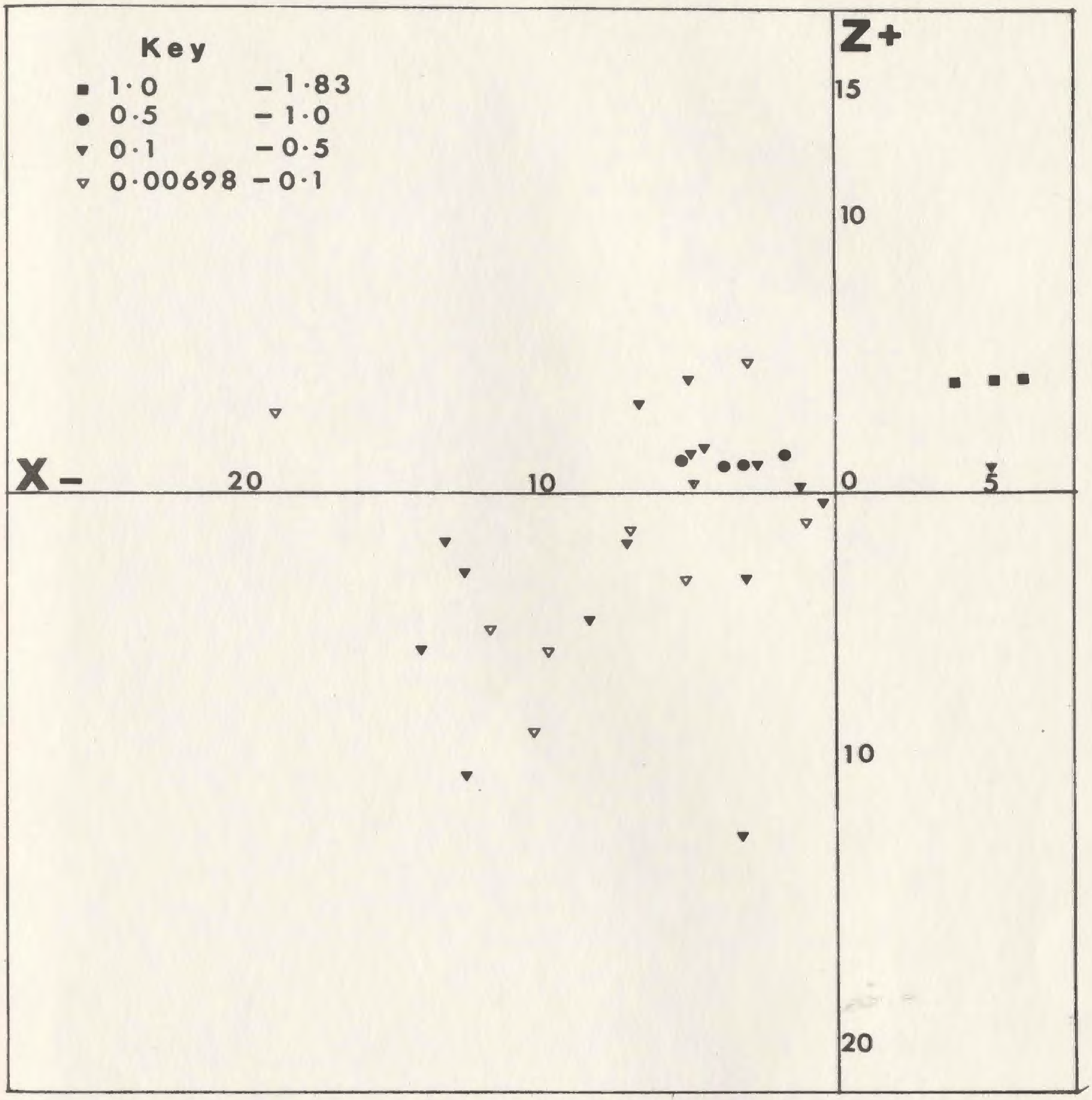


Figure 31. Distribution of available calcium (p.p.m.) within the XZ ordination

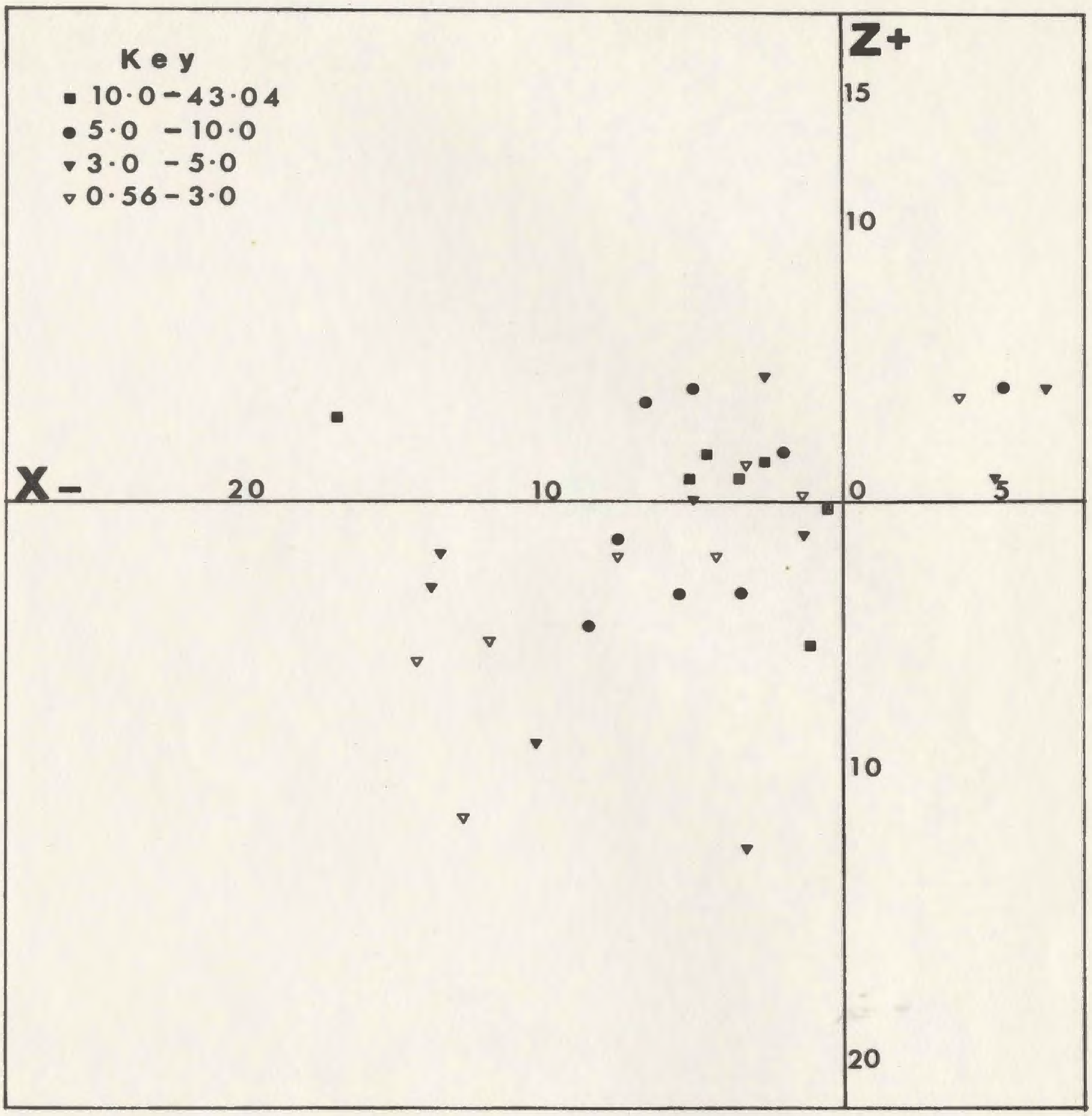


Figure 32. Distribution of organic content (%) within the XZ ordination

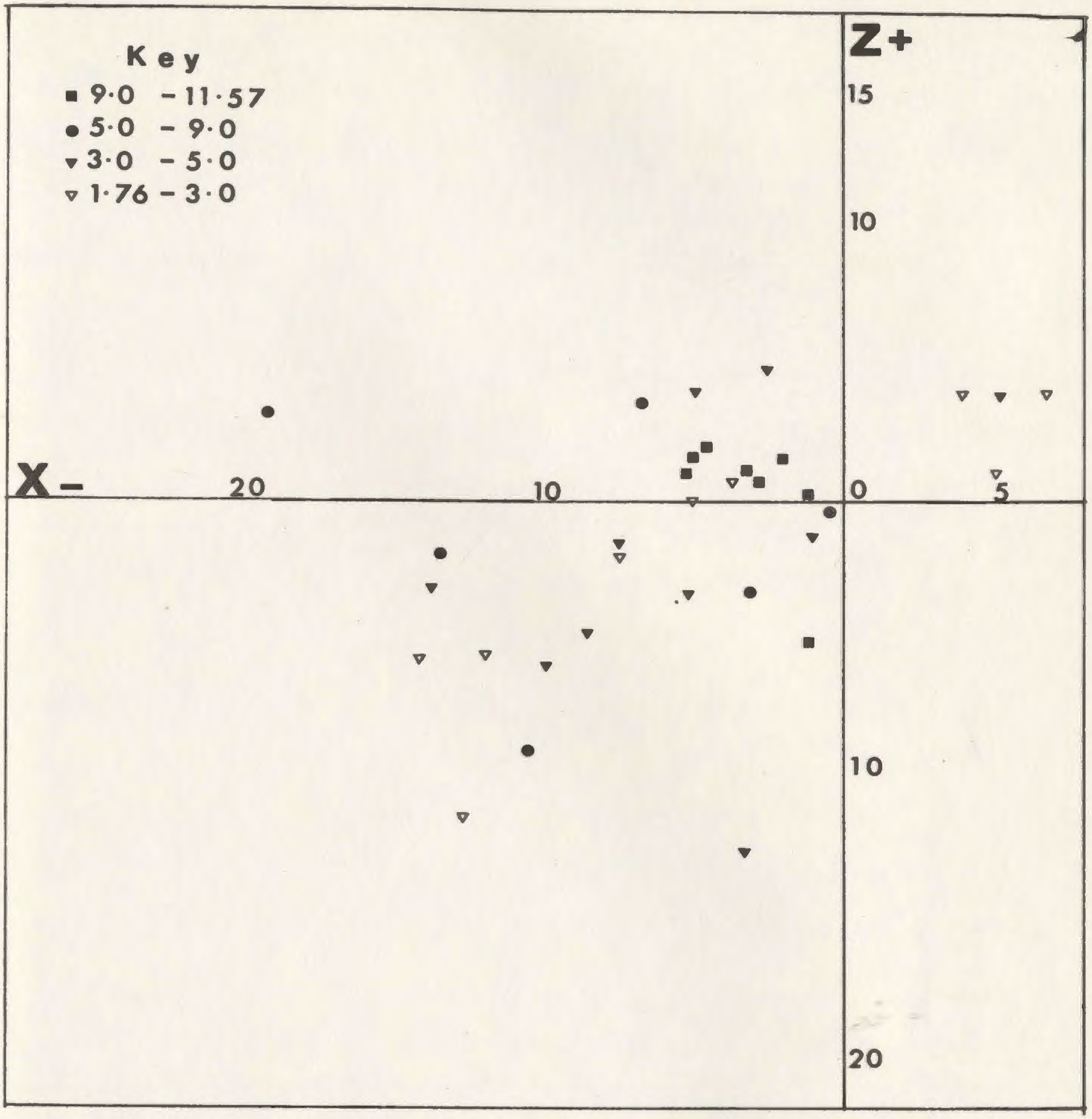


Figure 33. Distribution of water retention capability (%) within the XZ ordination

that relationships may be more apparent. Some factors, such as nickel (Figure 28) and available magnesium (Figure 29) show quite marked clustering in certain locations with steadily decreasing values toward the periphery, whereas others, such as pH (Figure 30) are not quite so localized. It is unwise to claim any causal link between soil chemistry and species distributions as shown in the graphs, which are presented merely to suggest relationships, and aid in the later interpretation of spatial variation and distribution of plant communities.

A more meaningful procedure is the calculation of correlation coefficients between phytosociological and edaphic properties and subsequently testing for significance with a 't' test. (Bray and Curtis 1957, p. 343). A probability value of .01 is a basis for rejecting a null hypothesis and is considered a highly significant correlation. A value of .05 is considered a significant correlation, while values of .05 are considered to represent no significant correlation (see Table 4).

The Y axis has significant correlations with three factors, pH, percent organic material and moisture that have no significance to the X and Z axes, but the latter two are significantly correlated to the amount of available calcium, the X axis highly so. The existence of such a highly significant relationship between the first and major axis of compositional variation and the amount of calcium available is very interesting (c.f. Chapter 2.0) and will be discussed in much greater detail later. Justification for a three rather than two axis ordination is provided by the correlation of the Y axis with soil properties not significant with X or Z values, and by the clearer phytosociological ordination obtained on the XZ compared to the XY axis. Thus no axis duplicates information which is apparent on another.

TABLE 4

Edaphic Correlations with Three Ordination Axes. Values in Table are the Probability that there is no Correlation.

	Edaphic Property					
	pH	% Organic Matter	Moisture Retention	Available Calcium	Available Magnesium	Total Nickel
X	0.10*	0.75*	0.45*	0.005***	0.25*	0.70*
Y	0.010***	0.010***	0.025**	0.1*	0.1*	0.70*
Z	0.30*	0.1*	0.30*	0.025**	0.50*	0.55*

*** highly significant correlation

** significant correlation

* no significant correlation

The correlations can be usefully envisaged within a three-dimensional hyperspace (Figure 9). For example the gradient of maximum variation of pH, percentage organic matter and moisture can be thought of as being vertical, whereas available calcium variation would be better represented in the horizontal plane. In this way it is possible to obtain some idea of the degree of continual change and interaction between the various species distributions and soil properties.

There is, of course, a possibility that the major environmental factor, or factors, influencing species distributions has not been included in the analysis. It is impossible to include all possible parameters in a precise and quantitative form in this way. More intangible combinations of factors affecting the total plant habitats, such as topography and micro-climatology may be of great importance. The combination of total environmental factors in relationship to plant community composition and distribution is discussed in detail in the next chapter.

