ASPECTS OF THE ECOLOGY OF COASTAL TUNDRA RAISED BEACH RIDGES IN NORTHWESTERN ONTARIO

By

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ABSTRACT

The structure of lichen dominated vegetation is described within a series of raised beach ridges found along the strip of coastal tundra in northwestern Ontario. The patterns of distribution of the most abundant species correlated with the topographic influences of individual beach ridges more than with the influences of the general developmental sequence of vegetation from the coast of Hudson Bay , inland.

The importance of topography to the structure of this vegetation was examined by comparing ridge top and bottom positions of raised beach ridges in terms of edaphic factors, snow cover and microclimatic factors. A new experimental system was developed to test for adaptation of net photosynthetic rates in the lichens *Alectoria ochroleuca* (Hoffm.) Massal. and *Cetraria nivalis* (L.) Ach. to the contrasting ridge surfaces from which they were collected. Morphological adaptations to these beach ridge surfaces were also examined.

Seasonal patterns of net photosynthesis in both species showed that intra and interspecific differences in seasonal acclimation were important to the observed patterns of distribution in the field. Thallus morphology was found to provide optimal water relations for photosynthetic production . Experiments showed further that the potential for control of evaporative loss is present in lichens.

This study shows that the patterns of distribution observed in the field , are consistently related to the topographic relations of individual

beach ridges . These patterns are also consistent with both the physiological and morphological requirements exhibited by the plants, and with the defined physical characteristics of the surfaces on which they grow.

ACKNOWLEDGEMENTS

I would like to extend my sincere thanks to my friend and supervisor Dr. K.A.Kershaw , for his continued interest and guidance in the completion of this study. I also thank the members of the supervisory committee , Drs. W.R.Rouse , D.E.N. Jensen , and G.P.Harris for their advice throughout this study. I would also like to thank Ms. Janet Edmonds, Mr. Eugene Maikawa , Mr. Herbert Deruyter and Ms. Margaret Webber for expert technical assistance both in the field and in the laboratory. Special thanks are offered to Ms. Jocelyn Voortman for her dedication in typing the final copy. Finally I wish to thank Ms. Dawn Ewings for her valuable criticisms , consolation and companionship in the final stages of this study.

This thesis is dedicated to my parents.

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Section 1

INTRODUCTION

Lichen dominated vegetation covers extensive areas of arctic, antarctic, and alpine environments (Billings, 1974). This particular type of vegetation has been shown to be important to the control of microclimatic patterns (Rouse and Kershaw, 1971), to the feeding behaviour of large mammals (Ahti and Hepburn, 1967; Andreev, 1954), and to the initial colonization of recently glaciated land (Webber and Andrews, 1973). Although lichens, as a group of plants, have been reported in abundance in high latitude or altitude sites, detailed studies of the structure of lichen dominated systems are few. As a result, there is very little information available regarding the factors controlling the distribution of individual lichen species. Although some studies have dealt with lichens from temperate-alpine and boreal forest environments, the complexity of these systems has prevented a clear understanding of those factors governing the distribution of the plants. In contrast arctic systems are much less complex than forested areas because the overlying canopy is absent. Yet intensive investigations in these regions has only recently been initiated.

Neal and Kershaw (1973a,b) and Kershaw and Rouse (1973) have studied coastal raised beach tundra at Cape Henrietta Maria and East Pen Island, respectively. This coastline supports a narrow strip of arctic tundra containing both poorly drained areas which support a productive meadow dominated by sedges, mosses, willows, and dwarf birches, and well-drained upland sites which support a lichen heath vegetation composed of lichens, mosses, and ericaceous shrubs. These upland areas are usually raised beach ridges formed as a result of isostatic uplift and subsequent recession of the coastline of Hudson Bay (Webber et al, 1970). In the upland areas the dominant plant association was a general lichen heath (Neal and Kershaw, 1973b; Kershaw and Rouse, 1973) composed of *Alectoria ochroleuca* (Hoffm.) Massal., *Cetraria nivalis* (L.) Ach., *C. islandica* (L.) Ach., *C. cucullata* (Bell.) Ach., *Cladina mitis* (Sandst.), *C. rangeferina* (L.) Wigg., *Dryas integrifolia* Wahl. and *Rhododendron lapponicum* (L.) Wahl. in varying abundance.

In the most recent study (Kershaw and Rouse, 1973) which took the form of a primary survey a general developmental sequence of vegetation from the coast inland was described. In the set of ridges adjacent to the coast two forms of the general lichen heath were separated based on the absence of *C. mitis* and *C. rangiferina*. It was thought that the general lichen heath II (containing both *C. mitis* and *C. rangiferina*) was associated with the older inland beach ridges while the general lichen heath I, lacking these two species, was associated with more recently uplifted beaches. Although the abundance of many species, for example, *Alectoria ochroleuca* and *Cetraria nivalis*, appeared visually to vary both between and within individual beach ridges in the ridge system, the primary survey (Kershaw and Rouse, 1973) was insensitive to these fluctuations, since the method was designed to demonstrate more general trends. Thus as an initial step in examining such patterns, a secondary survey of higher resolution was warranted to establish on a quantitative basis the distributional characteristics of individual species within this series of recently exposed beach ridges.

Such a survey should be sensitive to both the overall developmental sequence of vegetation and environmental factors from the coast inland and to effects independent of any age sequence which are characteristic of the contrasting topographic zones of the raised beach ridge surfaces. Since beach ridges show geomorphological consistency throughout this coastline, a series of independent samples may be taken, thus providing spatial replication of sampling units. Approaches utilizing spatial replicates of sampling units have been used by a number of authors (Sheard, 1968; Harris, 1972; Kershaw, 1964; Railton and Sparling, 1973) although most studies relating the distribution of plants to environmental factors have utilized samples taken from one site or a set of dependent sites (Bliss and Hadley, 1964; Lange, 1969; Adams, 1971a; Dinger and Patten, 1974; Barclay-Estrup and Nuttall, 1974). The lack of any spatial contrast and geomorphological consistency represents a major criticism of these studies.

If the pattern of species distribution is shown to be consistently related to either the inland developmental sequence or to the contrasting topographic positions of raised beach ridge surfaces, the design of the study must involve an examination of those factors which may be controlling. As shown in Figure 1, species distribution may be governed by 1) controls of growth rates by edaphic factors or physiological stresses present in the environment, 2) control of growth rates by limitations of photosynthetic production, 3) physical factors not related to growth rates, such as wind erosion and animal browsing. Approaches of this type have been used by many authors including Bliss and Hadley (1964), Reed and Waring (1974), Harris (1972), Karenlampi (1971), Bjorkman and Holmgren (1963), Eickmeier and Adams (1973), Lange and Kappen (1972), Lechowicz and Adams (1973), Kershaw and Rouse (1971), and Larsen (1971). These approaches are useful since they point to (by correlation) biologically important variables on a variety of time and spatial scales. Since no

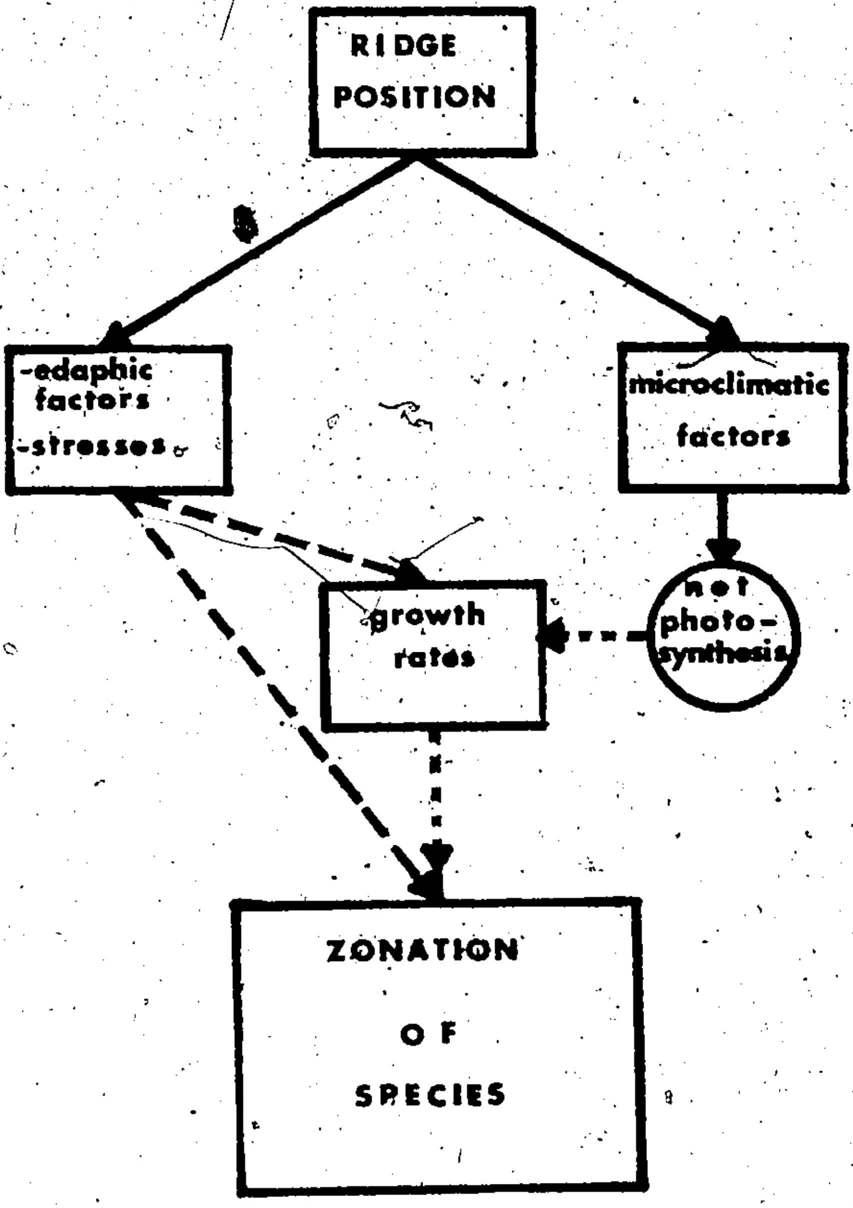
Figure 1.

Species distribution may be influenced by :

a) variables influencing growth rates directly, such as edaphic factors, environmental stresses, or microclimatic factors;

b) variables influencing the distribution of the plants directly by mechanical means such as wind erosion and animal browse.

In a situation in which growth rates are not measureable , it may be possible to determine the relative importance of these different variables by testing for specific adaptations in the plants (such as the responses of net photosynthesis) to these variables. Dashed lines refer to those factors not directly measureable, while solid lines refer to those directly measureable.


RIDGE POSITION
-edaphic factors
-stresses
microclimatic factors
net photo-synthesis
growth rates
ZONATION OF SPECIES

information was available regarding the coastline of Hudson Bay, (Kershaw and Rouse, 1973; Hare, 1972), an examination of both edaphic and microclimatic factors over raised beach ridge surfaces was required.

The measurement of soil moisture content, peat depth, topography and snow depth is relatively straightforward and could thus be made throughout the ridge system. Conversely, microclimatic factors such as windspeed, temperature, and evaporation rates were extremely difficult to measure. As a result, these variables would only be practically measured across individual beach ridge surfaces.

Topographically related differences in microclimate have been described only for clear-sky conditions when solar radiation predominates (Geiger, 1971). Yet conditions of diffuse radiation which are often associated with precipitation and low temperatures at these latitudes are of potentially great importance to a lichen dominated vegetation (Gannutz, 1968). Topographically related differences in microclimate under conditions of diffuse radiation are extremely small thus requiring very sensitive instrumentation.

Those measures of edaphic or microclimatic factors which correlate with observed zonation of individual species are ecologically interpretable if the species concerned show features which adapt them to these conditions. The demonstration of these adaptive characteristics, however, requires very careful selection of the proper experimental system. For example, if edaphic factors, physiological stresses and microclimatic factors all influence the distribution of plants over these raised beach ridge surfaces, detailed measurement of one or two characteristics exhibited by the vegetation may not adequately demonstrate adaptive patterns to the beach ridge environments. Such complex interactions can be avoided by the selection of the simplest experimental system which still contains significant ecological information. Since lichens do not have roots, and generally propagate by thallus fragmentation, it is reasonable to consider adaptation of these organisms to aspects of the atmospheric environment only. In addition, in these raised beach ridge systems lichens are the most abundant components of the vegetation and are likely to contain significant ecological information.

Throughout the literature dealing with the ecology of lichens considerable emphasis has been placed on correlations between spatial distribution and the physiological response to atmospheric conditions of moisture content, temperature, and light, as measured by CO_2 exchange. The use of growth studies, however, as independent tests of observed patterns of gas exchange (Karenlampi, 1971) is difficult since growth rates of lichen thalli are very low. Thus experimental approaches as would be used to study the ecology of a higher plant are not available. Investigations of the ecology of lichens must rely heavily on gas exchange studies. Accordingly rigorous examination of experimental methods and design is necessary. In addition, existence of genetic variation and acclimation as potentially important ecological parameters requires that the experimental data should be collected from as wide a range of environmental conditions as possible.