CHAPTER 6

DISCUSSION: THE COMPOSITION AND DISTRIBUTION OF PLANT COMMUNITIES ON TABLE MOUNTAIN

The subdivisions of the hyperspace produced in the ordination (Figure 27), provide the structural framework by which the abstract sample distributions can be related to reality and specific physiographic situations on Table Mountain. This section examines each subdivision of the ordination in turn describing its floristic composition and physiographic situation and location. A species list of plants found in each area is given and also detailed chemical and physical pedological information.

It is essential to remember that these areas are only divisions of the total environmental reality of Table Mountain, and thus considerable emphasis is given to the relationships of these areas to each other both phytosociologically and physiographically. Indeed each area may be characterized by several different floristic components, but these groups show greater similarity to each other than to other areas. In addition certain recurring geomorphological features may be colonized by different species depending upon their physiographic location. All such similarities and differences are discussed at length in the following Chapter.

6.1 Type A: Pioneer (mainly arctic-alpine) communities found in the most exposed locations.

This subdivision represents 'pioneer' communities on the exposed parts of Table Mountain. The sites are xeric, with a discontinuous, stunted vegetation cover. Dominant species are various arctic-alpine species and the bryophyte Rhacomitrium lanuginosum (See Table 5).

Lichens and bryophytes are the most common colonizers of unvegetated surfaces and instigators of soil development. However they

TABLE 5

Species list of Quadrats in Type A Communities

*Species found in association with sample quadrats, but not included in the ordination.

Trees

Betula pumila
Salix sp.

Shrubs

Andromeda glaucophylla
Juniperus communis
Ledum groenlandicum
Myrica gale
Potentilla fruticosa
Rhododendron lapponicum
Vaccinium ulinginosum var *alpinum*

Herbs

Androsace septenrionalis
Arenaria humifusa
**A. marcescens*
**A. rubella*
Armeria labradorica var *submutica*
Campanula rotundifolia
Cerastium arvense var *villosissimum*
**C. beeringianum*
**C. terrae-novae*
Conioselinum pumilum
Diapensia lapponica
Drosera intermedia
**Linum catharticum*
Lychnis alpina var Americana
Potentilla tridentata
Sagina nodusa
Sanguisorba canadensis
Saxifraga aizoides
S. oppositifolia
Senecio pauciflorus
S. pauperculus
Silene acaulis
Solidago multiradiata

Ferns

**Adiantum pedatum* var *aleuticum*

Grasses, sedges and rushes

Carex echinata
C. scirpoides
Deschampsia atropurpurea
D. flexuosa
Festuca rubra
F. scabrella
Juncus balticus
J. trifidus
Scirpus cespitosus

Mosses

Lycopodium annotinum
Rhacomitrium lanuginosum

are particularly scarce on Table Mountain because of the unfavourable chemical properties of the serpentine. This is illustrated in figure 34 where lichen colonization of the granite glacial erratic contrasts sharply to the bare surfaces of the adjacent serpentine boulders. Richards (1932) notes this sensitivity, "...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" (p. 369).

Lichens and bryophytes are not totally absent, indeed *Rhacomitrium lanuginosum* is one of the commonest species to be found on the serpentine, but their general absence does little to rectify the poor soil development. The soil is typically immature, a lithosol, and the distinction between soil and parent material is of necessity a little arbitrary. The lithosol is frequently patterned either in stone polygons or stripes (see Chapter 3.21). A typical soil profile of a gently sloping fine debris site is shown in figure 35. This profile is from an area of stone stripes on a 10^{o} slope, the very dry top layer being unconsolidated pieces of serpentine about 1 to 2 cms in diameter. With increasing depth the ochreous colour of the surficial layer changes to the grey unweathered stones below. At a depth of about 30 cms a brown, moist and fairly coarse clay appears and extends for a considerable depth (50 cms) before meeting the bedrock. Roots were found in this clay layer which were traced to a *Potentilla fruticosa* shrub rooted in the coarse debris of the stone stripe over a metre away.

P. fruticosa is perhaps the most widespread of the primary colonizers, being found from exposed rock crevices to the unstable fines in the polygon centres. The possession of such a highly developed root

Figure 34. Lichen colonization of granitic glacial eratic (centre), in contrast to the surrounding uncolonized serpentine blocks.

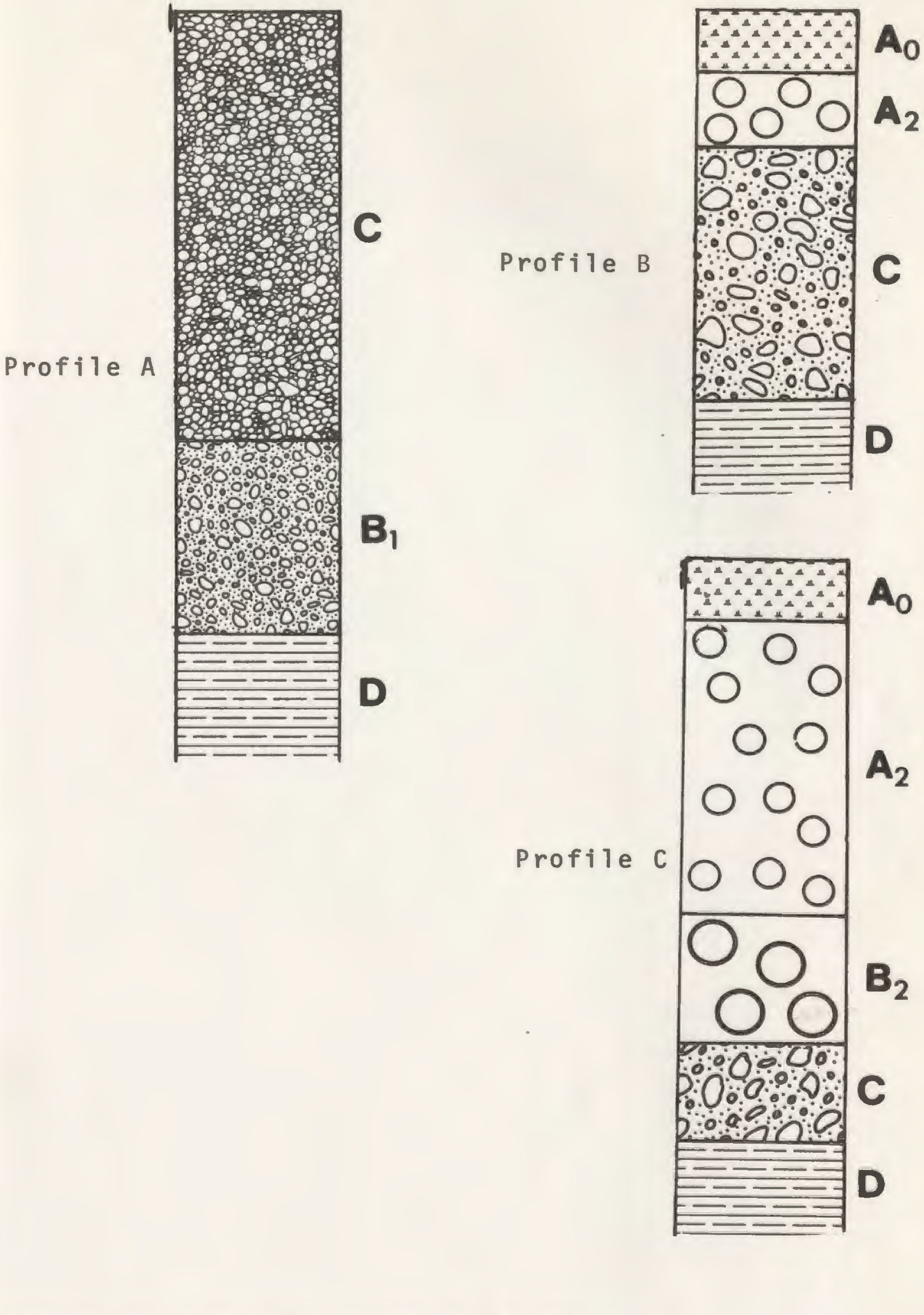


Figure 35. Soil profiles A, B and C

system must be a major factor, along with its ability to withstand xeric conditions, in the colonization of these habitats. Similar adaptations and tolerance levels aid other species to colonize these areas. In many arid communities of the temperate zone a discontinuous ground cover is evidence that the water supply is critical, not permitting a closed vegetation cover. 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 (Shacklette 1962).

The smaller crevices are often the result of the differential weathering rates of serpentine and peridotite, covering the thin serpentine layer to erode into a small fissure which may subsequently be colonized by chance by one of a number of species. Figure 36 illustrates colonization of such a fissure by Alnus crispa but other species like Arenaria humifusa and Cerastium terrae-novae are equally common. More sheltered and moist cracks are frequently colonized by the serpentinicolous fern Adiantum pedatum var aleuticum.

On patterned ground, vegetation is very much related to the local differences caused by the respective periglacial phenomenon. The frost action makes the substrate unstable. This instability is not restricted to slopes, although it is more intense there, for level soil surfaces may also be very unstable. When the soil is frozen most chemical and physical processes are immobilized, but on thawing the soil particles creep downslope. 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 downslope. The unstable nature of the

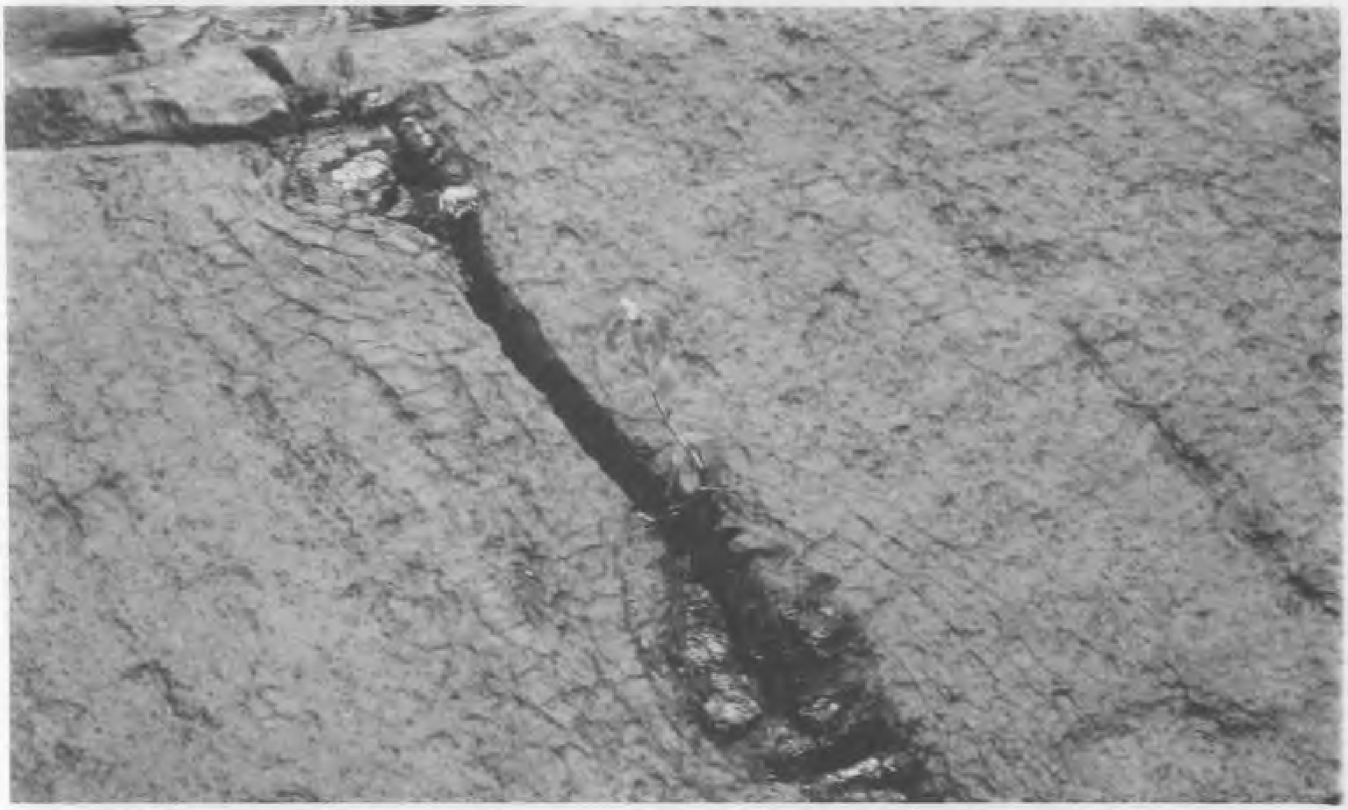


Figure 36. Alnus crispa colonizing a serpentine fissure in a peridotite boulder

substrate and its effect on vegetation is seen in figure 37 , where a plant, Juniperus communis has been almost totally covered by a mudflow.

Such instability has great implications in the development of a vegetation cover, for concepts of physiographic ecology are largely based on ideas of soil stability, and that because of this stability the vegetation has had time to develop. In this way the vegetation of Table Mountain, and in particular these Type A pioneer communities, has much in common with that of the tundra areas further north. The observation of Sigafoos (1952) for tundra regions is applicable to Table Mountain.

> "The ultimate limit of vegetation development is controlled in the final analysis by the length of time during which the environmental factors do not fluctuate beyond the limits of the ecological amplitude of the species. In tundra regions environmental factors frequently and periodically fluctuate beyond the limits of the ecological amplitude of the species. Frost action on soil (congeliturbation) because its intensity fluctuates widely and frequently, is the most important factor in the development of tundra plant communities" (p. 480).

Within the patterned ground areas there are several micro-habitats. The coarser boulders forming the boundaries of the polygons and stripes (A 1, Figure 38) are somewhat more stable than the fines. Surface water concentrates here resulting in a more moist habitat and hence a more continuous vegetation cover. The initial colonizer is typically Rhacomitrium lanuginosum which in turn is colonized by such species as Campanula rotundifolia, Rhododendron lapponicum, Lychnis alpina, Saxifraga oppositifolia, Cerastium terrae-novae, C. beeringianum, Sagina nodusa, Arenaria humifusa, A. marcescens and various Salix species. The wetter areas may be colonized by Sarracenia purpurea and Juncus trifidus.

The central, fine areas of the polygons (A 2, Figure 38) are colonized by species with a cushion growth form and long tap roots

Figure 37. Juniperus communis almost totally buried by a mudflow

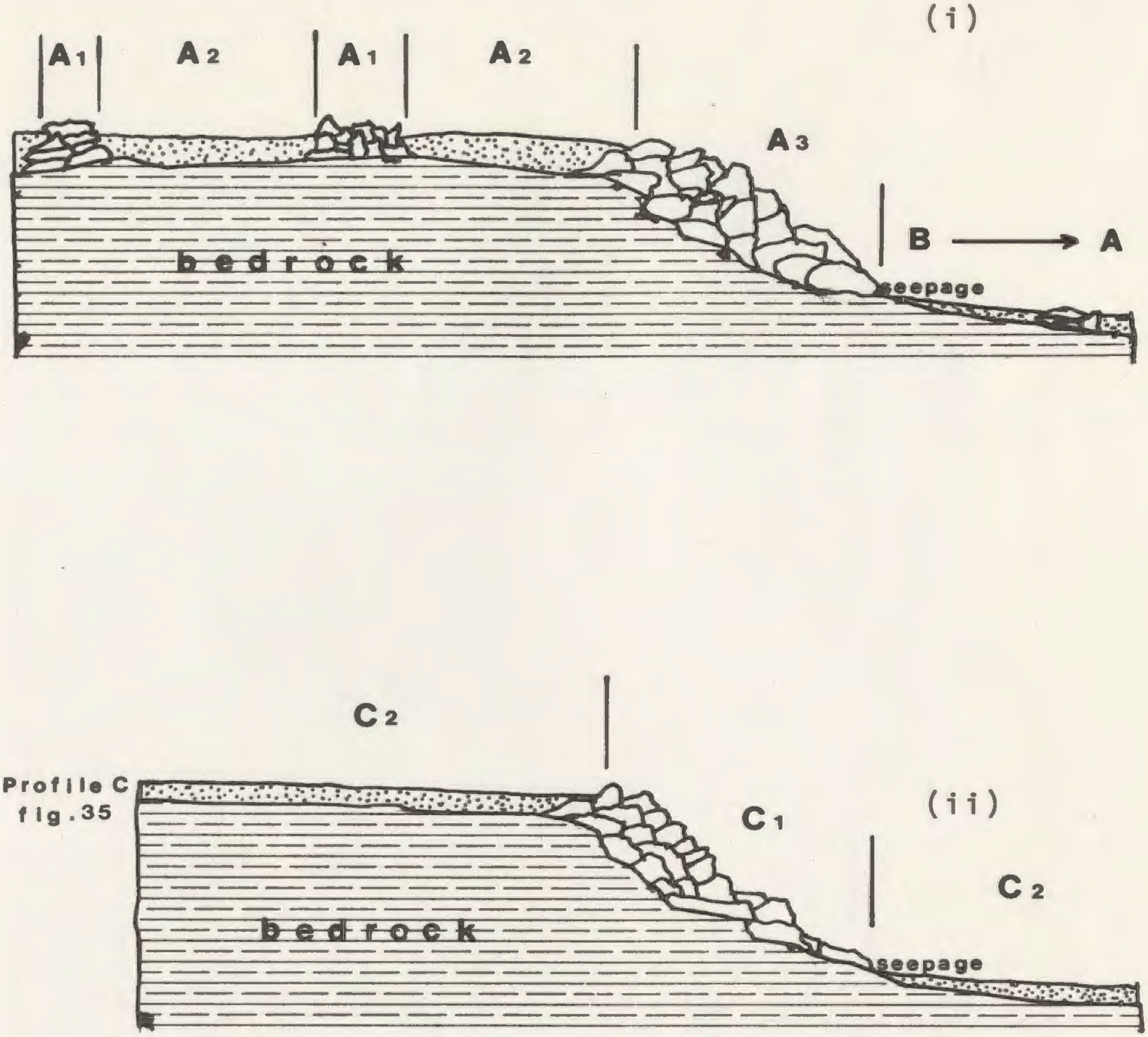


Figure 38. Schematic cross-section of (i) exposed, and (ii) sheltered solifluction terraces, indicating the vegetational response to changes in micro-topography

such as *Silene acaulis* (Figure 39), *Armeria labradorica* var *submutica* and *Diapensia lapponica*. This cushion growth form of many chamaephytes is an adaptation to the extreme environmental conditions, temperatures and also the exposure in winter because of removal of snow cover by high winds. Bliss(1962), for example, reports the ability of *Diapensia lapponica* to withstand sudden drops in temperature to well below freezing, while still in flower, and suffer no apparent ill effects. The same growth form has evolved in unrelated plant families in the tundra and in other harsh climates and is a good example of parallel evolution of a form well adapted for survival in severe environments such as Table Mountain. Similarly most of the shrub species in this habitat such as *Rhododendron lapponicum* are evergreen rather than deciduous, an adaptation which conserves energy, since the evergreen species do not put out an entirely new photosynthetic surface each year. Hadley and Bliss (1964) report that evergreen leaved shrubs, for example, *Diapensia lapponica*, *Rhododendron lapponicum* and *Juncus trifidus*, all found on Table Mountain, have lower photosynthetic and respiratory rates than the deciduous shrub *Vaccinium uliginosum* var *alpinum*, and conclude that,

> "the combination of lower energy balance and a cushion growth form which enhances the maintenance of a more favourable boundary layer, and thus higher leaf temperatures in spite of strong winds, are no doubt important factors in the habitat position of evergreen-leaved versus deciduous-leaved shrubs and herbs" (p. 351).

Where the polygons grade into stripes, communities may extend, and indeed move, downslope. This is illustrated in figure 40 , where from the original point of colonization by *Rhacomitrium lanuginosum* other species, notably *Betula pumila* and *Salix* sp. extend for quite a distance downslope, although still rooting in their original position. This results from a combination of soil creep, fluvial action and the

Figure 39. Silene acaulis, a common chamaephyte on Table Mountain. Note the cushion growth form and long tap root

Figure 40. Isolated clump of arctic-alpine species typical of Type A communities, extending downslope from the original point of colonization in the foreground

wind, the clumps typically having their long axis parallel to the greatest slope and prevailing wind direction.

A secondary component of the Type A communities are those sites which experience less environmental stress. These locations possess a higher species diversity, more continuous plant cover and larger individuals of the particular species. An exemplary habitat is the solifluction terrace. Local accumulation of snow reduces the impact of winter frosts and wind exposure, and groundwater seepage frequently occurs at the bank foot (Figure 38). On the terrace banks soil forms and collects within voids between the boulders and may become quite deep, especially if the bank has a continuous vegetation cover. The soils typically have a shallow (<5 cm) black humus layer over the brown, often sandyish soil pocket. As the angle of the bank decreases the soil becomes moister, and may even be clayey in certain flatter sites. Chemically they have above average pH values (6.50) but below average calcium and magnesium availability with low nickel content (Table 3).

The bank vegetation (A 3, figure 38) is dominated by prostrate tree species, *Betula pumila* and *Salix* in particular, their extensive root systems helping to stabilize the soil. Shrubs include those found on the more unstable sites, such as *Rhododendron lapponicum* and *Potentilla fruticosa*, but may include additional species such as *Vaccinium uliginosum* var *alpinum* and *Juniperus communis*. The arctic-alpine species, previously mentioned, are common herbs. Additional species are *Conioselinum pumilum*, often found in association with *Salix* species, and also species with great ecological amplitude, *Sanguisorba canadensis*, *Solidago hispida*, *S. multiradiata*, *Senecio pauciflorus* and *S. pauperculus*.

Those species better able to withstand dessication and winter exposure, particularly *Rhacomitrium lanuginosum*, dominate the wind blown heads of the solifluction banks. These areas are very exposed, the wind removing snow cover in winter and leaving them open to killing frosts. The height of the specimens on the bank is often quite even, due to the pruning effects of the wind and winter snow levels. The more diverse bank-foot vegetation may extend onto the terrace below, until increasing aridity and exposure allow only the primary colonizers to survive once more.

6.2 Type B: Pioneer communities found in less exposed locations.

Area B is composed of samples from communities which have typically a more diverse and closed vegetation than the pioneer communities, and yet still retain sufficient openness that pioneer species and arctic-alpine herb species, particularly *Lychnis alpina*, *Armeria labradorica* var. *submutica* and *Saxifraga aizoides* are not eliminated through competition. The soil development is greater, ranging from deep pockets within the coarse debris to quite well structured soils on flat terrain (e.g. sample 87, profile B, Figure 35). There is a shallow black humic A_0 horizon of anything up to 4 or 5 cms, a product of the greater supply of organic matter, grading into a horizon of brown stony soil with little organic matter. The boundary between the A_2 and B_2 horizons is often quite distinct, the B_2 horizon being a yellow serpentine clay, which gets stonier with depth until bedrock is reached. Chemical analysis (Table 3) indicates that typically they have a high pH level, with low nickel and available calcium levels and a variable available magnesium content. This is to be expected in that the values are somewhat less extreme than those of the pioneer communities, but still have the same characteristics of a relatively immature soil.

The less exposed environment and more mature soil is reflected in the vegetation composition and structure. The sparsely colonized

TABLE 6

Species list of Quadrats in Type B Communities

*Species found in association with sample quadrats, but not included in the ordination.

Trees

- _Alnus crispa_
- _Betula pumila_
- _Larix laricina_
- _Salix sp._

Shrubs

- _Arctostaphylos Uva-ursi_
- _Andromeda glaucophylla_
- _Empetrum nigrum_
- _Juniperus communis_
- _J. horizontalis_
- _Kalmia polifolia_
- _Ledum groenlandicum_
- _Myrica gale_
- _Potentilla fruticosa_
- *_Rubus acaulis_
- _Vaccinium Oxycoccus_
- _V. uliginosum_ var _alpinum_

Herbs

- _Anaphalis margaritacea_
- _Arenaria humifusa_
- _Armeria labradorica_ var _submutica_
- _Aster sp._
- _Campanula rotundifolia_
- _Cirsium vulgare_
- _Conioselinum pumilum_
- _Coptis groenlandicum_
- _Drosera intermedia_
- *_Euphrasia Randii_ var _Farlowii_
- *_Gnaphalium norvegicum_
- _Iris versicolor_
- _Lychnis alpina_
- _Pinguicula vulgaris_
- _Potentilla tridentata_
- _Primula mistassinica_
- _Sanguisorba canadensis_
- _Saxifraga aizoides_
- _Senecio pauciflorus_
- _S. pauperculus_
- _Silene acaulis_
- _Solidago hispida_
- _S. multiradiata_
- _Thalictrum alpinum_
- _Trientalis borealis_
- _Viola cucullata_

Ferns

Adiantum pedatum var _aleuticum_

Grasses, sedges and rushes

- _Carex echinata_
- _C. scirpoides_
- _Deschampsia atropurpurea_
- _D. flexuosa_
- _Eriophorum Chamissonis_
- _Festuca rubra_
- _F. scabrella_
- _Juncus balticus_
- _J. filiformis_
- _J. trifidus_
- _Poa glauca_
- _P. palustris_
- _Scirpus cespitosus_

Mosses

- _Dicranum bonjeani_
- _Hylocomium splendens_
- _Lycopodium annotinum_
- _Pleurozium schreberi_
- _Sphagnum sp._
- _Rhacomitrium lanuginosum_

polygons of the pioneer communities are now almost totally vegetated, with large areas dominated by colonized *Rhacomitrium lanuginosum*. The wetter habitats, particularly of the coarser polygon boundaries are colonized by *Scirpus cespitosus*, *Carex echinata*, and *Juncus trifidus*, the *R. lanuginosum* being replaced by *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum bonjeani* in wetter areas.

These colonized polygons eventually become indiscernable as the vegetation cover becomes continuous, and shrub growth more dominant. Thus Area B includes samples from the ecotone between the xeric pioneer communities (Type A) and the more mesic communities (Types C and D, Figure 41), where a typical mosaic occurs with large areas dominated by *J. trifidus*, *S. cespitosus* and *C. echinata* interspersed with shrubs such as *Ledum groenlandicum*, *Vaccinium uliginosum* var *alpinum*, *Myrica gale*, and prostrate *Betula pumila*. Accompanying herb species are *Viola cucullata*, *Coptis groenlandicum*, *Potentilla tridentata* and *Conioselinum pumilum*. Wherever the fenland substrate becomes coarser, with little peat development, then this community becomes dominant.

A similar community occurs in small depressions on the plateau, which are too small and well drained for peat development, and yet are less extreme than the pioneer communities (Figure 42). From the photograph two observations can be made. Firstly, that vegetation growth is restricted to the slight fluvial depression, presumably because of the greater water supply, and longer snow lie giving increased frost protection in winter. Secondly, the vegetation of the depression is by no means continuous, being broken by large boulders and areas of coarse debris. Large areas may be covered by *Juniperus communis* and *J. horizontalis*, giving an appearance of lush vegetation growth, when in fact there is only a single, very prostrate shrub.