Early studies by Stålfelt (1939) and Stocker (1927) and more recently by Lange (1969), Kallio and Heinonen (1971), Harris 1971b , Kershaw (1971) and Adams (1971a,b) have examined gas exchange characteristics in lichens from a variety of habitats and under a variety of experimental conditions. In all of these studies the time and space limitations of the experimental methods have permitted only uni- or bivariate experimental designs. For example, Adams (1971a,b) has examined the response of CO_2 fixation in Cladina rangiferina (L.) Wigg. to thallus moisture content, thallus temperature, and light intensity. In experiments examining the response of net photosynthesis to light intensity the thalli were held at optimal moisture content whereas when thallus moisture content was varied, all experiments were performed at a single constant light intensity. In this study (Adams, 1971a,b), aside from the experimental problems of maintaining thallus saturation levels constant, experiments did not show the interaction of variables. Similarly, Harris (1971b), examining three Parmelia species, measured separate responses of CO_2 fixation to light at 100% thallus saturation and to thallus moisture content at 1,600 foot candles. Models of primary production which utilize such limited data as input, assume that the response to thallus moisture content is the same at all light intensities. The basic assumption is that the model is linear and there are no secondary or tertiary interactions. This is not a valid assumption and necessitates the incorporation of corrective terms in the model to yield an acceptable result (Harris, 1972). An adequate description of such systems requires the basic data from factorially arranged experiments. Such experiments would display the important secondary or tertiary interactions among variables controlling net photosynthetic rates as a physiological data matrix. The limiting factor in the generation of such matrices lies in the slow gas analysis methods used. Both Lechowicz et al. (1974) and Lange (1969) have indicated their inability to handle clonal or seasonal variation because of the time required to conduct the more basic investigation. Methods to date typically involve gas-flow networks coupled to environmentally controlled cuvettes which were originally developed to study the photosynthetic characteristics of higher plants (Jarvis et al. 1971). While these methods may still be useful in studying higher plants, the use of such systems to examine gas exchange characteristics in lichens is difficult due to the low rates of carbon fixation, in the range of 0.1 to 3.0 mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$ dry wt. as compared with rates up to 140 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ in higher plants (Jarvis et al 1971). Examination of net CO_2 fixation rates of lichen material in such experimental systems is made possible only by striking a reasonable balance between the amount of plant material enclosed in the cuvette and the flow rate of air drawn over the material. If small amounts of material are used (Harris, 1971b; Kershaw, 1972), the low rates of fixation also demand a low flow rate of gas through the cuvette. These low rates can be made to provide reliable measures of net photosynthesis, but if flow rates are too low they may underestimate actual levels of fixation (Larson and Kershaw, 1975b, Kershaw, 1976; Kershaw, 1972). If large amounts of material are used (Lange, 1969; Kallio and Heinonen, 1971; Adams, 1971a,b), very rapid flow rates are required and the lichen material is thus exposed to a uncontrolled environmental condition (Larson and Kershaw, 1975b).

Unsuitable methods for measuring CO_2 exchange represent one of the major obstacles to research progress in lichen ecology and thus a new approach is a necessity. Any effective experimental system must satisfy the following three conditions: it must be able to measure very small levels of gas exchange using small weights, 0.5 to 2.0 grams, of lichen material. It must allow continuous measurement of the critical variables influencing gas exchange in the lichen material during the experiments. It must allow this to be done rapidly to afford examination of an entire matrix of environmental conditions, several times throughout a growing season. If a new method can be developed to satisfy these requirements, seasonal patterns of net photosynthesis in lichens can be examined in relation to the known physical characteristics of the beach ridge surfaces from which the lichens were collected.

An examination of the interaction between lichen morphology and water relations may also be useful in characterizing adaptations of lichens to specific physical environments. Differences in water relations due to morphology or growth habit alone have not been shown (Heatwole, 1966; Scofield and Yarman, 1943). In fruiticose lichens there are two aspects of the morphology, other than the internal structure of the lichen which may influence its water relations. Both the surface area of a thallus and its orientation to an air-stream will determine the area available for light interception and gas exchange. For example, the mat-forming Cladina alpestris shows very marked vertical stratification of thallus moisture content, temperature, and light because of the dense, finely-branched growth habit (Field, 1974). Similarly, Kershaw and Rouse (1971) found that moisture probes placed twenty cm below the lichen-air surface in this species remained saturated even after a full day of clear sky conditions. The morphology of C. alpestris contrasts markedly with that shown by Ramalina maciformis (Del)Bory in the Negev desert which has been show to imbibe and lose water much more rapidly (Lange, 1969). In these two cases the surfaces are exposed (or protected) from stresses in a very different manner. These mechanisms of control may be of adaptive significance and require examination in relation to the physical characteristics of the beach ridge environments from which the lichens were collected.

This thesis concerns itself with examining the relationships between the distribution of plants and the morphological and physiological adaptations linking them to measurable physical characteristics of the surfaces on which they grow. This study involves the objective determination of the structure of a piece of tundra vegetation on a series of raised beach ridges, the characterization of the physical environment of these raised beach ridge surfaces, and the examination of the relationships between physiological and morphological characteristics shown by the abundant species to defined environmental conditions.

The Research Sites

The main body of the research was conducted between 1972 and 1974 at the East Pen Island research site (lat. 57° 85', long. 88° 55') as shown in Figures 2&3. Details of the climate of the area are given in Figure 4. Additional information was collected in winter, 1973, near the community of Fort Severn, 85 miles southeast along the coast from the Pen Island camp.

While the main research camp at Pen Island is situated on the node of the most recently formed raised beach system (Figure 3) the initial study was restricted to five individual beach ridges, eight kilometers southeast along the coast, (Figure 3) designated area 1. More intensive investigation was directed to two topographic features adjacent to the main research site (area II). Site a was an area of hummock/hollow features, while site b was a typical beach ridge surface. A more pronounced ridge inland (area III) was also studied. Winter studies at Fort Severn were conducted on ridges whose general topographic and vegetational characteristics were similar to those found at Pen Island

Soils on all ridges were fine to coarse sands mixed with fine gravels.

A thin peat layer was present and continuous permafrost was found at depths varying from 0.5 to 2.0 meters during the summer.

Figure 2.

The Hudson Bay region showing the location of East Pen Island.

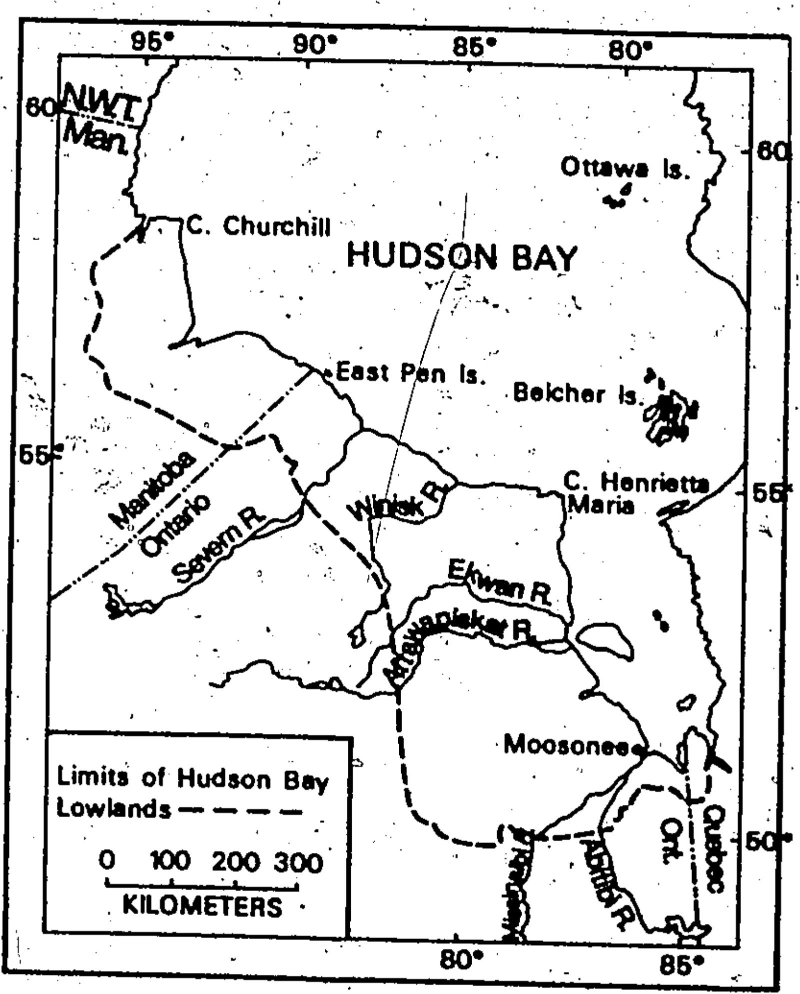

95°
90°
85°
80°
60°
NWT
Man.
60
Ottawa Is.
C. Churchill
HUDSON BAY
East Pen Is.
Belcher Is.
55°
55°
C. Henrietta Maria
Manitoba
Ontario
Severn R.
Winisk R.
Ekwan R.
Attawapiskat R.
Moosonee
Quebec
Ont.
Abitibi R.
50°
Limits of Hudson Bay Lowlands
0 100 200 300
KILOMETERS
80°
85°

Figure 3.

A diagrammatic representation of the raised beach system under study. The base camp, study ridges of area I , plus areas II and III are clearly shown. The hummock/hollow features in area II are found near a ; the raised beach ridge in area II is found near b.

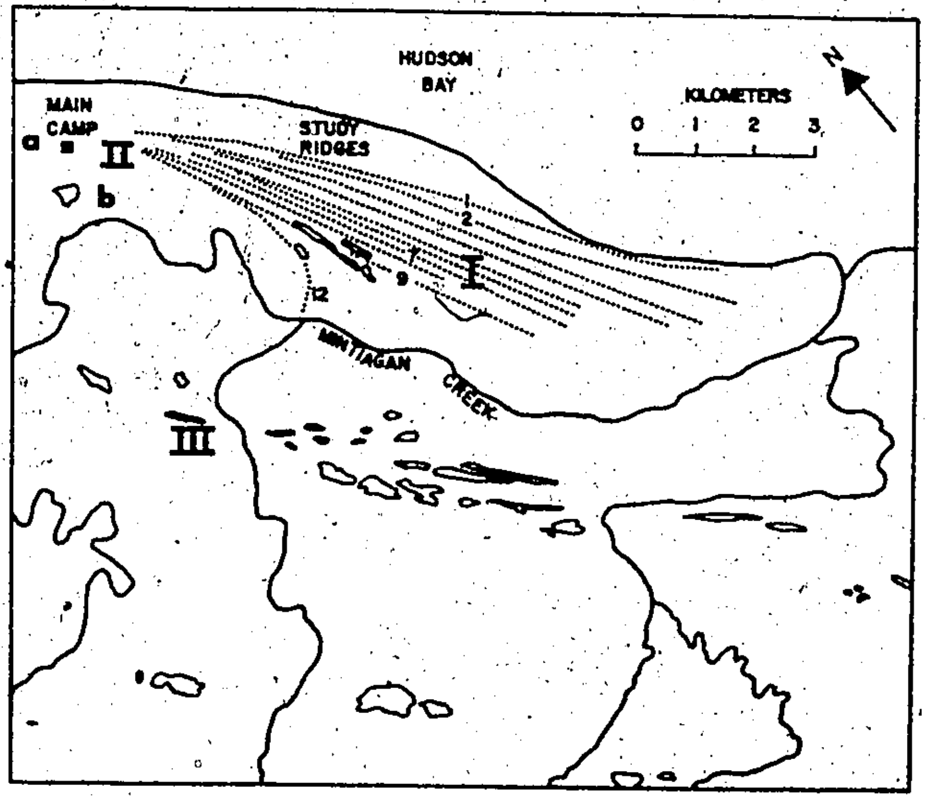
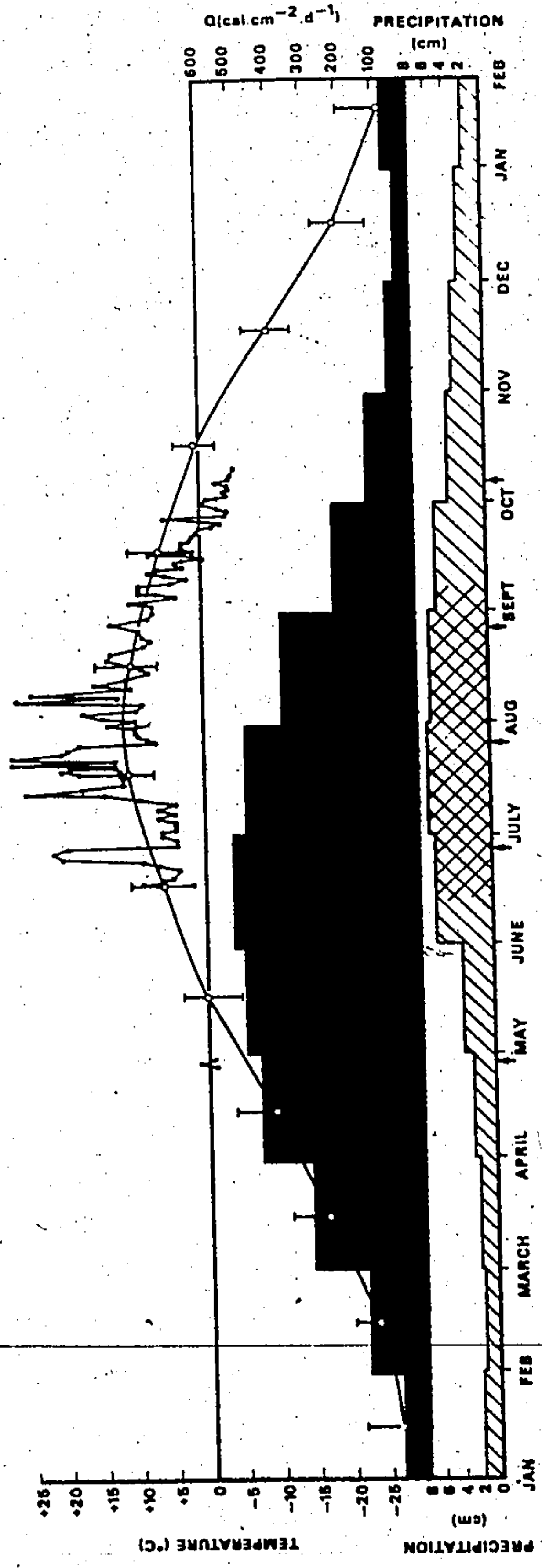

HUDSON
BAY
KILOMETERS
0
1
2
3
N
MAIN
CAMP
a
II
b
STUDY
RIDGES
1
2
7
9
12
I
MINTIAGAN
CREEK
III

Figure 4.

General features of the yearly climatic patterns of the Pen Island research site. Shown are averages for 1) precipitation as snow (hatching) and rainfall (cross-hatching) , 2) incoming solar radiation (stipple) , 3) screen height monthly mean, maximum and minimum dry bulb temperatures (open circles plus bars). Superimposed on these patterns are observed screen height daily average dry bulb temperatures for 1974 (solid circles) . Arrows indicate collection dates for samples described in the text. Data are abstracted from Thompson (1966) and from the Churchill weather office.


Q(cal.cm^{-2}.d^{-1})
PRECIPITATION
(cm)
600
500
400
300
200
100
8
6
4
2
FEB
JAN
DEC
NOV
OCT
SEPT
AUG
JULY
JUNE
MAY
APRIL
MARCH
FEB
JAN
+25
+20
+15
+10
+5
0
−5
−10
−15
−20
−25
8
6
4
2
0
TEMPERATURE (°C)
PRECIPITATION
(cm)

Section 2.

METHODS

(2.1) Quantitative Analysis of the Ridge Sequence

Five ridges were chosen for study on the basis of accessibility, adequate interridge separation, and the absence of gross topographic irregularities due to permafrost and wind erosion activity (Figure 3). Since the ridges are laid down from the node outwards, it was also necessary to obtain samples in a line perpendicular to the shore. This prevents any compounding of the inland vegetational change with that running along any one ridge to its most recently formed section.

Each ridge was sampled by six 33 m X 4 m transect zones orientated parallel to the ridge and spaced equally, 7 m apart, over the ridge profile. Six replicate 1 m^2 quadrats were then randomly placed within each transect. Each quadrat was subdivided into nine equal subquadrats. Results were averaged to give transect mean values. The ridge system is represented as 30 transect positions on five ridges.

The domin scale previously used by Neal and Kershaw (1973a,b) and Kershaw and Rouse (1973) is too insensitive to effectively demonstrate the actual variations in abundance levels found in this vegetation. Accordingly percent cover was chosen as the measure. Percentage cover is easily applied to arctic vegetation which characteristically has a low or prostrate habit. Although percent cover is a good estimate of the spatial abundance of a plant, it does not measure the vertical component of structure. This can only be achieved using cover repetition which is impossible in this particular vegetation type. Total standing biomass, however, is a particularly useful measure of the vertical component of lichen dominated systems since the plants have no root systems and the entire thallus can be collected for weight determinations. Three of the six m^2 quadrats in each transect were sampled for lichen biomass. A cylindrical 10 cm diameter core sampler was used, with samples being air-dried and weighed subsequently. These weights were then corrected for litter content and oven dry weight (80°C, 24 hrs). For determination of the biomass of each species, three of the nine samples from each m^2 quadrat were dissected to component species.

Dryas integrifolia represents by far the largest proportion of the vascular plant cover in the area, and in addition to cover value, an independent measure of its performance seemed appropriate. Total yield measurements are very time consuming and can only be realistically done on a small sample because of the spreading root systems. Conversely, rapidly obtained measurements of aerial plant parts over a large sample area have been found to be useful indices of performance (Phillips, 1954; Kershaw, 1960,1962). The index of performance chosen here was the product of leaf width and length (in mm^2) at the widest and longest points. In August, following the period of greatest growth, the m^2 quadrats, sub-sampled for biomass, were also sampled for Dryas performance. Six leaves were sampled from three shoots within each subquadrat.

Principle components analysis and linear regressions were used to analyse the vegetational data. The principle component analysis operates on a plot by plot similarity matrix (weighted similarity coefficient, Orloci, 1966) derived from the raw cover data. The technique has been shown to be a useful tool for extracting ecological information from a large data set (Orloci, 1966, 1967 ; Austin, 1968; Austin and Greig-Smith, 1968; Greig-Smith et al, 1967; Kershaw, 1968; Jesberger and Sheard, 1973; Neal and Kershaw, 1973b; Kershaw and Rouse, 1973). The data are presented in graphical form (Kershaw and Shepard, 1972) with each quadrat or transect having a set of coordinates on three orthogonal axes representing linear uncorrelated components in the solution of the original plot similarity coefficient matrix. The first axis extracts the greatest proportion of the total variance in the data cluster; successive axes remove the next largest proportion of the remaining variance until the residual is zero.

(2.2) Physical Characteristics of Individual Beach Ridges

(2.2.1) Edaphic Factors and Snow Cover

The depth of peat to the underlying sand surface was measured from a profile exposed on each subquadrat (see above). At the same time two 100 cm^3 soil samples were taken within each m^2 quadrat and sealed in plastic bags. Fresh weights and oven dry weights (110°C, 24 hrs.) were determined allowing calculation of surface soil moisture by both weight and volume.

For topographic measurements twenty-five points within each m^2 quadrat plus the end points of each transect were measured with reference to the coastal mud flats as a high tide datum point. The data were combined to give a profile of elevation within the ridge system. These measures provide estimates of both the degree of exposure to the north winds and age of each ridge.

The Pen Island research site is inaccessible between December and March. Raised beaches of morphology similar to those at the primary research site are found near the community of Fort Severn, eighty-five miles southeast along the Hudson Bay coast from the Pen Island camp. These ridges were examined between December, 1973 and March, 1974. In April, 1974 the Pen Island site was accessible and snow cover patterns over the raised beach ridge surfaces were examined at this time (for details see Larson and Kershaw, 1975a).

The depth and distribution of snow was measured over tundra raised beach ridge surfaces, sedge meadows, and forested areas. Vertical depth of snow was measured down the edge of snow pits dug out to expose 1 m^2 of the ground surface. Vegetation exposed in this manner at Fort Severn was found to be similar in species composition and abundance to ridges found at the Pen Island research site. Table 1 gives details of the distribution of sample pits both at Fort Severn and Pen Island sites. Elevations were made in reference to the nearest windward sedge meadow.

(2.2.2) Microclimatic Factors

The ridge over which microclimatic factors were measured was located five km inland at area III (Figure 3). The topographic profile of this ridge is shown in Figure 5.

Temperature Measurements

The measurement of temperature differences over the raised beach ridge surface at area III (Figure 5) was ideally achieved using thermocouples with their characteristic high sensitivity, accuracy, and low radiation errors (Tanner, 1963; Peiters and Schurer, 1973). The thermocouples used in this study were constructed of 42 (0.064 mm) gauge copper-constantan wire to maximize the above characteristics. Probes were built with five sensing junctions fanned out as shown in Figures 6a,b,c,. An ice reference temperature of 0°C was used; calibration from mv to degrees Calcius is linear from 0° to 30°C and accurate to 0.1°C. For air temperature the probes were exposed in a horizontal position whilst for thallus temperature the thermocouple element was inserted into the thallus. Air temperature probes were attached to support tubing at a height of 4 cm above the vegetation and the sensors fanned out in a horizontal plane. Thallus temperature probes completely covered with lichen were returned to their original positions in the lichen mat. Temperatures

TABLE I

Details of Sample Sites at Fort Severn and Pen Island.

Site Number and Location			Month	Distance Inland	Aspect	Dominant Vegetation	Number of Snow Pits and distribution
1	tundra raised beach	Fort Severn	Dec. Mar.	1.0 km.	60 E	*Alectoria ochroleuca* *Cetraria nivalis* *Dryas integrifolia*	11,1 transect perpendicular to ridge axis
2	tundra raised beach	Fort Severn	Dec. Mar.	5.0 km.	60 E	*Alectoria nitidula* *Dryas integrifolia* *Alectoria ochroleuca*	30,2 transects perpendicular to ridge axis
3(a-e)	forested raised beaches	Fort Severn	Dec. Mar.	6-10 km.	40-70 E	*Cladina alpestris* *Cladina rangiferina* *Ledum groenlandicum*	2 pits at crest of each of 5 ridges
4	tundra raised beach	Pen Island	Apr.		60 E	*Alectoria ochroleuca* *Cetraria nivalis* *Alectoria nitidula* *Dryas integrifolia*	11,1 transect perpendicular to ridge axis
5	tundra raised beach	Pen Island	Apr.	6.0 km.	90 E	*Alectoria nitidula* *Cladina alpestris*	5,1 transect perpendicular to ridge axis

Figure 5.

A cross sectional diagram of the raised beach ridge in area III some 5 km inland , is shown to the right. Mast I is situated on the ridge top, while mast II is on the ridge bottom.

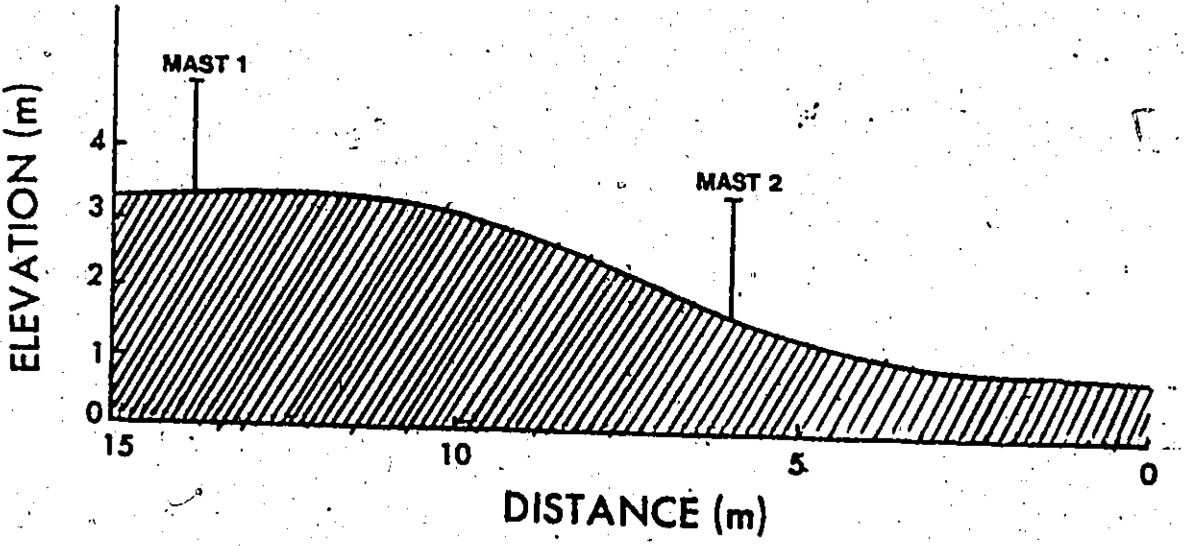

MAST 1
MAST 2
ELEVATION (m)
4
3
2
1
0
15
10
5
0
DISTANCE (m)

Figure 6.