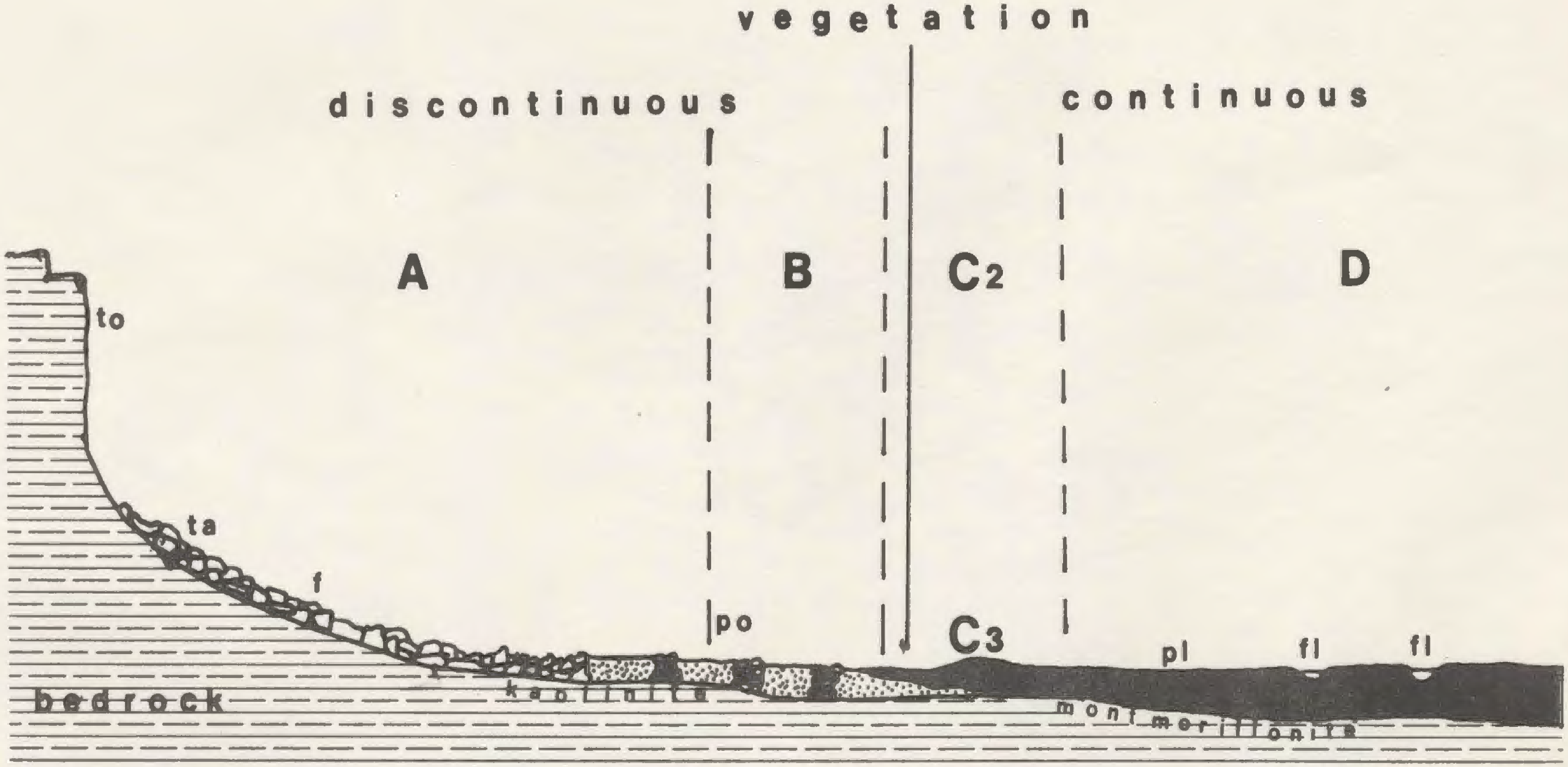


Figure 41. Schematic cross-section indicating the relationship between phytosociological groups A to D and physiographic location on the plateau of Table Mountain.

Key: to - tor, ta - talus, f - felsenmeer, po - stone polygons, pl - peatland, fl - flark

Figure 42. Typical Type B community in shallow depression on plateau surface

In sum, these areas are essentially ecotones between the more extreme pioneer communities and the mesic fenland and springline communities. Wherever conditions are not quite so exposed as to allow only the pioneer communities to exist, then characteristic species of these ecotone areas, Juncus trifidus, Ledum groenlandicum and Viola cucullata become increasingly dominant. However if conditions become too favourable then the arctic-alpine species become eliminated through competition, and the community grades into Type C. communities.

6.3 Type C: Ecotone communities occurring between the pioneer and more mesic communities.

Within Area C, three major vegetation trends are apparent, although all three are interrelated with each other and the adjacent areas. As the environment becomes increasingly mesic, an increased number of niches and hence phytosociological combinations becomes possible. The trend to more mesic conditions is essentially one of decreasing exposure. Secondary and indirect effects of this are numerous. Each will effect the distribution of different species in different ways, but generally the ecological amplitudes of an increasing number of species will no longer be exceeded. This leads to greater competition between species for essential nutrients, water and light, and consequently species better able to compete, particularly shrubs and trees, become increasingly dominant. Herbaceous species that are either able to compete successfully for light, (e.g. Sanguisorba canadensis, and Solidago multiradiata) or have lower light requirements (e.g. Trientalis borealis), become more frequent than the herbs dominating more open habitats (See Table 7).

The central part of the ordination (C 1, Figure 27), reflects these changes as, in general, competition increases giving a greater dominance of shrub and tree species. Juniperus communis, Myrica gale

TABLE 7

Species list of Quadrats in Type C Communities

*Species found in association with sample quadrats, but not included in the ordination.

Trees

Alnus crispa
Betula Michauxii
B. pumila
Larix laricina
Salix sp.

Shrubs

Andromeda glaucophylla
Empetrum nigrum
Juniperus communis
Kalmia polifolia
Ledum groenlandicum
Myrica gale
Rhododendron lapponicum
*Rubus pubescens
Vaccinium Oxycoccus
V. uliginosum var alpinum

Herbs

Armeria labradorica var submutica
Aster sp.
Campanula rotundifolia
Conioselinum pumilum
Coptis groenlandicum
Drosera intermedia
Potentilla tridentata
Prenanthes trifoliata var nana
Primula mistassinica
Sanguisorba canadensis
Sarracenia purpurea
Solidago multiradiata
Thalictrum alpinum
Trientalis borealis
Viola cucullata

Ferns

Adiantum pedatum var aleuticum
Osmunda regalis

Grasses, sedges and rushes

Carex Buxbaumii
C. capilaris
C. limosa
C. paupercula
Danthonia intermedia
Deschampsia atropurpurea
Eriophorum Chamissonis
Festuca rubra
Juncus balticus
Poa palustris
Schizachne purpurascens
Scirpus cespitosus
Scirpus hudsonianus
Triglochin palustris

Mosses

Dicranum bonjeani
Hylocomium splendens
Lycopodium annotinum
Lycopodium selago
Microlepiodizia sefaceae
Mylia anomala
Pleurozium schreberi
Rhacomitrium lanuginosum
Sphagnum sp.

and Betula pumila dominate large areas, a typical habitat being the steep banks of the solifluction terraces (C 1, figure 38). These species are able to dominate the more sheltered and moist banks to the virtual exclusion of the arctic-alpine species. Typical herbs are Sanguisorba canadensis and Solidago multiradiata, although primary colonizers Potentilla tridentata and Campanula rotundifolia still appear to be able to compete successfully.

The soil is now more mature, although in this habitat it is still essentially in pockets between the larger boulders. The humic A_0 horizon is quite well developed with much organic matter before it merges into a lighter brown, fine, friable loam, which can be anything up to 50 cms in depth before bedrock is reached. A yellow clay may overlie the bedrock, especially in flatter situations. Chemically the soil continues the trend so far established (Table 3), in that pH levels are high and calcium availability low, although the values in each case are not extreme. Available magnesium and total nickel show considerable variability for this community type.

The samples in the top left of the C subdivision (C 2, Figure 27) represent a trend toward wetter conditions from those of the centre. They are a continuation of the gradient from the bare patterned ground and the closed vegetation of the peatland areas. Increasingly they become dominated by Scirpus cespitosus, S. hudsonianus, Carex scirpoides, Juncus balticus and Thalictrum alpinum, with few shrub species. A similar community (C 2, Figure 38) occurs on the moist level terraces, particularly where there is an active seepage zone at the bank foot. This provides an interesting phytosociological contrast with the more exposed terraces of Type A.(Figure 38).

Figure 43. Type C community in foreground gradually changes into Type B and ultimately Type A communities as exposure increases with altitude

A typical soil profile (e.g. sample 41, profile C, Figure 35) has a rather thin humus layer of poorly decomposed sedges. The A_2 horizon is a light brown, coarse, stony soil that gradually merges into the much darker illuvial B_2 horizon. With increasing depth this becomes moister, stonier and more yellow in colour until bedrock is reached. Chemically it continues the trend of high pH and low calcium availability, although nickel content is higher than average (Table 3).

The lower right hand side of the C area in the ordination represents the driest parts of the true peatland (C_3, Figure 27). Frequently these are large hummocks, up to one metre above the water table. The driest, highest hummocks are deep clumps (>50 cms) of black, undecomposed *Rhacomitrium lanuginosum*, colonized by *Vaccinium ulinginosum* var. *alpinum*, *Potentilla fruticosa* and dwarf *Betula pumila*.

The *Rhacomitrium lanuginosum* is often rooted on other moss species, *Sphagnum papillosum*, *S. nemoream*, *S. fuscum*, *S. palustre*, *Mylia anomala* and *Microlepiodizia sefaceae*. These species are characteristic of wetter peatland habitats (Type D). Towards the base of the hummocks *Kalmia polifolia* and *Vaccinium Oxycoccus* become increasingly important. These species are accompanied by *Drosera rotundifolia* and more rarely *D. intermedia*, and various sedges, *Carex Buxbaumii*, *C. capilaris*, *C. limosa*, *C. paupercula*, *Eriophorum angustifolium* and *E. Chamissonis*.

6.4 Type D: Peatland and sedge meadow communities

Type D communities represent a well-defined group associated with wetland habitats. Within the group there is a clear division between fenland communities based on an organic substrate and sedge meadow communities on a mineral substrate. Each substrate is, however, underlain by a clay horizon.

Clay formation from serpentine has been reported from many different areas, (Japan; Harada 1953, Nagatsuka 1967; Borneo; Schellmann 1964; Italy; Veniale and Van der Marel 1963: California; Wildman _et al_ 1968) and various weathering sequences have been proposed covering a wide range of clay minerals: montmorillonite (Wildman _et al_ 1968), vermiculite, chlorite (Nagatsuka 1967), and kaolinite (Harada 1953). De Kimpe and Zizka (1973) studying the weathering of dunite at Asbestos (Quebec) found that,

> "the major features in the chemical compositions were the loss of MgO throughout the profile, the enrichment of SiO_2 in the A horizon, of Fe_2O_3 in the B horizon and of Al_2O_3 in the A and B horizons. The clay mineralogy indicated that the dunite transformed, through interstratified minerals and vermiculite, to montmorillonite and chlorite" (p. 1539).

This contrasts to the findings of Harada (1953), studying serpentine weathering in a similar climate in northern Japan who concludes that "in the early stage of weathering of serpentine the predominant clay mineral is halloysite, and with the progress of weathering kaolinite increases" (p. 48).

However it is possible that, given the conditions for clay formation, such as sufficient silicon and aluminum in the weathered material, two areas of serpentine bedrock in close proximity to each other can have montmorillonite and kaolinite respectively, because of the local water conditions. The two are distinguished by the arrangement of their laminae, kaolinite having one silica and one alumina layer, and montmorillonite one alumina layer between two silica layers. Because of the greater interface area of the montmorillonite clay particles, their smaller size, and the greater space between laminae, they are much more active in promoting chemical reaction and in forming a plastic cohesive soil. If not counteracted by other factors, a wet substrate favours the predominance of clays of the montmorillonite group, whereas a dryer substrate favours the formation of the kaolin group.

It is thought that on Table Mountain, the clay underlying the drier habitats of areas A, B, C and the sedge meadows (D_2) is essentially kaolinite. Ross and Hendricks (1946) state that, "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" (p. 60). In the drier areas over most of Table Mountain the orange red colour of the clay is evidence of both oxidizing conditions and hence ferric rather than ferrous iron. Similarly the sedge meadows are thought to experience oxidizing conditions for at least part of the year, because of the underlying orange clay. Kaolin formation contributes to the development of an infertile soil for vegetation and the resulting poor development of vegetation in turn reduces the amount of organic colloids produced.

Furthermore, in respect to the effect of organic material on clay development Ross and Hendricks (1946) state that, "organic material in association with certain bacteria results in reducing conditions in the clay forming system. This would favour montmorillonite formation..." (p. 60). All the peatlands on Table Mountain were found to have a reducing environment as evidenced by the fine bluish grey clay at their base, so coloured by ferrous iron, and found only in an anaerobic environment.

The high plasticity and cohesion of the montmorillonite clays contributes to the maintenance of the wet substrate by the formation of a layer impervious to percolation. This in turn favours their continued production in the weathering process, while kaolin formation is prevented by the reducing environment maintained by the impervious layer of montmorillonite.

On Table Mountain organic matter has accumulated in large, shallow depressions to form peatlands. In better drained fluvial depressions and below seepage lines of sheltered terraces, conditions favour the formation of sedge meadows. These two categories represent sub-divisions of Type D communities, although floristically the division is not very distinct.

Peatlands are the product of a steady accumulation of dead plant residues in the water-logged, flatter areas. This process is aided by the depleted oxygen supply, lack of soil bacteria and poor drainage conditions. Over time, peat may accumulate to a depth of two metres (profile D_1, Figure 44).

From the surface to a depth of 4 cms are pure undecomposed plant, predominantly sedge, remains. Below this is a more dense, brown peat layer up to 30 cms in depth in which the plant remains may still be discernible. This merges into a black, decomposed, homogenous, and often very wet, peat layer. The local water table is in this zone. There is an abrupt boundary with the C horizon, a blue-grey, coarse, stony clay, which is quite wet on the surface, but becomes increasingly drier and finer with depth until it meets the unweathered blue-grey bedrock. This type of profile was ubiquitous on peatland sites, with variation only in the depth of peat accumulation.

Chemically peatland soils are not radically different from the other soils found on the serpentine, but there is greater variation between the samples (Table 3). Generally, however, they have low pH, but high available calcium magnesium and total nickel levels reflecting their illuvial position, and, as to be expected high organic matter and moisture retention capability. Between different horizons, particularly the B_2 and C horizons, mineral levels can change dramatically (Table 9).