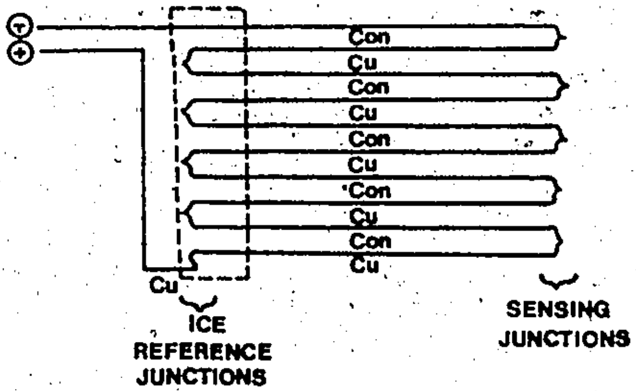
Construction of the thermocouple probes.

a) This shows a diagrammatic view of the probe, with five sensors wired in series. Cu represents copper, Con represents constantan.

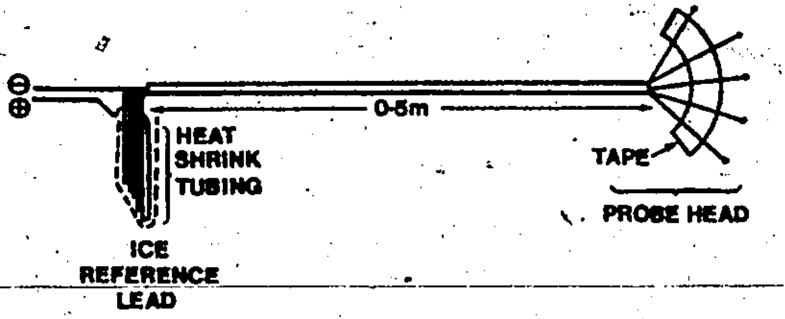
b) The completed probe has five tips fanned out. All ice reference junctions must be completely immersed in the ice bath.

c) Photograph showing the orientation of a temperature probe over a lichen surface. The sensors are fanned out in a horizontal plane 4 cm above the vegetation.

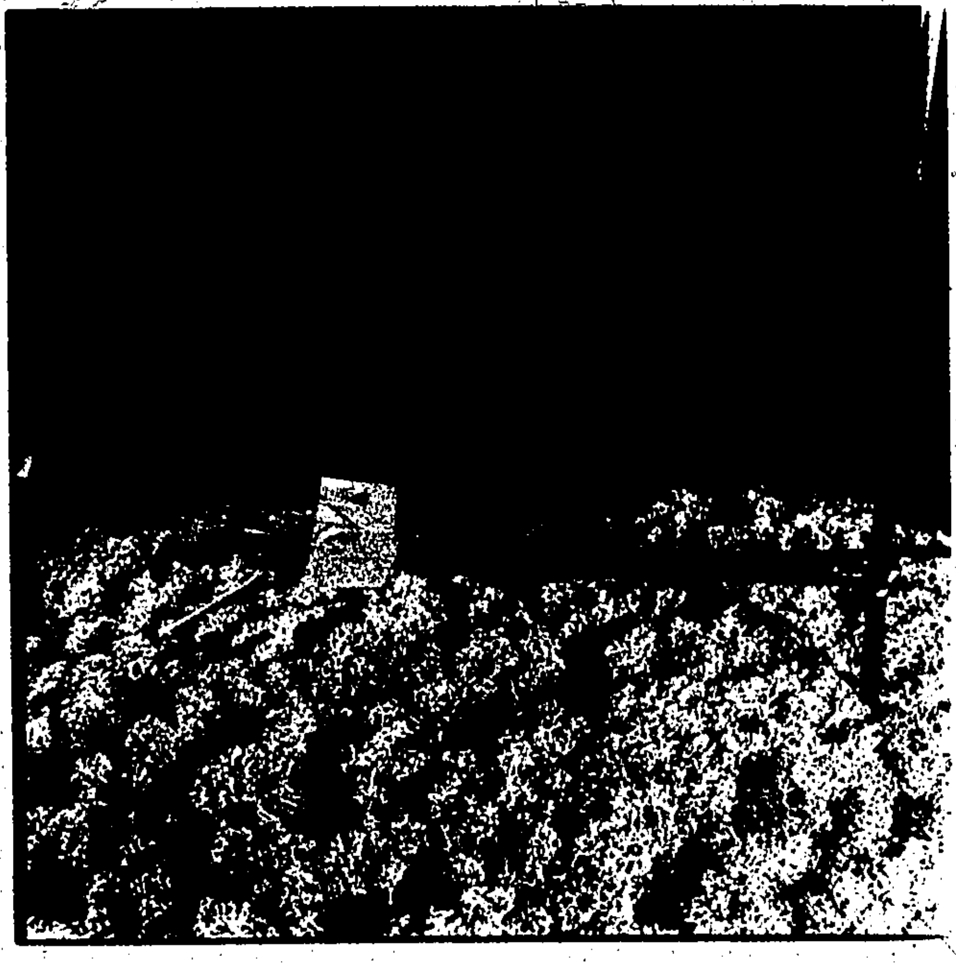
A


⊖
⊕
Con
Cu
Con
Cu
Con
Cu
Con
Cu
Con
Cu
Cu
ICE REFERENCE JUNCTIONS
SENSING JUNCTIONS

B


⊖
⊕
0·5m
HEAT SHRINK TUBING
TAPE
PROBE HEAD
ICE REFERENCE LEAD

C



were measured at both ridge top and bottom positions and recorded on strip chart recorders housed in a tent 35 m downwind.

Windspeed Measurements

Similar requirements of rapid response time, great sensitivity, and high accuracy, demanded of the temperature system, were also necessary in the measurement of windspeed. These requirements are adequately met by constant temperature hot-film anemometry (Tanner, 1963; King, 1914; Simmons, 1949). A thermo-systems 1051-2 power supply and monitor were connected to a constant temperature anemometer module 1054-B containing a wheatstone bridge circuit as shown in Figure 7. The sensing probe (model 1270) and its support (model 1170) are shown in Figure 8a,b respectively. The probes work in the following way: the temperature of an electrically heated quartz film on a glass rod of diameter 0.025 mm (Figure 8a) is maintained at a constant level by voltage supply from a modified wheatstone bridge circuit. The variations in windspeed at the probe surface are sensed by the bridge which modifies the heating voltage supply to the sensor to maintain its temperature. These small variations in voltage supply are measured and can be read as $m \cdot sec^{-1}$ windspeed by reference to a calibration curve. Since the temperature of the sensor is maintained at $550^{\circ}C$, fluctuations in voltage caused by changes in ambient temperature are insignificant (Thermo-Systems Incorporated, 1973). Windspeed was measured at either 4, 16, and 128 cm or 8, 16, and 64 cm at both stations on the ridge. The signals were gathered by automatic stepping switches of new design (Field et al., 1974) and directed into single channel laboratory recorders housed in a tent. A diagrammatic layout of the system is shown in Figure 9. (for details see Kershaw and Larson, 1974).

Figure 7.

Block diagram of the hot-film anemometry system, adapted from Thermo-Systems Inc. 1973 .

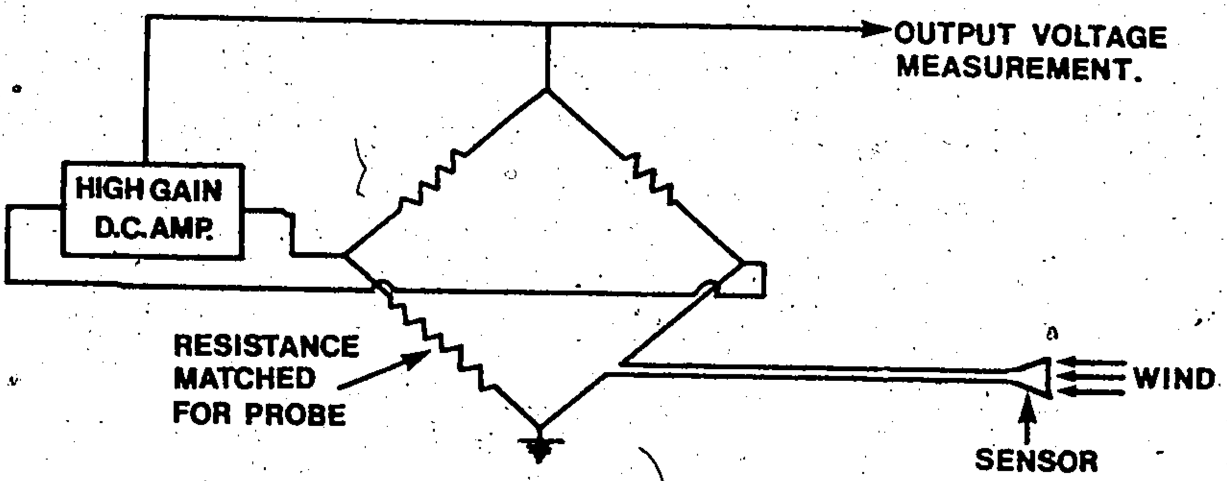

OUTPUT VOLTAGE MEASUREMENT.
HIGH GAIN D.C. AMP.
RESISTANCE MATCHED FOR PROBE
WIND
SENSOR

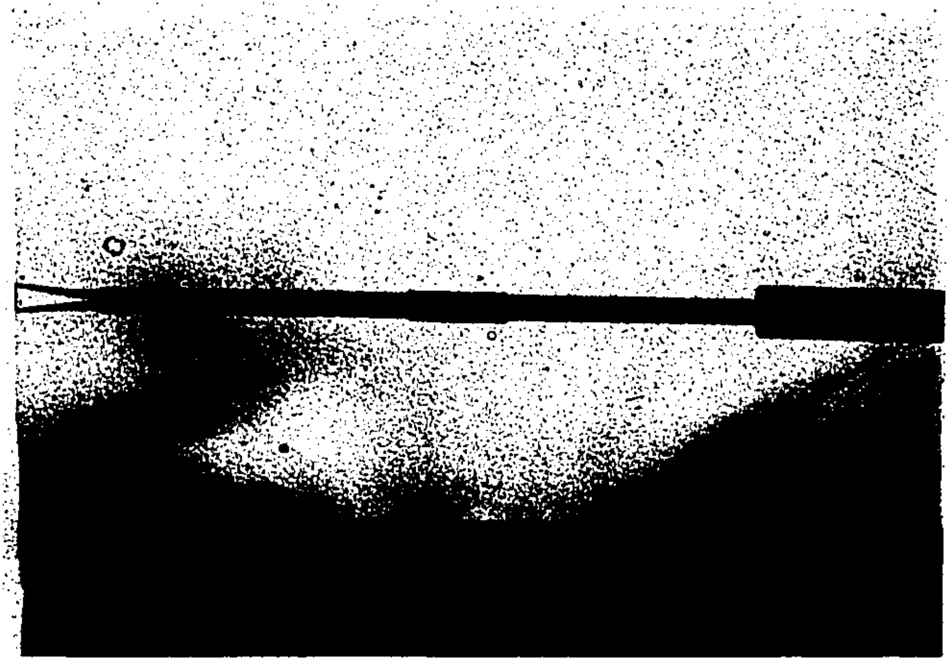
Figure 8.

Photographs showing the details of the windspeed sensors.

a) Detail of the sensing element and the probe support (x 3) .

b) Detail of the positioning of the wind sensor over the vegetated surface (x 0.5).

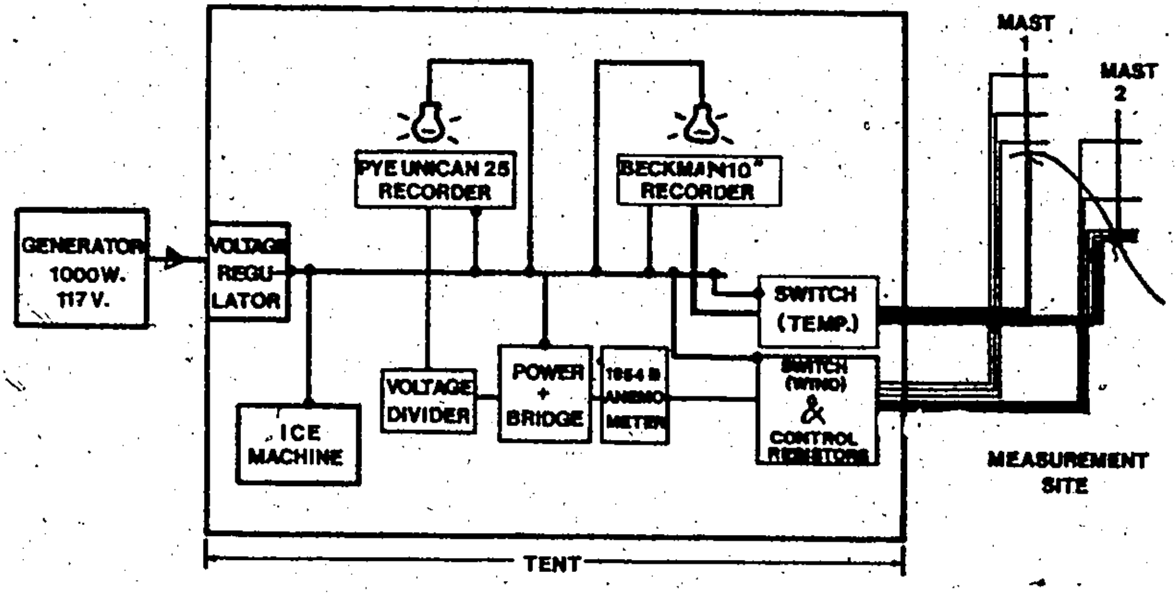
A



B

Figure 9.