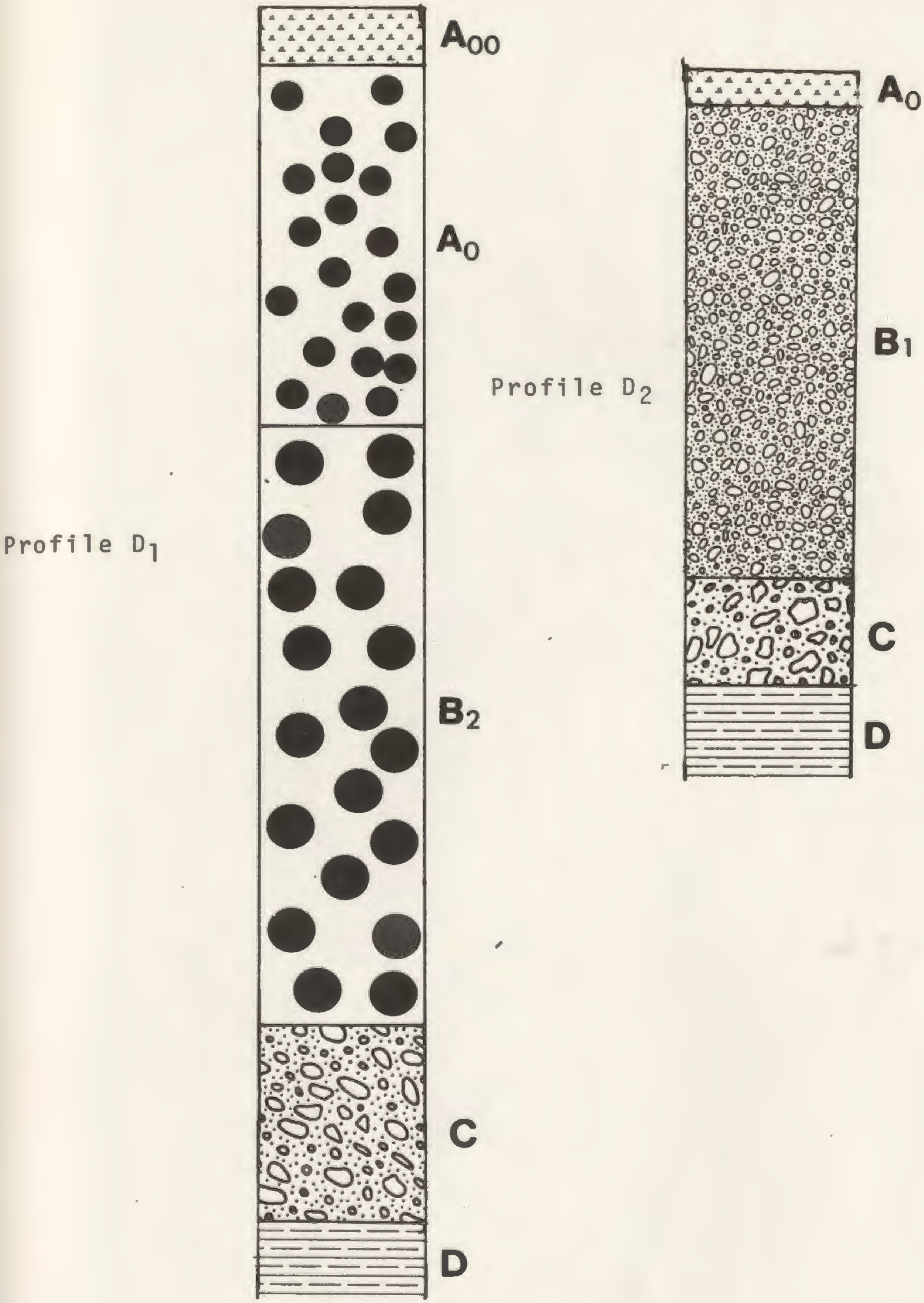


Figure 44. Soil profiles D_1 and D_2

TABLE 9

Chemical and Physical Properties of Different Horizons of Some Peatland Soils

Sample		Property					
Site	Horizon	Organic Matter	Moisture Retention	pH	Available Calcium	Available Magnesium	Total Nickel
58	C	17.42	6.76	4.89	0.559	5.08	0.112
58	B_2	47.95	13.35	4.70	0.869	5.62	0.204
58	Ao	38.08	11.57	4.59	0.665	5.63	0.0757
68	C	1.74	1.83	5.80	0.0497	2.58	0.0276
68	A_o	43.04	9.58	5.40	0.294	7.84	0.0152
76	C	0.33	2.93	7.02	0.0601	2.11	0.00772
76	B_2	12.31	6.89	5.73	0.0786	2.75	0.0113

Available calcium, magnesium and total nickel are expressed as mg/gm. Organic matter and moisture retention capability are both percentages

The underlying clay layer has lower available calcium and magnesium, and total nickel, but higher pH values than the surface layer. This is as anticipated, the more soluble minerals, calcium and magnesium, having accumulated in the illuvial B_2 horizon.

These peatlands are fens in the terminology of Zoltai *et al* (1973):

> "Fens are peatlands characterized by surface layers of poorly to moderately decomposed peat, often with well decomposed peat near the base. They are covered by a dominant component of sedges, although grasses and reeds may be associated in local pools. *Sphagnum* is often subordinate or absent, with the more exacting mosses being common. Often there is much low to medium height shrub cover and sometimes a sparse layer of trees. The waters and peats are less acid than in bogs of the same area, and sometimes show somewhat alkaline reactions. Fens usually develop in restricted drainage situations where oxygen saturation is relatively low and mineral supply is restricted. Usually very slow internal drainage occurs through seepage down very low gradient slopes although sheet surface flow may occur during spring melt or periods of heavy precipitation" (p. 6-7).

The Table Mountain fens have clearly defined boundaries (Figure 45) within which vegetation is continuous except for the wet hollows or flarks, running at right angles to the greatest angle of slope. Quite a distinctive hummock and hollow pattern exists on all the fens. The floristic composition varies somewhat from fen to fen, the main factor appearing to be exposure.

At the base of the fen hummocks there are various *Sphagnum* species (*S. fuscum*, *S. papillosum*, *S. palustre* and *S. nemoreum*) whereas at a higher level above the water table, the dominant moss species are *Hylocomium splendens*, *Dicranum bonjeani* and *Pleurozium schreberi*. The hummocks on the less exposed, drier fens may support *Rhacomitrium lanuginosum* on top. The larger hummocks are sometimes colonized by prostrate *Picea mariana*, *Larix laricina* and *Betula pumila*. The exposed fens on the plateau have but a sparse scattering of the latter, *Betula*

Figure 45. Typical fen at base of scarp, showing finite borders surrounded by sparsely vegetated serpentine debris

Michauxii being far more common, often accompanied by *Vaccinium ulinginosum* var *alpinum*, *V. Oxycoccus* and *Empetrum nigrum*, all of which are absent on the lower less exposed fens. However all the fen hummocks have many species in common such as *Myrica gale*, *Vaccinium angustifolium*, *Kalmia polifolia*, *Ledum groenlandicum*, *Andromeda glaucophylla*, *Sanguisorba canadensis*, *Coptis groenlandicum* and *Drosera rotundifolia*.

The remainder of the fens are dominated almost exclusively by sedges (Figure 46), with the occasional patch of *M. gale*, *S. canadensis* and *B. Michauxii*. The main sedges are *Carex exilis*, *C. echinata*, *C. limosa*, *C. paupercula*, *C. livida*, *C. Buxbaumii* and *C. scirpoides*, although *Scirpus cespitosus* and *S. hudsonianus* are still abundant, and *Juncus balticus* and *J. filiformis* occur on slightly better drained areas. The cotton grasses *Eriophorum angustifolium*, *E. viridi carinatum* and *E.* Chamissonis are widely distributed with *Rhynchospora alba* and *Carex flava* being dominant near the borders of fern pools. Accompanying herbs include *Sarracenia purpurea*, *Habenaria dilatata*, *Thalictrum polygamum* and various species of *Aster*.

Sedge meadows form the second subdivision of Type D communities. The substrate of the sedge meadows differs considerable from that of the peatlands (profile D_2, Figure 44). There is only a very thin humic layer before the dark brown, moist clayey B_1 horizon. The base of this horizon is distinctly bounded by the kaolin of the C layer, which grades into the bedrock. Chemically it has relatively high available calcium and magnesium levels with quite a low pH (Table 3). Although the substrate is often very wet standing water is infrequent because of the steeper angle than the peatland areas.

Floristically there is much in common with the peatlands for large areas are dominated by the Cyperaceae family with shrubs such as *Myrica*

TABLE 8

Species list of Quadrats in Type D communities

*Species found in association with sample quadrats, but not included in the ordination

Trees

Alnus crispa
Betula Michauxii
B. pumila
Larix laricina
Picea mariana

Shrubs

Andromeda glaucophylla
Arctostaphylos Uva-ursi
*Chamaedaphne calyculata
Empetrum nigrum
Epigea repens var glabrifolia
Gaultheria procumbens
Gaylussacia dumosa var Bigeloviana
G. baccata
Juniperus horizontalis
Kalmia polifolia
Lonicera villosa
Myrica gale
Nemopanthus mucronata
Potentilla fruticosa
Rubus pubescens
Vaccinium angustifolium
V. macrocarpon
V. Oxycoccus
V. Vitis-Idaea

Herbs

Anaphalis margaritacea
Aster sp.
Campanula rotundifolia
Castilleja septenrionalis
Clintonia borealis
Commandra Richardsiana
Conioselinum pumilum
Coptis groenlandicum
Cornus suecica
Drosera intermedia
D. rotundifolia
Habenaria dilatata
Iris versicolor
Linnaea borealis
*Nuphar variegatum
Potentilla tridentata
Prenanthes trifoliata
Primula mistassinica
Pyrus floribunda
Sanguisorba canadensis
Sarracenia purpurea
Senecio pauperculus
Solidago multiradiata
Thalictrum alpinum
Thalictrum polygamum
Trientalis borealis
Utricularia cornuta
Viola cucullata

Ferns

Osmunda regalis

Grasses, sedges and rushes

Carex Buxbaumii
C. echinata
C. exilis
C. flava
C. lasioscarpa
C. limosa
C. livida
C. paupercula
C. scirpoides
Danthonia intermedia

D. spicata
Eriophorum angustifolium
E. Chamissonis
E. viridi-carinatum
Festuca rubra
Juncus balticus
J. filiformis

Poa glauca
P. palustris
Rhynchospora alba
Schizachne purpurescens
Scirpus cespitosus
S. hudsonianus
Triglochin maritima
T. palustris

Mosses

Dicranum bonjeani
Hylocomium splendens
Lycopodium annotinum
L. selago
Mylia anomala
Pleurozium schreberi

Rhacomitrium lanuginosum
Sphagnum fuscum
S. nemoreum
S. palustre
S. papillosum
S. rubellum

Figyre 46. Typical sedge dominated fen on plateau surface

gale, *Potentilla fruticosa*, *Juniperus communis* and *J. horizontalis*. The fern *Osmunda regalis* is a distinctive member of this community which is not found on the peatlands. Accompanying herbs are similar to those of the peatlands particularly *Thalictrum polygamum* and *Sanguisorba canadensis* but also with species such as *Viola cucullata*, *Primula mistassinica*, *Trientalis borealis*, *Linnaea borealis* and *Castilleja septenrionalis*, which are rare on the fens.

6.5 Type E: Fellfield communities, isolated vegetation hummocks in exposed locations at low altitude.

Type E represents areas of hummock colonization (Figure 47) in localities at lower altitude than the hummocks of the pioneer (Type A) communities, and consequently with a far greater number of species (Table 10). Similar forms have been reported from cold and wet environments elsewhere, for example in the Mount Kosciusko area in Australia (Barrow, *et al.* 1968), and the Cairngorm Mountains in Scotland (Watt and Jones 1948, Burges 1951). They occur on gentle slopes (5°-15°) of sorted debris up to 10 cms in diameter.

The substrate varies widely on this type of terrain from the unstable, sparsely colonized lithosol (profile A, Figure 35), to a more mature and humic soil in the more stable areas of greater vegetation cover (profile E, Figure 48, of sample 94). The soil is typically moist, but dry in the upper layers, with a large number of small stones, especially in the B_2 horizon. The A_2 horizon may be quite sandy and of a lighter colour than the more moist illuvial B_2. The latter is dark brown and varies considerably in depth from a few to 30 or 40 cms, before meeting the underlying orange kaolin of the C horizon. Samples in this area (Table 3) typically have quite high pH values but low calcium and magnesium availability.

TABLE 10

Species list of Quadrats in Type E Communities

*Species found in association with sample quadrats, but not included in the ordination

Trees

Alnus crispa
Betula pumila
Larix laricina
Picea mariana

Shrubs

Andromeda glaucophylla
Arctostaphylos Uva-ursi
Empetrum nigrum
Epigea repens
Juniperus communis
J. horizontalis
Ledum groenlandicum
Myrica gale
Potentilla fruticosa
Rhododendron canadense
Rubus acaulis
Vaccinium angustifolium
V. Vitis-Ideae

Herbs

Anaphalis margaritacea
**Artemisia canadensis*
Aster sp.
Campanula rotundifolia
Cirsium vulgare
Commandra Richardsiana
Conioselinum pumilum
Coptis groenlandicum
**Gnaphalium norvegicum*
Linnaea borealis
**Linum catharticum*
Potentilla tridentata
Pyrola rotundifolia
**Rhinanthus Crista-Galli*
Sanguisorba canadensis
Sarracenia purpurea
Senecio pauciflorus
S. pauperculus
Solidago hispida
S. multiradiata
**Taracetum huronense var terrae-novae*
Thalictrum alpinum
Trientalis borealis

Grasses, sedges and rushes

Deschampsia cespitosus
D. flexuosa
C. scirpoides
Festuca rubra
F. scabrella
Juncus balticus

Mosses

Hylocomium splendens
Dicranum sp.
Lycopodium annotinum
L. selago
Pleurozium schreberi
Rhacomitrium lanuginosum

Figure 47. Large hummocks typical of Type E fellfield areas. The hummocks are remarkably uniform in species composition, size and distance apart.

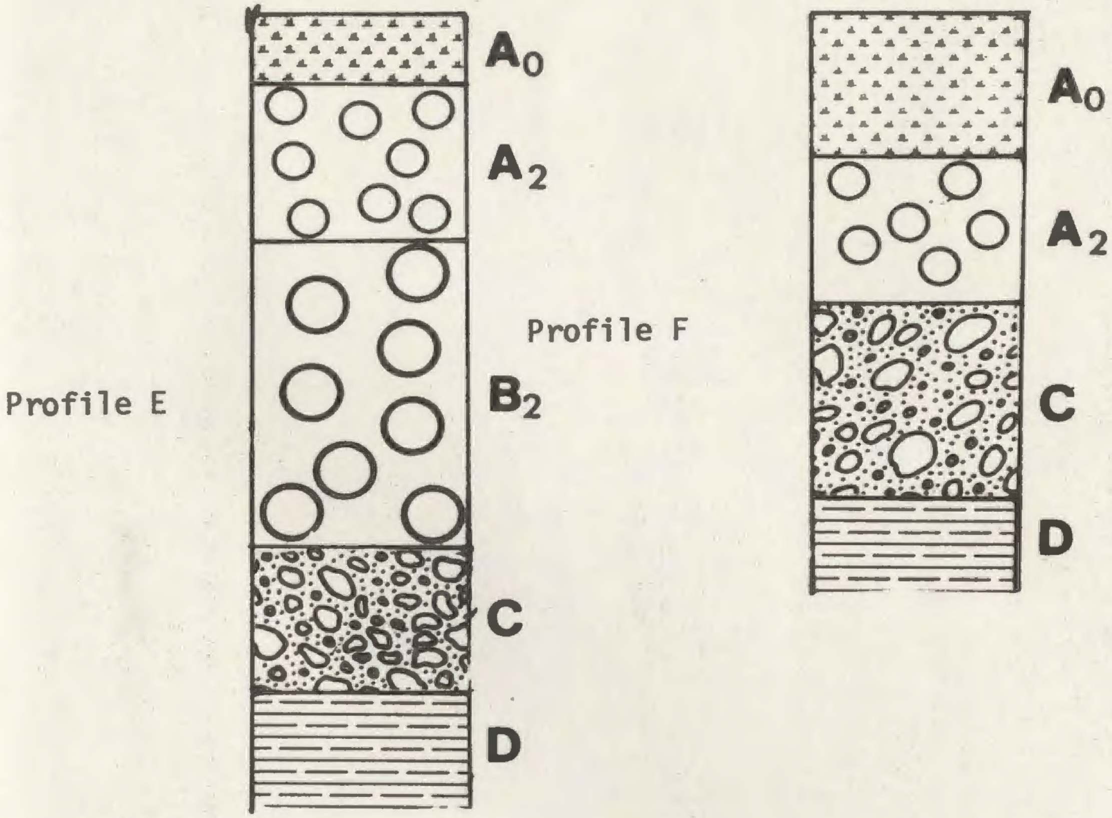


Figure 48 . Soil profiles E and F

Floristically they are very uniform with a large number of species. They usually have a base of *Rhacomitrium lanuginosum* but other mosses, *Hylocomium splendens*, *Pleurozium schreberi* and various *Dicranum* species also occur. The relative positions of the different species is remarkably uniform from hummock to hummock. The foremost part is typically *Alnus crispa*, the roots being at the highest point of the gradient and the boughs stretching back along the slope. This gives way downslope to other prostrate tree species such as *Larix laricina* and *Betula pumila*, and the shrubs *Potentilla fruticosa*, *Rhododendron canadense* and *Ledum groenlandicum*. As the exposure becomes less critical towards the centre of the hummock, the tree and shrub species are not quite so prostrate, and the community is more open. Herbs, particularly *Senecio pauperculus*, *S. pauciflorus*, *Solidago multiradiata*, *S. hispida*, *Coptis groenlandicum*, *Pyrola rotundifolia* and *Trientalis borealis* dominate with grass species *Festuca rubra*, *F. scabrella* and *Deschampsia cespitosa*.

The lowest part of the hummock are dominated by prostrate *Juniperus communis* and *J. horizontalis*, the roots of which may be established well to the forefront of the clump. Surrounding the clumps such primary colonizers as *Lychnis alpina*, *Campanula rotundifolia*, *Cerastium beeringianum*, *C. terrae-novae* and *Linum catharticum* are once more in evidence as competition decreases and the habitat becomes less stable.

The establishment of vegetation hummocks on this type of terrain is very limited. It is thought that they originate on the lee side of protecting boulders, probably initially with *Rhacomitrium lanuginosum* and other primary colonizers. As the small plants grow out from the shelter of the stones they are exposed to the effects of the wind and to abrasion by wind-blown soil, ice and snow. Some of the abrading material and erosion debris from the plants themselves are deposited on the leeward side, and if growth can be established in this area before the original roots are killed by exposure through erosion then the clump continues to develop. Once established it provides a rooting medium and protection for any further colonizers, and the process becomes self generating.

The regular wave form of the hummocks and of the wind scoured spaces in between is difficult to explain. Perhaps the uneven distribution of the plants initially modifies the wind profile, and is itself modified by the wind, until a fairly regular wave form is produced which is maintained thereafter. Barrow, *et al.* (1968) suggest that:

> "The approximate equality in the length of the *Epacris* clumps [which are very similar to the hummocks on Table Mountain] and of the spaces in between in some transects suggests that the *Epacris* plants are acting essentially as impermeable wind breaks, with a very restricted zone of reduced wind action downwind from the leading edge, then a zone of strong eddies with a high erosive potential beyond (c.f. Caborn 1957 p. 5). As this erosive energy is dissipated, and just before the zone at which there would be a return to undisturbed flow, the next *Epacris* clump develops" (p. 94-95).

A similar mechanism may be proposed to explain the regularities of occurrence and form of the hummocks on Table Mountain.

6.6 Type F: Scarp-foot communities, dominated by trees and shrubs and occurring in the most sheltered localities.

This type has the most fully developed vegetation structure on the Mountain. It is continuous within itself, has the greatest number of species, the tallest specimens, and is the most favourable environment for plant growth. This community is restricted to the lowest altitudes and most sheltered position, wherever conditions become more extreme it grades into one of the previously described communities, depending upon local conditions. One of the favoured locations for its development is at the sheltered scarp foot (Figure 49). This zone is well drained and yet has a high water availability. In winter, snow accumulation at the break of slope protects the plant species and later in Spring provides good moisture availability levels.

The substrate is usually stable, even though local topography may be quite steep (20^{0}), held together by the interlocking root systems. The humus layer (profile F, Figure 48) is quite deep ($>$10 cms), because of the greater vegetation growth with more deciduous species than elsewhere on the Mountain. This is underlain by a moist light brown stony loam (A_2) that may have quite an abrupt boundary with the moist kaolin clay beneath. Chemically the soil is quite distinct with the highest pH and available calcium levels and the lowest available magnesium and nickel values (Table 3). This is of great interest in view of the many autecological studies (see Chapter 2.12) which indicate that in particular high levels of magnesium and nickel, and low available calcium are the major factors in producing the distinctive serpentine vegetation. Thus the concurrence of the chemically least extreme soil on the Mountain, with low magnesium and nickel and high calcium availability, and the least distinct serpentine vegetation, would appear to substantiate these hypotheses.

This same community occurs in other sheltered positions, such as on the floors of the canyons and more sheltered cirques where local topography creates a slightly raised and drier habitat than that occupied

TABLE 11

Species list of Quadrats in Type F Communities

*Species found in association with sample quadrats, but not included in the ordination

Trees

Abies balsamea
Acer rubrum
Alnus crispa
Betula borealis
B. paperyfera
B. pumila
Larix laricina
Picea mariana
*Pinus strobus

Shrubs

Andromeda glaucophylla
Arctostaphylos Uva-ursi
Empetrum nigrum
Epigea repens
Gaultheria procumbens
Gaylusacia baccata
G. dumosa var Bigeloviana
Juniperus communis
J. horizontalis
Kalmia polifolia
Ledum groenlandicum
Nenopanthus mucronata
Potentilla fruticosa
Rhamnus alnifolia
*Rosa nitida
*Rubus acaulis
Vaccinium angustifolium
V. macrocarpon
V. Vitis-Ideae

Herbs

Anemone parviflora
Campanula rotundifolia
Circaea alpina
Clintonia borealis
Commandra Richardsiana
Cornus canadensis
Cypripedium calceolus
Dryas integrifolia
Erigeron hyssopifolius var villicaulis
Linnaea borealis
Mainanthemum canadense
Pinguicula vulgaris
Pyrola grandiflora
Sanguisorba canadensis
Senecio pauciflorus
S. pauperculus
Solidago hispida
S. multiradiata
Thalictrum alpinum
Tofieldia pusilla
T. glutinosa
Trientalis borealis

Ferns

Osmunda regalis

Grasses, sedges and rushes

Carex scirpoides
C. rupestris
Festuca rubra
F. scabrella
Scirpus cespitosus
*Triglochin maritima
*T. palustris

Mosses

Dicranum bonjeani
Hylocomium splendens
Lycopodium annotinum
L. selago
Pleurozium schreberi
Selaginella selaginoides

Figure 49. A typical habitat for the well developed Type F communities at the sheltered and moist scarp foot

by the sedge meadows (D_2). These two communities can be seen in adjacent positions in Figure 50 taken at the mouth of Winterhouse Canyon (Figure50) looking north-west. The ecotone between them is especially rich in species, the tree-growth being less dominant and therefore allowing greater light penetration to the ground layer.

Although some dominant species of the Type F community notably *Larix laricina*, *Juniperus communis*, and *J. horizontalis* occur occasionally in other habitats, many species (*Acer rubrum*, *Betula papyrifera*, *Nemopanthus mucronata* and *Pinus strobus*) are restricted to these sheltered locations. Similarly very common shrubs in this habitat (*Gaylussacia dumosa*, *Lonicera villosa*, *Vaccinium Vitis Ideae*, *V. angustifolium*, *V. macrocarpon*, *Rhododendron canadense*, *Kalmia polifolia*, *Gaultheria hispidula* and *Epigeae repens*) are found very rarely elsewhere. Herbs are dominantly those of the understorey, well adapted to low light supplies, such as *Circaea alpina*, *Cornus canadensis*, *Mainanthemum canadense* and *Trientalis borealis*. Other species such as *Pinguicula vulgaris*, *Thalictrum polygamum* and *Sanguisorba canadensis* become more abundant in the surrounding ecotones.

An important variation of this community is that found below the five calcium seepage outflows on the northern flank of the Mountain. These are relatively small seepage zones below which has been deposited a highly calcareous tufa deposit. This deposit, because of its lack of soil, is very sparsely colonized only by occasional clumps of *Dryas integrifolia*, its only station on the mountain. The hard deposit eventually becomes fragmented away from the seepage zone and is colonized by various plant species, which are also not found elsewhere on the Mountain, particularly *Carex rupestris*, *Erigeron hyssopifolius* var *villicaulis*, and *Cyprepedium calceolous*, all indicators of high calcium

Figure 50. Type F communities dominated by trees and shrubs occupy the slightly higher, better drained ground to the left compared to the flatter, poorly drained sedge meadows (D_2) to the right

levels. The effect of these deposits on the vegetation extends for a considerable distance downslope presumably because of the higher calcium levels made available in the groundwater. There is little active water flow from the deposits themselves in summer, although flow may occur when the water table is higher. The downslope community is dominated by the main Type F species supplemented by Anemone parviflora, Tofieldia pusilla, Comandra Richardsiana and the moss Selaginella selaginoides.

CHAPTER 7

CONCLUSION

The aim of this thesis has been to describe and analyze the plant community composition and distribution on the serpentine bedrock of Table Mountain. Serpentine vegetation has everywhere been noted for its distinctive growth in contrast to the vegetation on adjacent bedrocks. In particular it is characterized by a discontinuous plant cover of stunted species somewhat different to the species found on other geological formations in the locality. Edaphic and autecological studies (see Chapter 2.1, 2.2) have ascribed these differences mainly to four edaphic properties: low available calcium, high available magnesium and high total nickel and chromium contents. It was hypothesized that these edaphic properties in conjunction with other environmental variables, particularly topographic situation, may be of potential importance in explaining the distribution and composition of plant communities on the serpentine massif itself.

The vegetation and soils were rigorously sampled and the results subjected to an indirect phytosociological ordination. The first axis extracted, that is the one representing the major gradient of phytosociological variation of the samples (axis X), had an extremely significant (0.005 probability value) relationship to the amount of available calcium. In the area where available calcium is highest (Type F communities), are the tallest specimens and most diverse species assemblages. This supports the results of recent autecological studies (Proctor 1971a, 1971b) which indicate that low calcium availability along with relatively high magnesium levels are the most important factors in serpentine ecology. Furthermore it confirms the possibility that calcium availability is of importance in explaining community distribution and composition on a serpentine massif.

It is interesting to note that areas with the second highest levels of available calcium are the peatlands. It seems inconsistent that they should have a relatively high calcium content and yet be acidic, with pH values as low as 4.59 (see Table 3). However, the absorptive capacity of peat for exchangeable cations is so high that such a soil may carry an exceptionally large amount of calcium and yet contain a preponderance of exchangeable hydrogen. Under such conditions the dominance of the hydrogen ions will be equilibrium adjustments maintain an acid soil solution in the presence of large quantities of calcium.

Two further compositional gradients (axes Y and Z) were extracted to give a three dimensional ordination. It was found that phytosociological relationships were most clearly apparent when plotted on the X and Z axes. Therefore the distribution of ten important and characteristic species were plotted on the XZ axes to illustrate their phytosociological relationship. In addition the soil properties, available calcium, and magnesium, total nickel, pH, organic matter content and water retention capability were plotted on the same axes to facilitate identification of soil properties with phytosociological distributions.

The main trend represented by these two axes (see figure 27) from lower left (Type A communities) to top right (Type F communities) is basically one of decreasing exposure. The Type A communities represent the most exposed, xeric colonized sites on the Mountain whereas the Type F communities constitute the most sheltered, mesic and vegetationally diverse sites. It would be erroneous to ascribe causal relationships on the basis of such an interpretation for ecological relationships are seldom, if ever, linear. This exposure gradient is related to the entire environmental complex, from which it would be futile to extract and specify causal relationships. However, the ordination provides in an abstract space the compositional similarity of the samples, and clarifies phytosociological and environmental relationships.

Within these graphical representations certain areas of relative homogeneity (Community Types A to F, Figure 27) can be recognized for descriptive purposes. These areas relate to certain topographic features of the Mountain which often recur in the same relative positions in different locations. For example the solifluction terrace - patterned ground interaction covering large areas of the Mountain. The exposure of a particular terraced patterned area is reflected by the vegetation cover. If the terrace is exposed then it will be colonized by Type A/B communities, if it is sheltered by Type C/D communities (Figure 38). This provides a model of plant community composition and distribution that can be applied for all vegetation types (A to F) recurring on the serpentine of Table Mountain.

Such a recurrence has been termed a catena by Morison *et al.* (1948), who define a catena as,

> "A grouping of soil-vegetation types linked in their occurrence by conditions of topography and repeated in the same relationship to each other whenever the same conditions occur" (p. 6).

This is based on two beliefs: firstly that "the development of the soil on any site is mainly determined by the local topography through its effect on water movement," and secondly, "the vegetation which develops ... likewise follows the form of a catena, and the detail of the vegetation within any one of the sites is, like the soil pattern, complicated by micro-relief" (p. 5).

This concept of the catena aptly summarizes the relationships between topography, soil development and plant community composition and distribution on Table Mountain. Recurring topographic situations (for example, see Figure 41) are associated with specific repeated soil-vegetation types that vary only with exposure.