This is a diagrammatic view of the complete measurement system on the raised beach ridge in area III. Instruments housed in the tent are clearly shown. The distance between the tent and the ridge is 35 m.


GENERATOR
1000 W.
117 V.
VOLTAGE REGULATOR
PYE UNICAN 25 RECORDER
BECKMAN 10" RECORDER
ICE MACHINE
VOLTAGE DIVIDER
POWER + BRIDGE
1054 B ANEMOMETER
SWITCH (TEMP.)
SWITCH (WIND) & CONTROL RESISTORS
MAST 1
MAST 2
MEASUREMENT SITE
TENT

Measurements of Drying Rates

Relative rates of water loss were compared for ridge surfaces which showed contrasting exposed and sheltered zones. At area II the rates of drying from exposed hummocks dominated by Dryas integrifolia were compared to rates found on adjacent hollows dominated by Alectoria ochroleuca (Figure 10, a,b,c). The relief from hummock to hollow was about 0.1 m. These results were compared to results from a similar study conducted over the ridge profile at area III (see Figure 5) some 5 km inland. Drying rates were determined as the change in resistance shown by 0.5 cm^2 resistance grid moisture probes (Harris, 1971b; Kershaw and Rouse, 1971) as the filter paper sandwich dries out. This instrumentation permits an examination of the differential drying rates over these two surfaces. Twenty probes were placed on both the top and bottom ridge positions in area III. Ten probes were used on the hummock/ hollow features of area II. Barnstead resistance bridges interfaced through manual stepping switches were used to determine resistance changes. During the drying runs, values for all probes at one position were averaged. Experiments using the grids were initiated whenever the lichen mat and adjacent grids were saturated which occurred after rainstorms or during mists.

(2.3) Net CO_2 Exchange

The experimental system necessary for this study requires the measurement of CO_2 fixation in each species as a function of temperature, thallus moisture content, light intensity, time of year, and topographic position to form a physiological data matrix . Initial testing of older flow systems of design after Kershaw (1972) (see Figure 11a) showed these methods to be much too time consuming and insufficiently sensitive leading to severe underestimation of net CO_2 exchange. A modified flow system was

Figure 10.

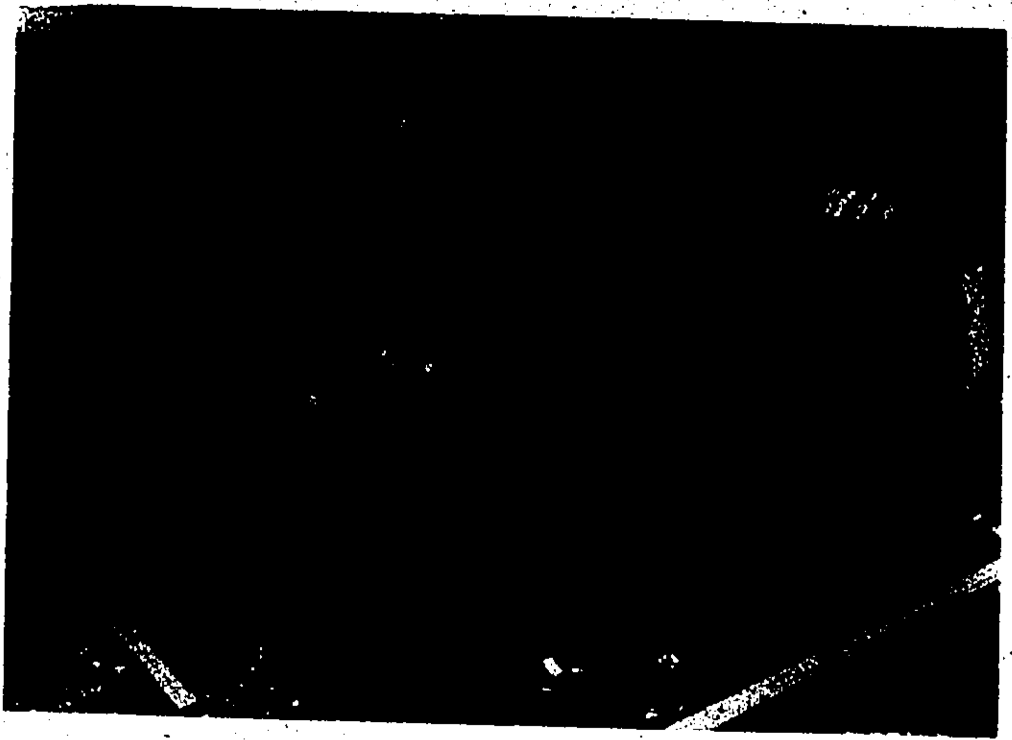
One of the hummock/ hollow features in area II near the coast.

a) Site 2 instrumented for drying runs. Meter sticks giving reference scale are removed during experiments.

b) Close-up of the same surface as in (a) above. North is towards the left.

c) Microrelief of this same surface. Position of probes is marked: X- hummock probes ; 0 - hollow probes. Contour in cm.

A



3

c

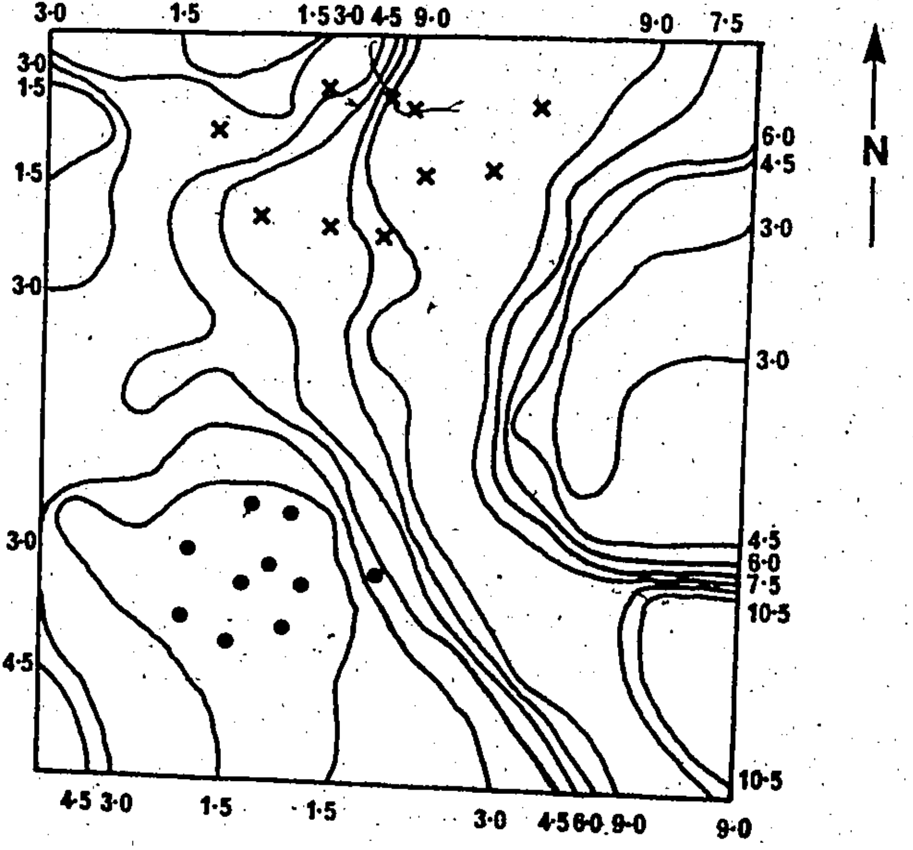

3·0
1·5
1·5 3·0 4·5 9·0
9·0
7·5
3·0
1·5
1·5
3·0
6·0
4·5
3·0
3·0
N
3·0
4·5
4·5
6·0
7·5
10·5
10·5
4·5 3·0
1·5
1·5
3·0
4·5 6·0 9·0
9·0

Figure 11.

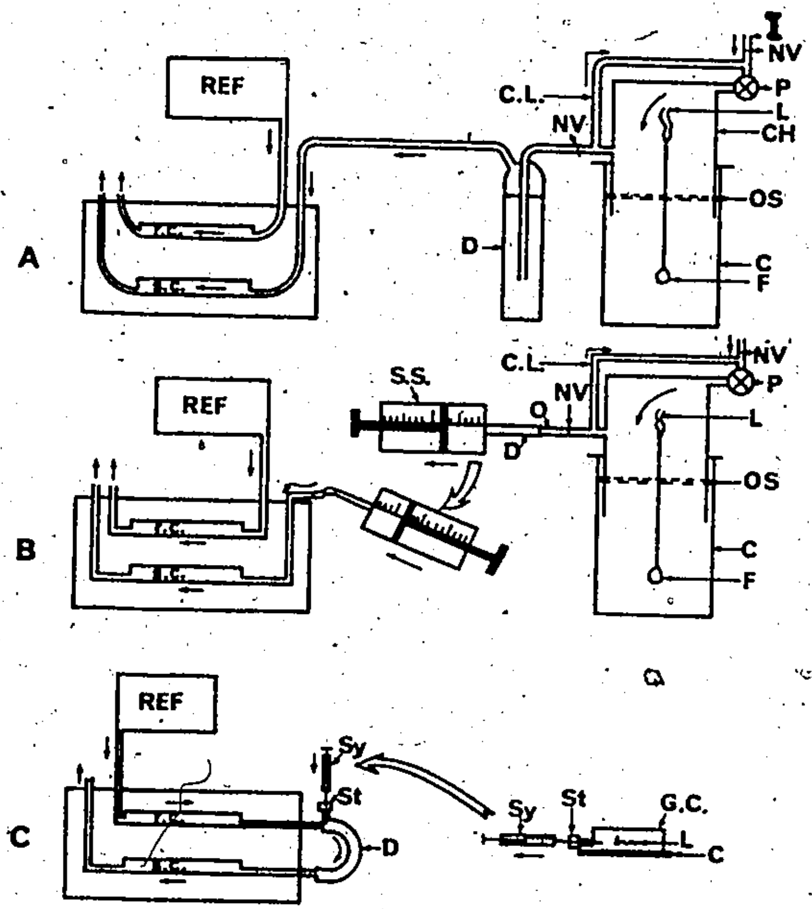
The various gas analysis systems used in this study are illustrated here.

a) The gas flow system designed after Kershaw (1972) , volume 2.0 l .

b) The modified flow system reduced to 0.8 l in volume, incorporating the use of a gas sampling syringe.

c) The new experimental system utilizing gas exchange cells.

Symbols : I, inlet; NV, needle valve; P, pump; L, lichen; CH, assimilation chamber; OS, oil seal; C, cover; F, float; CL, circulating loop; D, drying apparatus; r.c., reference cell of IRGA; s.c., sample cell of IRGA; REF, reference gas supply; O, output; S.S., gas sampling syringe (500 ml) ;G.C., gas exchange cell ; st. serum stopper; Sy., 2 ml. sampling syringe.

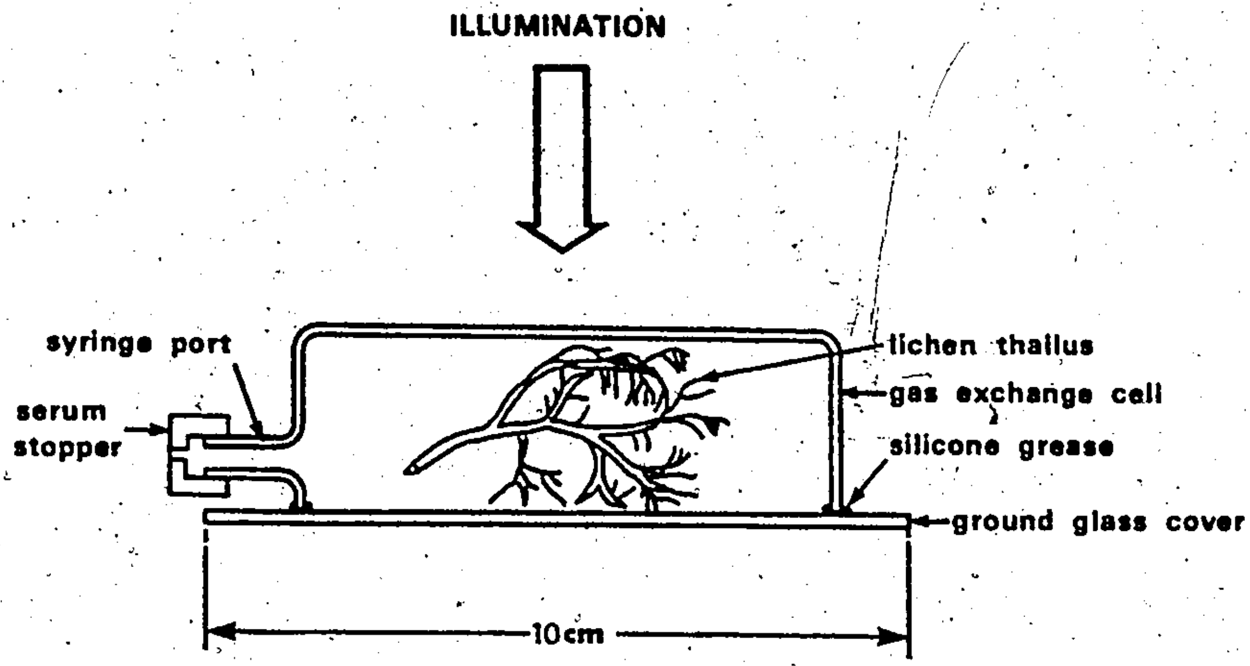

A
REF
C.L.
NV
NV
P
L
CH
OS
D
C
F
B
REF
S.S.
C.L.
NV
NV
P
L
Q
D
OS
C
F
C
REF
Sy
St
D
Sy
St
G.C.
L
C

then developed which provided reliable results but was still extremely slow (Figure 11b). By blending concepts used in gas chromatography and infrared gas analysis, a new rapid method, specially designed for cryptogams, was developed which permits physiological matrices to be constructed (Figure 11c). These matrices are generated by following the response of net photosynthesis to thallus moisture content (one of the primary controlling factors of carbon assimilation in lichens, Farrar, 1973) at a variety of light intensities, thallus temperatures, and times of year for each collection.

Instead of using an assimilation chamber of standard design (Jarvis et al, 1971) gas exchange cells as shown in Figure 12 were designed with ground glass covers sealed with Dow Corning high vacuum silicone grease and with small syringe ports for removal of gas samples. Saturated lichen material is placed within the cell under given experimental conditions. A 2 ml gas sample is removed to permit the measurement of the input concentration of CO_2 to which the lichen is exposed. The plants are sealed in the gas exchange cells until positive or negative fixation of CO_2 changes the concentration of that gas by about 50-100 ppm. A second 2 ml gas sample is then taken. The difference between input and output concentrations, standardized to ppm per unit time, measures CO_2 fixation in mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$ under the given experimental conditions. The lichen material is then removed, weighed, and the process is repeated until the thallus is air-dry. Thus each replicate sample shows the response of net CO_2 fixation to thallus water content from saturation to air-dry. Tests were conducted to show that the silicone grease is impermeable to CO_2 and that the levels of fixation at any water content of the thallus are equilibrium levels. All experiments were conducted within a walk-in growth chamber with the gas analyzer mounted outside as a precautionary measure.

Figure 12.

A diagrammatic representation of the gas exchange cells. Volume 100 ml.


ILLUMINATION
syringe port
serum stopper
lichen thallus
gas exchange cell
silicone grease
ground glass cover
10cm

The CO_2 concentration is measured in the following way: A Beckman 215A infrared gas analyzer (IRGA) is used on maximum sensitivity. A carrier reference gas (200 ppm CO_2/N_2, 200 ml/ min)flows first through the reference cell, then through a short (30 X 1 cm) drierite packed column into the sample cell of the IRGA. An injection port is placed at the junction of the reference cell and drierite column. After injection of a 2 ml gas sample into the injection port, the CO_2 concentration in the IRGA sample cell changes to a maximum and then rapidly returns to the same concentration as the reference cell. Recorder deflections appear as sharp peaks with a zero line set at the known concentration of the reference carrier gas. Peak height is calibrated against known standards and is accurate to 5 ppm. The calibration is linear for each flow rate/sensitivity setting. The gas analyzer is thus analogous to the detector unit of a simple gas chromatographic system (for details see Larson and Kershaw, 1975b).

There are many advantages of the new experimental system. The IRGA requires no separate calibration. There are no problems related to evaporative cooling of thalli as is found when using ventilated cuvettes since evaporation proceeds only between incubations. Any number of replicates can be accommodated in experimental situations.

Jarvis et al (1971) have critically reviewed infrared gas analysis techniques as used to monitor carbon uptake in higher plants and two aspects of such methods, CO_2 limitation and ventilation, should be examined in relation to the measurement of net photosynthesis in lichens using this method. The level at which CO_2 limitation occurs was determined experimentally for the gas exchange cells under a range of environmental conditions. The possible depression of CO_2 exchange rates due to a ventilation effect was examined in several ways:

by a direct comparison of results obtained with those using a modified flow system (both methods using *Alectoria ochroleuca* at 14°C and a light intensity of 150 µ einsteins · m^2 · sec^{-1} from maximum thallus moisture content to air-dry); by comparing results obtained with the new system against rates previously reported in the literature; and by mixing the air within the dish during experimental periods which was achieved by pumping a 3 ml syringe during the incubation periods producing a minimum air-speed of 1.25 m/sec as measured by hot-wire anemometry.

The results from these tests show that the rate of CO_2 fixation at a given level of thallus saturation is constant in *A. ochroleuca*, *C. nivalis*, and *Parmelia caperata* (L.) Ach. between 150 and 350 ppm (Figure 13). A safe lower limit of CO_2 concentration was subsequently taken as 200 ppm during all experiments. The experiments conducted to test for the requirements of ventilation utilized the flow system shown in Figure 11b. This design was modified after Kershaw (1972) in such a way that reliable results were obtained (see Figure 14 for comparison).

Comparison of the results obtained from a ventilated flow system modified after Kershaw (1972) and from the new gas exchange cells both run at 14°C and 150 µ einsteins · m^{-2} · sec^{-1} show differences only at high water contents (Figure 14). These slight differences reflect the much greater sensitivity of the new method at the start of any experiment. Similarly the experiments conducted using *C. nivalis* and *P. caperata* show rates of fixation which are the same as those quoted by Kallio and Heinonen (1971), Scholander et al. (1952), Bliss and Hadley (1964), for *C. nivalis* and by Harris (1972) for *P. caperata*, thus confirming the general lack of requirement for ventilation (Table II). In another test using *Peltigera polydactyla* (Neck.) Hoffm. the experimental atmosphere in the gas exchange cells was mixed using a syringe. The results show no differences between mixed and unmixed incubations (Table III).

Figure 13.

The response of CO_2 fixation to CO_2 concentration shows reduction in rates of uptake near 150 ppm., in the three species tested. Points indicate individual determinations : ● , *Alectoria ochroleuca* O , *Cetraria nivalis* , and X , *Parmelia caperata*.

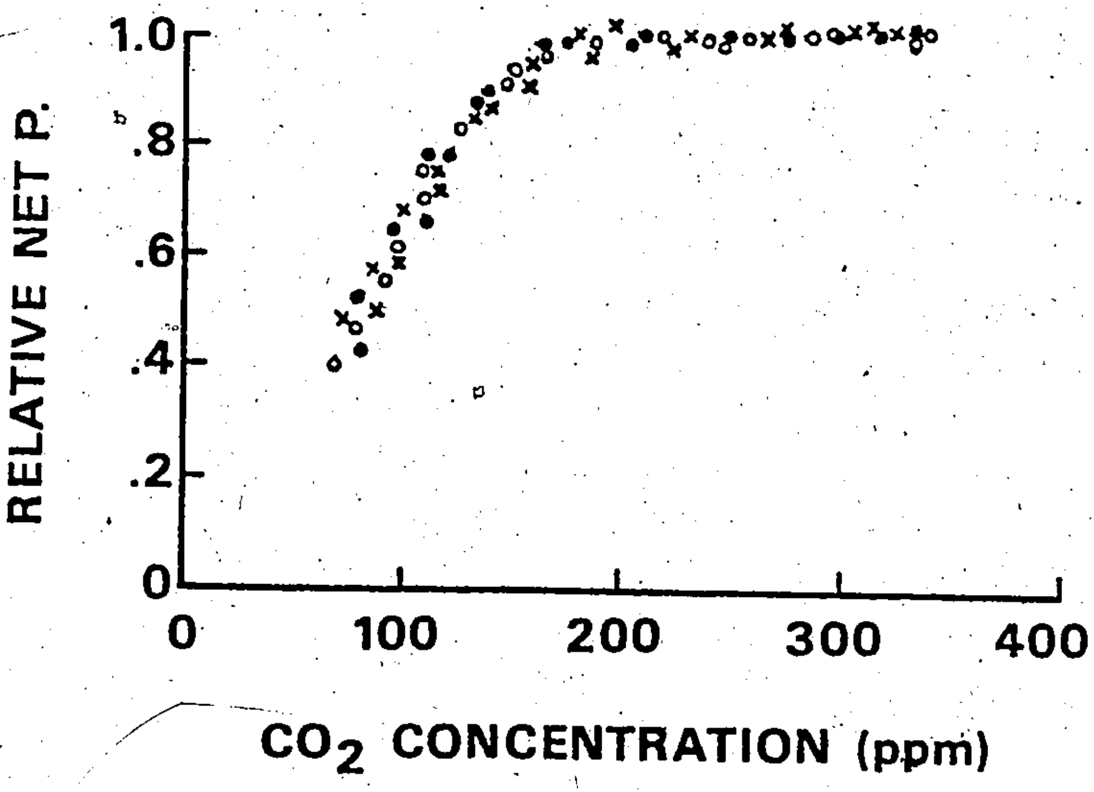

RELATIVE NET P.
1.0
.8
.6
.4
.2
0
0
100
200
300
400
CO2 CONCENTRATION (ppm)

Figure 14.

The response of net photosynthesis of <u>Alectoria</u> <u>ochroleuca</u> at 150 μeinsteins $\cdot m^{-2} \cdot sec^{-1}$ (above the zero line) and dark respiration (below the zero line) both at 14°C, using the methods described in the text. Symbols used: Filled circles(●) using the gas flow system of Kershaw (1972) and 0.3 $l \cdot hr^{-1}$. Open circles (O) , using the same system at 1.2 $l \cdot hr^{-1}$. Filled squares (■) using the modified flow system (with ventilation) at 1.8 $l \cdot hr^{-1}$. Triangles (△) , using the new experimental system with sealed gas exchange cells. Standard error of the mean given.

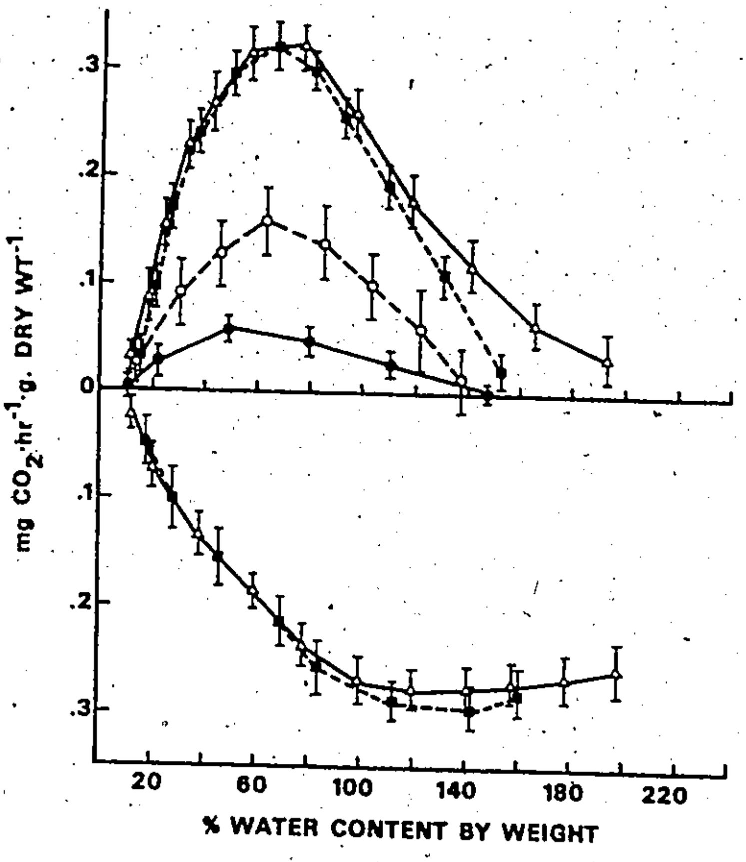

.3
.2
.1
0
.1
.2
.3
mg CO$_2$·hr^{-1}·g. DRY WT^{-1}
20
60
100
140
180
220
% WATER CONTENT BY WEIGHT

TABLE II

Comparison of net photosynthetic rates between (I) previously published work and (II) the new experimental system, at similar environmental conditions. Net photosynthesis (Net P.) expressed as mg $CO_2 \cdot hr^{-1} \cdot g \cdot$ dry wt.$^{-1}$. The type of analysis system is indicated.