Spence (1957, 58, 59) has suggested that the degree of plant cover on serpentine is an indication of seral position. He proposed a series of seral communities from the pioneer phase (up to 5.3% cover), through grass (19.4% cover) and sedge (33.7% cover) phases to a climax of a *Calluna vulgaris* serpentine heath. This is a very attractive theory in its simplicity and accord with traditional Clementsian views on succession and climax (Clements 1934). Furthermore Spence proposes cyclical succession based on this prisere. Initially the closed vegetation mat is broken by erosion and bare loam appears. This is progressively removed to expose the underlying stone layer, and an area of typical debris is established which is then colonized by pioneer species.

No evidence whatsoever was found on the serpentine of Table Mountain to substantiate either of these hypotheses. It is thought that colonization is almost permanently retarded in most localities, that the vegetation is the environmental climax and not just a seral stage that will ultimately lead to a closed vegetation cover over most of the Mountain. This is not necessarily an effect of the peculiar chemistry of the serpentine soils, but also reflects their shallowness and unstable nature. Indeed the periglacial phenomena evident on Table Mountain emphasize its similarity to the unstable arctic-alpine environment found many miles further north. In sum, the vegetation is felt to be in dynamic equilibrium with the environment, the sparsely colonized Type A communities being no less of a climax relationship than the closed vegetation of Type D and F communities.

APPENDICES

Appendix I

Location of sample areas on Table Mountain

Appendix I

The aerial photograph (see rear pocket), covering most of Table Mountain, shows the areas selected for detailed sampling. The numbers refer to the number of vegetation samples taken in each area. One sample area is on the southern edge of the plateau overlooking Trout River Pond; its location is indicated by the arrow along the southern margin. The photograph can be used in conjunction with the map of the study area (Figure 1), to give greater familiarization with the area. The scale is approximately 3.75" (9.5 cms) to 1 mile (1.609 kms).

Key

W.H.C. - Winter House Canyon

T.R.P. - Trout River Pond

● - Location of the five calcium seepage zones on the northern flank

Appendix II

Position of each stand on the three ordination axes.

Position of Each Stand on the Three Ordination Axes

Sample	Axis			Sam-ple	Axis			Sam-ple	Axis		
	X	Y	Z		X	Y	Z		X	Y	Z
1	0.9	-3.2	-2.1	37	-3.3	-9.5	-12.5	73	-6.1	3.7	-5.4
2	2.0	-0.7	1.2	38	-1.4	-4.5	1.8	74	-2.3	1.9	-4.4
3	-6.6	-2.2	3.7	39	-13.6	-6.6	7.3	75	-5.7	3.1	0.0
4	-4.3	1.5	2.1	40	2.0	-2.7	7.9	76	-19.0	-1.2	3.2
5	-8.2	-2.0	1.5	41	-3.2	0.1	-3.4	77	-26.6	2.5	-2.4
6	3.7	-1.1	2.4	42	-13.1	-10.3	-1.8	78	-26.2	10.3	-0.7
7	-1.8	-2.7	1.7	43	-10.1	-1.5	-7.8	79	-1.4	-1.7	0.4
8	5.1	-2.1	0.7	44	-10.3	-0.5	-8.8	80	-5.1	7.0	1.1
9	6.6		4.2	45	-7.9	-11.0	-4.8	81	-7.5	8.3	1.6
10	5.5	0.5	4.2	46	-3.1	2.5	1.0	82	-3.4	4.4	1.2
11	2.5	-2.0	2.3	47	-9.8	-3.9	-5.9	83	-3.8	3.6	1.1
12	4.0	0.5	4.0	48	-5.3	-5.8	-1.7	84	-2.3	3.3	1.2
13	5.7	0.0	2.7	49	1.6	-2.3	0.8	85	-1.3	6.5	-0.4
14	4.8	1.8	2.4	50	-3.9	-5.7	1.1	86	-4.4	1.9	-2.6
15	4.5	0.7	-1.3	51	-14.0	8.8	-5.7	87	-8.3	-1.6	-4.5
16	-1.2	-3.3	-1.0	52	-0.6	-0.7	0.2	88	-13.1	-6.1	-8.7
17	-1.0	-3.7	-4.9	53	-4.5	-0.2	-5.7	89	-7.3	1.3	-10.2
18	-0.6	-0.5	-2.4	54	-5.3	5.0	-0.9	90	-5.2	-2.1	-3.4
19	-4.9	-4.4	-4.2	55	-19.3	3.2	2.0	91	-11.9	-2.4	-5.1
20	-0.2	-1.9	-0.2	56	-4.1	-0.6	-1.8	92	-11.7	-1.5	-7.5
21	2.4	-2.1	-11.7	57	-9.7	-2.9	-4.7	93	-4.5	3.0	-6.7
22	-3.5	2.0	-1.9	58	-2.6	7.9	1.2	94	-2.5	2.6	4.9
23	-7.3	2.9	-1.5	59	-3.5	10.2	0.4	95	-1.2	1.4	7.0
24	-7.3	-2.2	-1.9	60	-5.9	3.7	2.3	96	-4.8	4.1	1.7
25	-4.9	-6.0	-0.2	61	-1.3	0.6	0.1	97	-3.4	4.8	2.6
26	-5.9	-13.0	-5.0	62	-0.6	-1.7	-2.5	98	-9.8	6.4	2.7
27	-12.5	-4.2	-11.1	63	-0.8	1.8	-1.8	99	-2.3	6.3	0.6
28	-3.6	-6.3	12.5	64	-0.5	-2.3	-0.3	100	-9.6	7.7	2.6
29	-7.5	-2.5	-9.6	65	-0.8	-1.3	-2.1	101	-2.8	3.4	1.3
30	-13.6	0.8	-2.9	66	-1.0	3.7	-0.7	102	-2.0	4.1	0.9
31	-10.9	1.4	-10.7	67	-1.0	-2.7	-0.7	103	-2.1	1.6	0.1
32	-4.7	4.1	-10.3	68	-1.1	-1.6	-5.4	104	1.3	0.6	8.0
33	-4.5	4.4	1.0	69	0.0	0.6	-1.4	105	2.4	-2.0	6.6
34	-5.4	6.5	3.6	70	-1.7	2.5	-1.1	106	1.5	-2.7	6.3
35	-7.2	6.6	1.6	71	-1.0	4.9	0.0	107	0.9	-7.3	6.1
36	-3.9	3.1	-2.3	72	-1.3	0.2	-5.8	108	-2.1	-9.0	-6.2

Appendix III

List of all the plant species found on the serpentine of Table Mountain, June 1st to August 25th 1974. All species identification and nomenclature follows Fernald (1950).

APPENDIX III

Trees

Abies balsamea
Acer rubrum
Alnus crispa
Amelanchier Bartramiana
Betula borealis
B. Michauxii
B. papyrifera
B. pumila
Larix laricina
Nemopanthus mucronata
Picea mariana
Pinus strobus
Prunus depressa
Salix sp.
Viburnum cassanoides

Shrubs

Andromeda glaucophylla
Arctostaphylos Uva-ursi
Chamaedaphne calyculata
Empetrum Nigrum
Epigaea repens var *glabrifolia*
Gaultheria procumbens
Gaylussacia baccata
G. dumosa var *Bigeloviana*
Juniperus communis
J. horizontalis
Kalmia polifolia
Ledum groenlandicum
Lonicera villosa
Myrica gale
Potentilla fruticosa
Pyrola gradiflora
Rhamnus alnifolia
Rhododendron canadense
R. lapponicum
Rosa nitida
Rubus pubescens
Vaccinium angustifolium
V. macrocarpon
V. Oxycoccus
V. uliginosum var *alpinum*
V. Vitis-Idaea

Herbs

Androsace septenrionalis
Anaphalis margaritacea
Anemone parviflora
Arenaria humifusa
A. marcescens
A. rubella
Armeria labradorica var *submutica*
Artemisia campestris
Aster nemoralis
Campanula rotundifolia
Castilleja septenrionalis
Cerastium arvense var *villosissimum*
C. beeringianum
C. terrae-novae
Circaea alpina
Cirsium vulgare
Clintonia borealis
Comandra Richardsiana
Conioselinum pumilum
Cornus canadensis
C. suecica
Cypripedium calceolus
Diapensia lapponica
Drosera intermedia
D. rotundifolia
Dryas integrifolia
Erigeron hyssopifolius var *villicaulis*
Euphrasia Randii var *Farlowii*
Gnaphalium norvegicum
Habenaria dilatata
Iris versicolor
Linnaea borealis
Linum catharticum
Lychnis alpina var *Americana*
Maianthemum canadense
Nuphar variegatum
Pinguicula vulgaris
Potentilla tridentata
Prenanthes trifoliata var *nana*
Primula mistassinica
Pyrus floribunda
Rhinanthus Crista-Galli
Sagina nodusa
Sanguisorba canadensis

Sarracenia purpurea
Saxifraga aizoides
S. bronchialis
S. oppositifolia
Senecio pauciflorus
S. pauperculus
Solidago hispida
S. multiradiata
Silene acaulis
Tanacetum huronensa var *terra-novae*
Thalictrum alpinum
T. polygamum
Tofieldia glutinosa
T. pusilla
Trientalis borealis
Utricularia cornuta
Viola cucullata

Grasses, Sedges and Rushes

Carex Buxbaumii
C. echinata
C. exilis
C. flava
C. lasioscarpa
C. limosa
C. livida
C. paupercula
C. rupestris
C. scirpoides
Danthonia intermedia
D. spicata
Deschampsia atropurpurea
D. cespitosa
D. flexuosa
Eriophorum angustifolium
E. Chamissonis
E. viridi-carinatum
Festuca rubra
F. scabrella
Juncus balticus
J. filiformis
J. trifidus
Poa glauca
P. palustris
Rhynchospora alba
Schizachne purpurascens
Scirpus cespitosus
S. hudsonianus
Triglochin maritima
T. palustris

Ferns

Adiantum pedatum var *aleuticum*
Osmunda regalis

Mosses

Dicranum bonjeani
Hylocomium splendens
Lycopodium annotinum
L. selago var *patens*
Microlepidozia sefacea
Mylia anomala
Pleurozium schreberi
Rhacomitrium lanuginosum
Selaginella selaginoides
Sphagnum fuscum
S. nemoreum
S. palustre
S. papillosum
S. rubellum

BIBLIOGRAPHY

Antevs, E. 1932. Alpine Zone of Mt. Washington Range. Merrill & Webber Co., Auburn, Maine, 54.

Austin, M.P. and Orloci, L. 1966. Geometric models in ecology. II. An evaluation of some ordination techniques, J. Ecol. 54:217-227.

Ayyad, M.A.G. and Dix, R.L. 1964. An analysis of a vegetation-microenvironmental complex on prairie slopes in Saskatchewan, Ecol. Monogr. 34 (6):421-441.

Bannister, P. 1968. An evaluation of some procedures used in simple ordinations, J. Ecol. 56:27-34.

Barrow, M.D., Costin, A.B. and Lake, F. 1968. Cyclical changes in an Australian fjaeldmark community, J. Ecol. 56:94-95.

Beals, E.W. 1973. Ordination: mathematical elegance and ecological naivete, J. Ecol. 61:23-35.

Bellair, P. 1969. Soil stripes and polygonal ground in the subarctic islands of Crozet and Kerguelen, in The periglacial environment--past and present, Ed., T.L. Pewe. McGill-Queen's University Press, Montreal.

Billings, W.D. and Mark, A. 1961. Interactions between alpine tundra vegetation and patterned ground in the mountains of southern New Zealand, Ecology 42:18-31.

Birrell, K.S. and Wright, A.C.S. 1945. A serpentine soil in New Caledonia, New Zeal. J. Sci. Tech. 27A:72-76.

Bjørlykke, B. 1938. Vegetasjonen pa olivinsten pa Sunmøre, Nyt Mag. f. Naturvid 79:51-126.

Bliss, L.C. 1962. Adaptation of arctic and alpine plants to environmental conditions, Arctic 15:117-144.

Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston and Co., Philadelphia.

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin, Ecol. Monogr. 27:325-349.

Brookes, I. 1964. The upland surfaces of western Newfoundland. M.Sc. thesis, McGill University.

Burges, A. 1951. The ecology of the Cairngorms. III. The Empetrum-Vaccinium zone, J. Ecol. 39:271-284.

Caborn, J.M. 1957. *Shelterbelts and microclimate*. Bull. For. Comm. Land, 29.

Cailleux, A. and Taylor, R. 1954. *Cryopédologie etude des sols geles*. Exped. Polaires franc. IV. Hermann, Paris.

Clements, F.E. 1934. The nature and structure of the climax. *J. Ecol*. 24:252-284.

○ Cooper, J.R. 1936. Geology of the souther half of the Bay of Islands igneous complex; Newfoundland, Dept. Nat. Res., *Geol. Sec. Bull. 4*.

Cox, C.B., Healey, I.N. and Moore, P.D. 1973. *Biogeography, an ecological and evolutionary approach*. Blackwell Scientific Publications, London.

○ ✓ Damman, A.W.H. 1965. The distribution patterns of northern and southern elements in the flora of Newfoundland, *Rhodora*, 67:363-391.

Dansereau, P. 1950. Flora and vegetation on the Gaspé Peninsula, *Wild Flower*, April 1950:26-39.

Deevey, E.S. 1949. Biogeography of the Pleistocene, *Bull. Geol. Soc. Am*. 60:1315-1416.

De Kimpe, C.R. and Zizka, J. 1973. Weathering and clay formation in a dunite deposit at Asbestos, *Can. J. Earth Sci*. 10:1533-1540.

Drury, W.H. 1966. Plant persistence in the Gulf of St. Lawrence, pp. 105-148, in *Essays in plant geography and ecology*, Ed., K.N.H. Greenridge. Nova Scotia Museum, Halifax.

Fernald, M.L. 1907. The soil preferences of certain alpine and subalpine plants, *Rhodora* 9:149.

○ ✓ Fernald, M.L. 1911. A botanical expedition to Newfoundland and southern Labrador, *Rhodora* 13:109-162.

○ ✓ Fernald, M.L. 1918a. The geographic affinities of the vascular floras of New England, the Maritime Provinces and Newfoundland, *Am. J. of Bot*. 5:219-237.

○ ✓ Fernald, M.L. 1918b. The contrast in the floras of eastern and western Newfoundland, *Am. J. of Bot*. 5:237-247.