Species and Reference	Conditions	Net P. (I)	Net P. (II)
Cetraria nivalis Kallio and Heinonen (1971) Summer - 10,000 lx, 300% water content (flow system)	5°C	.22	.20
	10°C	.23	.25
	15°C	.23	.28
	20°C	.20	.17
	25°C	.10	.10
	30°C	-.19	-.14
Cetraria nivalis Bliss and Hadley (1964) Summer - 16,000 lx 250% water content (flow system)	10°C	.26	.25
	15°C	.30	.28
	20°C	.30	.30
	24°C	.24	.20
Parmelia caperata Harris (1971) Fall- 16,000 lx 250% water content (flow system)	20°C	1.20	1.50
Cetraria nivalis Scholander et al (1952) Winter - Dark Respiration 300% water content (respirometer)	0°C	.07	.06
	10°C	.13	.17
	20°C	.30	.40
	30°C	.43	.70

TABLE III

Comparison of the net photosynthetic rates between ventilated and unventilated three minute incubations (300 einsteins $\cdot m^{-2} \cdot sec^{-1}$, 250 % moisture content, and 20 °C) using *Peltigera polydactyla* . Rates of fixation as mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$ ± the standard error of the mean.

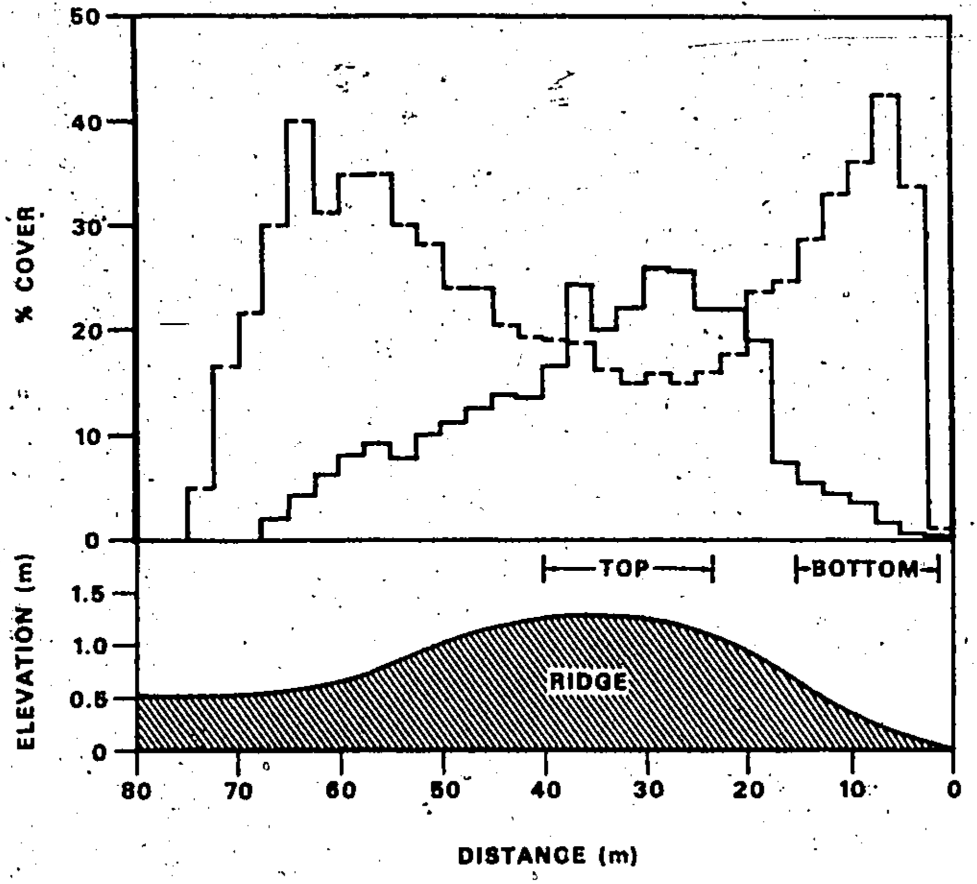
Treatment	number of trials	rates
ventilated	10	0.39 ± 0.01
unventilated	10	0.39 ± 0.02

Two characteristics of these lichens permit their use in this new experimental system. First, the CO_2 limitation point is low relative to higher plants, reflecting the reduced rates of CO_2 exchange in lichens. Second, lichens show no physical barriers to gas exchange. Although a thick cortex is found in some lichens (Blum, 1973), this does not appear to create a large resistance to gas flow when the material is saturated. These two characteristics prevent the development of large potential gradients of CO_2 between the algal cells and the atmosphere. Whether observed patterns of response to ventilation and low CO_2 concentrations are characteristic of all lichens is not known. This requirement for ventilation must be tested on each new species for which a physiological data matrix is to be generated using this method.

The experimental system was used to examine gas exchange characteristics in the lichens Alectoria ochroleuca and Cetraria nivalis from the raised beach ridge surface at area II. The relief of this ridge is shown in Figure 15. The structure of vegetation on this ridge was determined using similar but more intensive sampling than that described above. Samples of these two species were collected randomly from within both the top and bottom positions of the ridge to provide intraspecific control for later comparisons. Collections from the ridge top were made April 27, June 27, July 26, August 27, and October 6, 1974. Similar collections of ridge bottom material were made except for April 27, 1974 when the ridge bottom was still under 30 cm of snow. The lichens were collected brittle-dry, stored in plastic bags, and transported to laboratory facilities. In this dry state lichens are metabolically

Figure 15.

The lower panel of this figure shows the topographic profile of the raised beach ridge in area II. The upper panel shows the percentage cover of *Alectoria ochroleuca* (solid line) and *Cetraria nivalis* (broken line) over this ridge profile.


50
40
30
20
10
0
% COVER
TOP
BOTTOM
1.5
1.0
0.5
0
ELEVATION (m)
RIDGE
80
70
60
50
40
30
20
10
0
DISTANCE (m)

inactive and cannot adjust to new environmental conditions quickly (Hale, 1967). The duration of this uncontrolled storage period never exceeded four days. The dry material was then placed in a environmental controlled growth chamber, at 10°C and 12 hours dark/12 hours light (150 μ einsteins $\cdot$ m^2 $\cdot$ sec^{-1}). This set of conditions represented the standard pretreatment of thalli.

Fluorescent light tubes were used to provide light intensities of 0, 50, 150, and 250 μ einsteins $\cdot$ m^2 $\cdot$ sec^{-1} as measured using a Lamda quantum sensor at the thallus surface. Temperature control was achieved by control of the air temperature around the gas exchange cell. Since no evaporation occurs inside the dish and the fluorescent tubes have no infrared output, thallus temperatures at 250 μ einsteins $\cdot$ m^2 $\cdot$ sec^{-1} were only 1-2°C above the chamber air temperature. Thallus temperatures of 0, 7, 14, 21, and 28°C were used as measured with the thermocouples described previously. Each experiment starts with material soaked twelve hours to reach maximum water content and to eliminate a respiration burst found in these lichen species (see also Smith and Molesworth, 1973). Equilibrium levels of CO_2 fixation are found from 0 to 38 hours soaking.

During the experiments the lichen material was exposed to air containing 330-350 ppm CO_2. The material is permitted to dry slowly between incubations with the covers removed from the gas exchange cells, so that experiments last 8-12 hours. Dead lichen thalli were used as controls and showed no gas exchange. Thallus moisture content was determined by weighing on an analytical balance.

By arranging the light and temperature experiments factorially a simple physiological data matrix is formed for each clone of each species for each season examined. These basic matrices were completed using April and June collections. Further tests for seasonal variation were conducted by testing the matrix across light levels at 14°C (except for dark respiration) and across the various temperatures at 150 μ einsteins · m^2 · sec^{-1}. Other tests of different cells in the matrix were spot checked throughout the experimental program. It was not possible to repeat the entire matrix for each season since 4 separate matrices were generated simultaneously. This resulted in incomplete and non-symmetrical arrays of data which present some minor difficulties in analysis.

Additional material of <u>Alectoria ochroleuca</u> was collected July 27, 1974 from two other widely spaced geographical locations. Material was collected from a polar desert near Little Point, Melville Island, Northwest Territories (75° 5'N 25° 5'W) as well as from a palsa mound 40 miles inland from the tree-line at the Pen Island site. These two collections contrast markedly with <u>A. ochroleuca</u> found on open tundra ridges at Pen Island (Figure 16). Using this material which received the standard pretreatment, experiments were performed at 150 μ einsteins · m^2 · sec^{-1} at 1°, 7°, 14°, and 21°C plus dark respiration at 21°C, and 250 μ einsteins · m^2 · sec^{-1} at 14°C.

All experiments for each collection were completed within four weeks of the collection date. It was found that although general "viability" was not influenced after six weeks storage, net photosynthetic rate at 20°C had dropped by 20%. After four weeks, however, no effects were noticeable.

Results are expressed as mg CO_2 · hr^{-1}·g^{-1} dry weight of the thallus (80°C, 12 hours) versus thallus moisture content. Thallus moisture is

Figure 16.

Random samples of lichen material used in this study.

a) thalli of A. ochroleuca from the top of the beach ridge at Pen Island.

b) thalli of A. ochroleuca from the bottom of the beach ridge at Pen Island.

c) thalli of C. nivalis from the ridge top at Pen Island.

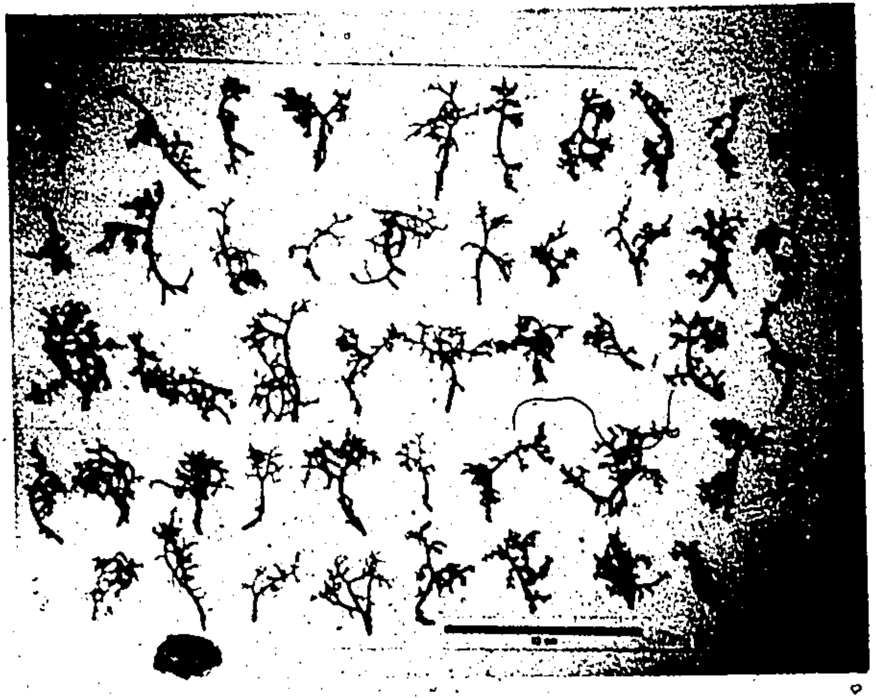
d) thalli of C. nivalis from the ridge bottom at Pen Island.

e) thalli of A. ochroleuca from Little Point, Melville Island, Northwest Territories.

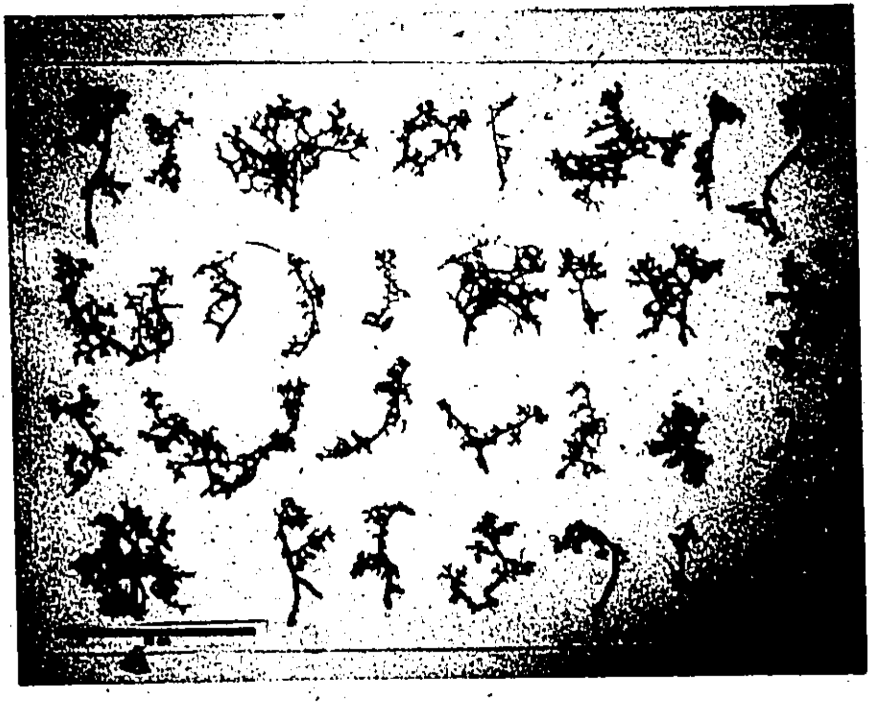
f) thalli of A. ochroleuca from the palsa mound 40 miles south of the treeline at Pen Island.