Fernald, M.L. 1924. Isolation and endemism in north-eastern America and their relation to the age and area hypothesis, *Am. J. of Bot*. 11:558-572.

Fernald, M.L. 1925. Persistence of plants in unglaciated areas of boreal America, *Mem. Amer. Acad. Arts Sci*. 15:238-342.

Fernald, M.L. 1926. Two summers of botanizing in Newfoundland, *Rhodora* 28:49-63, 74-87, 89-111, 115-129, 145-155, 161-178, 181-204, 210-225, 234-241.

13085
13084

Fernald, M.L. 1933. Recent discoveries in the Newfoundland flora, *Rhodora* 35:1-16, 47-63, 80-107, 120-140, 161-185, 203-223, 231-247, 265-283, 298-315, 327-346, 364-384, 395-403.

Fernald, M.L. 1950. *Manual of botany: a handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada*. American Book Co., New York.

Ferreira, R.E.C. 1963. Some distinctions between calciphilous and basiphilous plants. I. Field data, *Trans. Bot. Soc. Edinb*. 39: 399-421.

Ferreira, R.E.C. 1964. Some distinctions between calciphilous plants and basiphilous plants. II. Experimental data, *Trans. Bot. Soc. Edinb*. 39:512-524.

Gauch, H.G. 1973. The relationship between sample similarity and ecological distance, *Ecology* 54:618-622.

Gause, G.F. 1934. *The struggle for existence*. Johns Hopkins University Press, Baltimore.

Gittens, R. 1965. Multivariate approaches to a limestone grassland community, *J. Ecol*. 53:385-425.

Goodall, D.W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis, *Aust. J. Bot*. 2:304-324.

Goodall, D.W. 1973. Sample similarity and species correlation, pp. 107-149 in *Ordination and classification of communities*, Ed., R.H. Whittaker, Pt. 5 of *Handbook of Vegetation science series*, Ed., R. Tuxen. Pub. W. Junk, The Hague.

Gordon, A. and Lipman, C.B. 1926. Why are serpentine and other magnesian soils infertile? *Soil Sci*. 22:291-302.

Grant, D.R. 1969. Late pleistocene re-advance of Piedmont glaciers in western Newfoundland, *Maritime Sediments* 5:126-128.

Gregory, S. 1963. *Statistical methods and the geographer*. Longman, London.

Greig-Smith, P. 1964. *Quantitative plant ecology*. Butterworths, London.

Hadley, E.B. and Bliss, L.C. 1964. Energy relationships of alpine plants on Mt. Washington, New Hampshire, *Ecol. Monogr*. 34:331-357.

Harada, A.M. 1953. The weathering of serpentine in Wakasa-Machi, Tottori Prefective, J. Sci. Soil and Manure 23:137-140.

Harshberger, J.W. 1903. The flora of the serpentine barrens of southeast Pennsylvania, Science N.S. 18:339-343.

Harshberger, J.W. 1904. A phyto-geographic sketch of extreme southeastern Pennsylvania, Bull. Torrey. Bot. Club 31:125-159.

Hesse, P.R. 1971. A textbook of soil chemical analysis. Chemical Publishing Co., Inc., New York.

Hunter, J.G. and Vergano, O. 1952. Nickel toxicity in plants, Ann. Appl. Biol. 39:279-284.

Huxley, C. and Odell, L.C. 1924. Notes on surface markings in Spitsbergen. Geog. Jour. 63:207-229.

Jackson, M.L. 1958. Soil chemical analysis. Prentice-Hall, London.

Johnson, C.M., Pearson, G.A. and Stout, P.R. 1952. Molybdenum nutrition of crop plants. II. Plant and soil factors concerned with molybdenum deficiencies in crop plants, Plant and Soil 4:178-196.

Kanno, I.,Tokudome, S., Arimura, S., and Onikura, Y. 1965. Genesis and characteristics of brown forest soils derived from serpentine in Kyushu, Japan. Part 2. Genesis and characteristics of brown forest soils, Soil Sci. Plant Nutr. 11:1-10.

Kotilainen, M.J. 1944. Kasvit erikoislaatuisen substraatin indikaattoreina, Arsbok Soc. Sci. Fern. 22B (6):1-18.

Kruckeberg, A.R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. Am. J. Bot. 38: 408-419.

Kruckeberg, A.R. 1954. Plant species in relation to serpentine soils, J. Ecol. 35:267-274.

Lämmermayr, L. 1934. Ubereinstimmung und Unterschiede in der Pflanzendecke über Serpentin und Magnesit, Naturw. 72:27-38.

Loew, O. and May, D.W. 1901. The relation of lime and magnesium to plant growth. I. Liming of soils from a physiological standpoint. II. Experimental study of the relation of lime and magnesia to plant growth, U.S. Dept. Agr. Plant Ind. Bull. 1.

Low. 1884. Geol. Surv. Can. Rep. for 1882-3-4, Pt. F7, 8.

Lyon, G.L., Peterson, P.J., Brooks, R.R., and Butler, G.W. 1971. Calcium, magnesium and trace elements in a New Zealand serpentine flora, J. Ecol. 59:421-430.

Maarel, E. van Der. 1969. On the use of ordination models in phytosociology, Vegetatio 19:21-46.

Marie-Victorin, F. 1938. Phytogeographical problems of eastern Canada, Am. Midland Naturalist 19:489-558.

Mason, H.L. 1946. The edaphic factor in narrow endemism. I. The nature of environmental influences, Madrono 8:209-226.

McIntosh, R.P. 1967. The continuum concept of vegetation, Bot. Rev. 33:130-187.

Morison, C.G.T., Hoyle, A.C. and Hope-Simpson, J.F. 1948. Tropical soil-vegetation catenas and mosaics. A study in the south-western part of the Anglo-Egyptian Sudan, J. Ecol. 36:1-84.

Morrison, J.L. 1941. A monograph of the section Streptanthus Nutt. I. Two new species in the section Euclisia Nutt. Ph.D. Dissertation, University of California, Berkeley.

Nagatsuka, S. 1967. Genesis of a soil derived from serpentine in Mikkali-Cho Shizuoka Prefecture, J. Sci. Soil and Manure, 38:187-192.

Novak, F.A. 1928. Quelques remarques relatives au probleme de la vegetation sur les terrains serpentiniques, Preslia 6:42-71.

Orloci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods, J. Ecol. 54:193-227.

Pennell, F.W. 1910. Flora of the Conowingo Barrens of southeastern Pennsylvania, Proc. Acad. Nat. Sci. Philadelphia 62:541-584.

Pennell, F.W. 1913. Further notes on the flora of the Conowingo or Serpentine Barrens of southeastern Pennsylvania, Proc. Acad. Nat. Sci. Philadelphia 64:520-539.

Pennell, F.W. 1930. On some critical species of the Serpentine Barrens, Bartonia 12:1-23.

Pichi-Sermolli, R. 1948. Flora e vegetazione delle serpentine e delle altre ofioliti dell 'Alta Valle del Tevere (Toscana). (English summary). Webbia 6:1-380.

Polunin, N. 1934. The vegetation of Akpatok Island, J. Ecol. 22:337-395.

Proctor, J. and Woodell, S.R.J. 1971. The plant ecology of serpentine. I. Serpentine vegetation of England and Scotland, J. Ecol. 59:375-395.

Proctor, J. 1971a. The plant ecology of serpentine. II. Plant response to serpentine soils, J. Ecol. 59:397-410.

Proctor, J. 1971b. The plant ecology of serpentine. III. The influence of a high magnesium/calcium ratio and high nickel and chromium levels in some British and Swedish serpentine soils, J. Ecol. 59:827-842.

Radford, A.E. 1948. The vascular flora of the olivine deposits of North Carolina and Georgia, Jour. Elisha Mitchell Sci. Soc. 64: 45-106.

Raup, H.M. 1941. Botanical problems of boreal America, Bot. Rev. 7: 147-248.

Richards, P.W. 1932. Ecology, pp. 366-396 in Manual of bryology, Ed., Verdoorn, F. Martinus Nijhoff, The Hague.

Robinson, W.O., Edgington, G., Byers, H.G. 1935. Chemical studies of infertile soils derived from rocks high in magnesium and generally high in chromium and nickel, U.S. Dept. Agr. Tech. Bull. 471.

Ross, C.S. and Hendricks, S.B. 1946. Minerals of the montmorillonite group, U.S. Geol. Survey Prof. Paper 205:23-79.

Rune, O. 1953. Plant life on serpentines and related rocks in the north of Sweden, Acta. Phytogeog. Suecica 14:101-106.

Sasaki, S., Matsuno, T. and Kondo, Y. 1968. A podzol derived from serpentine rocks in Hokkaido, Japan, Soil Sci. Plant Nutr. 14: 99-109.

Schellmann, W. 1964. Zur lateritischen Verwitterung von Serpentinit, Geol. Jahrb. 81:645-678 (English Abst.).

Seddon, B. 1971. Introduction to biogeography. Duckworth, London.

Sedletski, I.E. 1945. Colloid-dispersoid mineralogy, Acad. Sci. U.S.S.R., 114. (Cited in Y.F. Yoffre's Pedology. Pedology Publications, New Brunswick, N.J.)

Shacklette, H.T. 1962. Influences of the soil on boreal and Arctic plant communities. Ph.D. Dissertation, University of Michigan.

Sharp, R.P. 1942. Soil structures in the St. Elias Range, Yukon Territory, J. Geomorph. 5:274-293.

Shreve, F. 1910. The ecological plant geography of Maryland, Midland Zone, Lower Midland District, pp. 199-219 in The plant life of Maryland, by F. Shreve, M.A. Chrysler, F.H. Blodgett and F.W. Besley. Johns Hopkins University Press, Baltimore.

Sigafoos, R.S. 1952. Frost action as a primary physical factor in tundra plant communities, Ecology 33:480-487.

Smith, C.H. 1958. Bay of Islands igneous complex western Newfoundland. Geological Survey of Canada Memoir 290, Dept. Mins and Tech. Surveys.

Spence, D.H.N. 1957. Studies on the vegetation of Shetland. I. The serpentine debris vegetation of Unst, *J. Ecol*. 45:917-945.

Spence, D.H.N. 1958. The flora of Unst, Shetland, in relation to the geology, *Trans. Bot. Soc. Edinb*. 37:163-173.

Spence, D.H.N. 1959. Studies on the vegetation of Shetland. II. Restriction of the exclusive pioneers to serpentine debris, *J. Ecol*. 47:641-649.

Spence, D.H.N. 1970. Scottish serpentine vegetation, *Oikos* 21:22-31.

Stevens, R.K. 1970. Cambro-Ordovician flysch sedimentation and tectonics in west Newfoundland and their possible bearing on a proto-Atlantic Ocean, *Geol. Assoc. Can*. Spec. Paper No. 7:165-177.

Strong-Moorhead, Sigsby Ltd. 1971. *Gros Morne National Park*. *Analysis of existing factors and constraints*. Report submitted to: Dept. of Indian Affairs and Northern Develop., National and Historic Parks Branch, National Parks Service--Atlantic Region.

Swan, J.M.A. 1970. An examination of some ordination problems by use of simulated vegetational data, *Ecology* 51:89-102.

Taber, S. 1943. Perenially frozen ground in Alaska: its origin and history, *Bull. Geol. Soc. Am*. 54:1433-1548.

Taylor, B.W. 1955. Terrace formation on Macquarie Island, *J. Ecol*. 43: 133-140.

Tidmarsh, C.E.M. and Havanga, C.M. 1955. The wheel-point method of survey and measurement of semi-open grasslands and karoo vegetation in South Africa, *Mem. Bot. Surv. S. Afr*. 29:1-49.

Tivy, J. 1971. *Biogeography. A study of plants in the ecosphere*. Oliver and Boyd, Edinburgh.

Tricart, J. 1970. *Geomorphology of cold environments*. Macmillan and Co., London.

Twenhofel, W.H. and MacClintock, P. 1940. Surface of Newfoundland, *Bull. Geol. Soc. Amer*. 51:1665-1728.

Venaile, F. and Van der Marel, H.W. 1963. An interstratified saponite swelling chlorite mineral as a weathering product of lizardite rock from St. Margherita Staffora (Pavia province), Italy, *Beit. Mineral. Petrog*. 9:198-245.

Vlamis, J. and Jenny, H. 1948. Calcium deficiency in serpentine soils as revealed by adsorbent technique, *Science* 107:549-552.

Vlamis, J. 1949. Growth of lettuce and barley as influenced by degree of calcium saturation of soil, *Soil Sci*. 67:453-466.

Walker, R.B. 1948. Molybdenum deficiency in serpentine barren soils, Science 108:473-475.

Walker, R.B. 1954. The ecology of serpentine soils. II. Factors affecting plant growth on serpentine soils, Ecology 35:259-266.

Watt, A.S. 1947. Pattern and Process in the plant community, J. Ecol. 35:1-22.

Watt, A.S. and Jones, E.W. 1948. The ecology of the Cairngorms. Part I. The environment and the altitudinal zonation of the vegetation, J. Ecol. 36:283-296.

Watts, P. 1971. Principles of biogeography. McGraw-Hill, London.

Whittaker, R.H. 1954. The ecology of serpentine soils, Ecology 35:258-288.

Whittaker, R.H. 1967. Gradient analysis of vegetation, Biol. Rev. 42: 207-264.

Whittaker, R.H. 1973. (Ed.) Ordination and classification of communities, Part 5 of Handbook of vegetation science series, Ed. R. Tuxen. Pub. W. Junk, The Hague.

Whittaker, R. H. 1973. Wisconsin comparative ordination, Ch. 8 in Ordination and classification of communities, Ed. R.H. Whittaker, (ibid.).

Wildman, U.E., Jackson, M.L. and Whittig, L.D. 1968. Iron-rich montmorillonite formation in soils derived from serpentinite, SSSA Proc. 32:787-794.

Williams, H. 1971. Mafic-ultramafic complexes in western Newfoundland Appalachians and the evidence for their transportation: a review and interim report, Geol. Assoc. of Can. Proc. 24:9-25.

Wilson, J. 1952. Vegetation patterns associated with soil movement on Jan Mayen Island, J. Ecol. 40:249-264.

Zoltai, S.C., Pollett, F.C., Jeglum, J.K. and Adams, G.D. Developing a wetland classification for Canada. (Manuscript.)

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