(All magnified x 0.25)

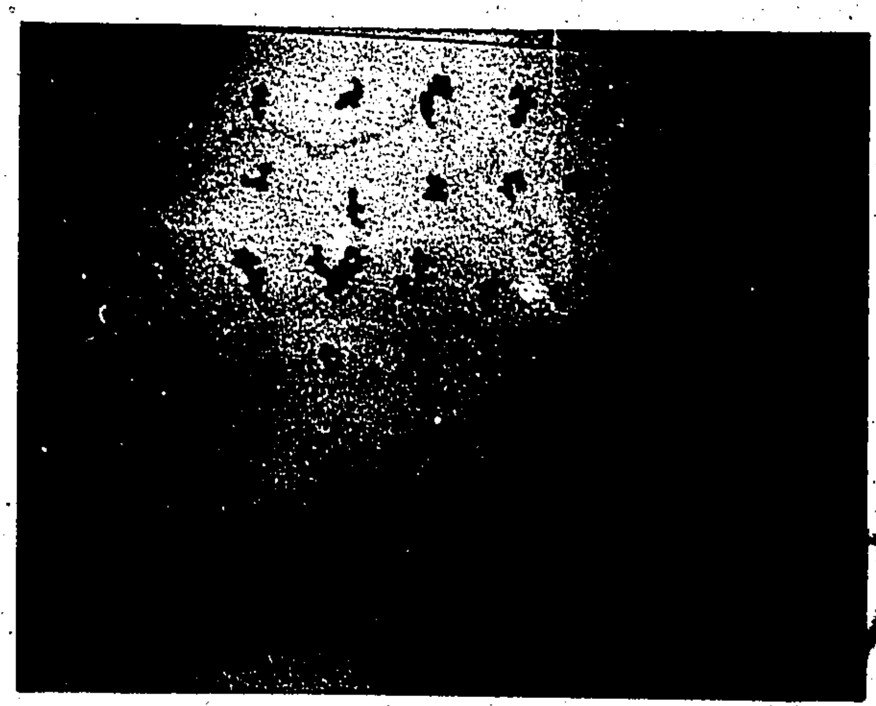
A



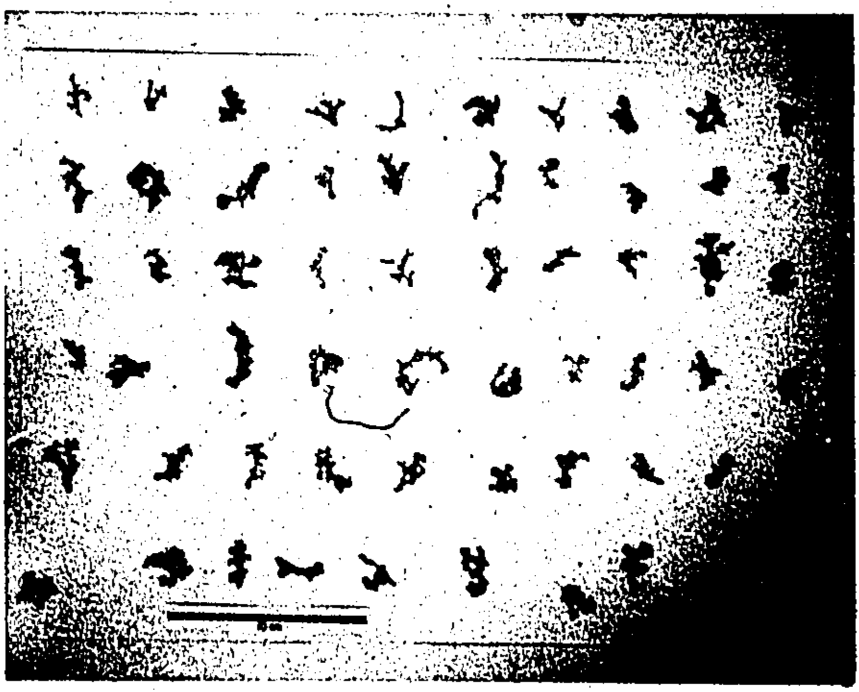
B



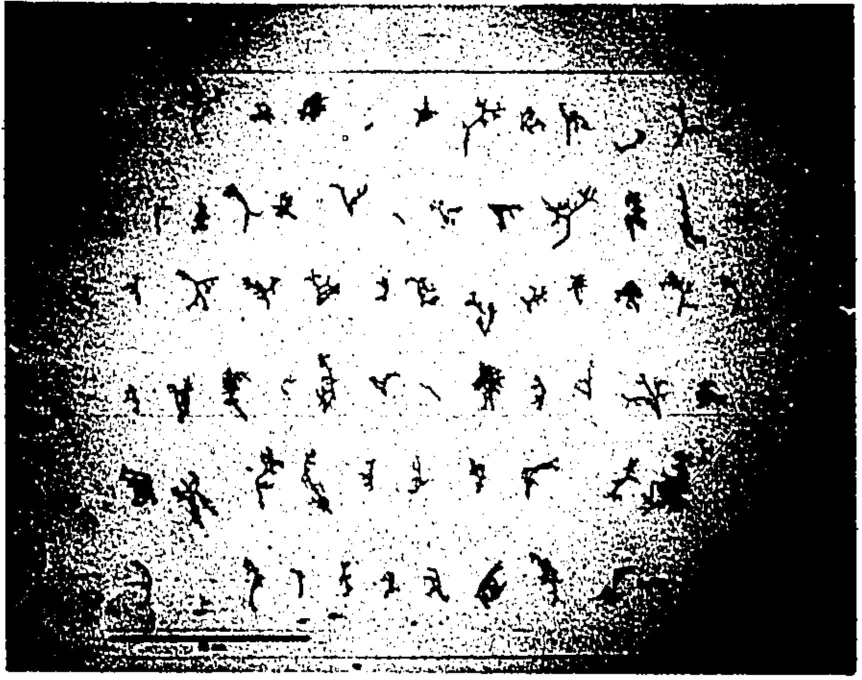
C



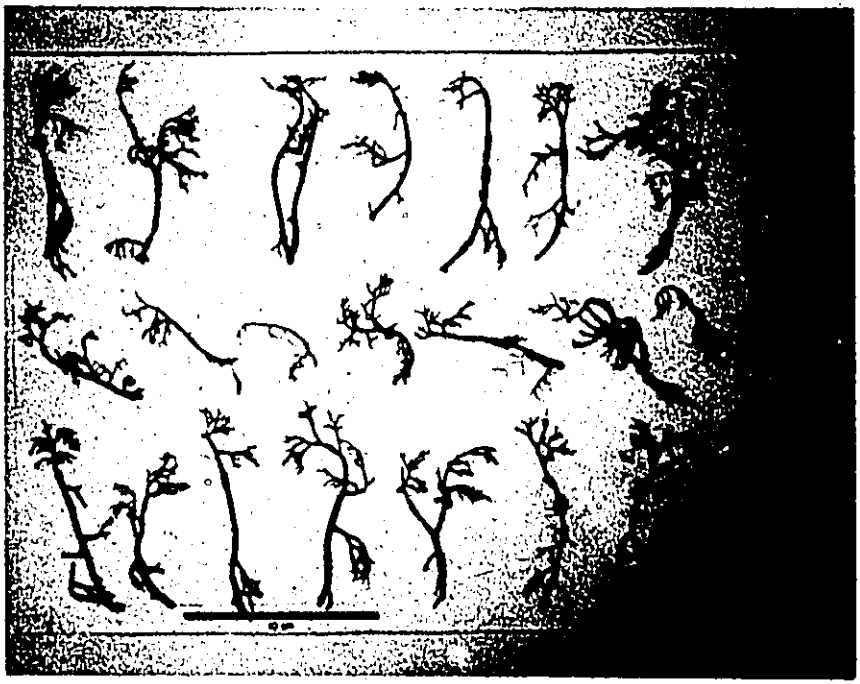
D



E



F



expressed as percent water content relative to dry weight. Each curve is the mean of four to ten replications.

(2.4) Statistical Testing of Results from Net CO_2 Exchange Experiments

(2.4.1) Establishment of the Simultaneous Confidence Interval

A number of methods are available which permit statistical testing of results from this type of study. For example, multivariate analysis of variance is best suited to large factorially arranged experimental designs but requires symmetrical and complete arrays of data. In this case, incomplete data make the analysis difficult to handle. Alternatively Lechowicz and Adams (1974) have fitted parabolic regression lines through data with subsequent analysis performed on the parameters of the fitted curves. These approaches are of dubious worth if the same information can be extracted from a simpler analysis. In this case it was found that the magnitude and distribution of the experimental variances over all these experiments using these methods were sufficiently small to permit the calculation of an extremely conservative simultaneous confidence interval for multiple comparisons (Wonnacott and Wonnacott, 1971). Although this interval provides such a conservative estimate of significance at the 5% level, a large number of ecologically significant differences were demonstrated. Thus more refined statistics were unneccessary. This confidence interval was 0.05 mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$ dry weight and was applied to 97% of the experiments: the remaining 3% (five experiments) required 0.07 mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$ to establish significant differences when two points were compared.

(2.4.2) Intra and Interspecific Comparisons of Net Photosynthetic Rates

Two points on each curve of the physiological data matrix which lend themselves to comparisons are the net photosynthetic rates at maximum and half maximum thallus water content. These two points are important ecologically. The 100% relative water content level is likely to be found much of the time since mists and light rain are common at Pen Island. The 50% relative water content level is important because it is the optimum water content for maximum net photosynthetic rate in both lichen species. Comparisons were made between different collections under identical experimental conditons for those experiments repeated for each collection.

Using these two points as comparisons, tables were constructed for each intra and interspecific comparison. These tables show the significant differences in means across all experimental conditions. A zero difference was entered if the two samples under comparison were within 0.05 mg $CO_2 \cdot hr^{-1} . g^{-1}$ (or 0.07 mg $CO_2 \cdot hr^{-1} . g^{-1}$) of each other. If for example the net photosynthesis of A. ochroleuca (ridge bottom) was significantly greater than A. ochroleuca (ridge top), a negative difference and its magnitude was recorded. In the reverse case a positive difference was recorded. Totals of zeros, positives, and negatives were then determined for each comparison. A perfect comparison yields only zeros. Each time a non-zero is recorded, it it is significant and requires examination. Subsequent to these tabulations, the proportion of positives and negatives were examined for trend. If the significant deviations from zero were without trend, then the probability of either species exceeding the other is 50%. The sign test, the Wilcoxon signed rank test for two related samples, and a chi square test were performed on each set of accumulative deviations. These tests determine for each distribution of positive and negative differences the probability of achieving this distribution assuming no trend favoring one sign or the other. Probabilities of less than 0.05 for all three tests were accepted as evidence for significant difference. The symmetrical matrix thus produced permitted an examination of row (seasonal) or column (temperature) variations in the accumulated significant differences, represented as totals for each comparison. These procedures achieve the same result as would be available using multivariate analysis of variance in that the distribution of significant differences can be separated to effects of season and temperature.

(2.5) Morphology and Water Relations

(2.5.1) Surface Area Determinations

Random samples of lichen material were selected to provide an estimate of the average weight of individual thalli using the following procedure. Lichen material was placed in water for five minutes which was sufficiently long to achieve near maximum thallus water content, and lightly blotted. Porapak 80-50 mesh chromatographic column packing material, made of small plastic beads of uniform diameter, was poured over the lichen material, adhering to exposed wet thallus but not to itself. Thalli were examined microscopically to insure that a monolayer of beads covered the entire thallus. As the thalli dried, the packing material fell off and was subsequently weighed to provide an estimate of surface area by calibration against known standards.

(2.5.2) Thallus Water contents under Rainfall of Differing Intensity

To determine the levels of saturation to which *A. ochroleuca* and *C. nivalis* from Pen Island were raised in the field, air-dry samples of both species were placed out-of-doors and exposed for approximately five hours to rainfall of four different intensities. Since no data concerning the microclimates of the Melville Island or the palsa mound sites were available, these samples were not included in these experiments. Rainfall intensity was measured in cm/h. Twenty subsamples of each species were sealed in plastic tubes at the end of each experiment. Weights taken before and after drying at 60^{o}C for 20 hours provided a measure of thallus moisture content.

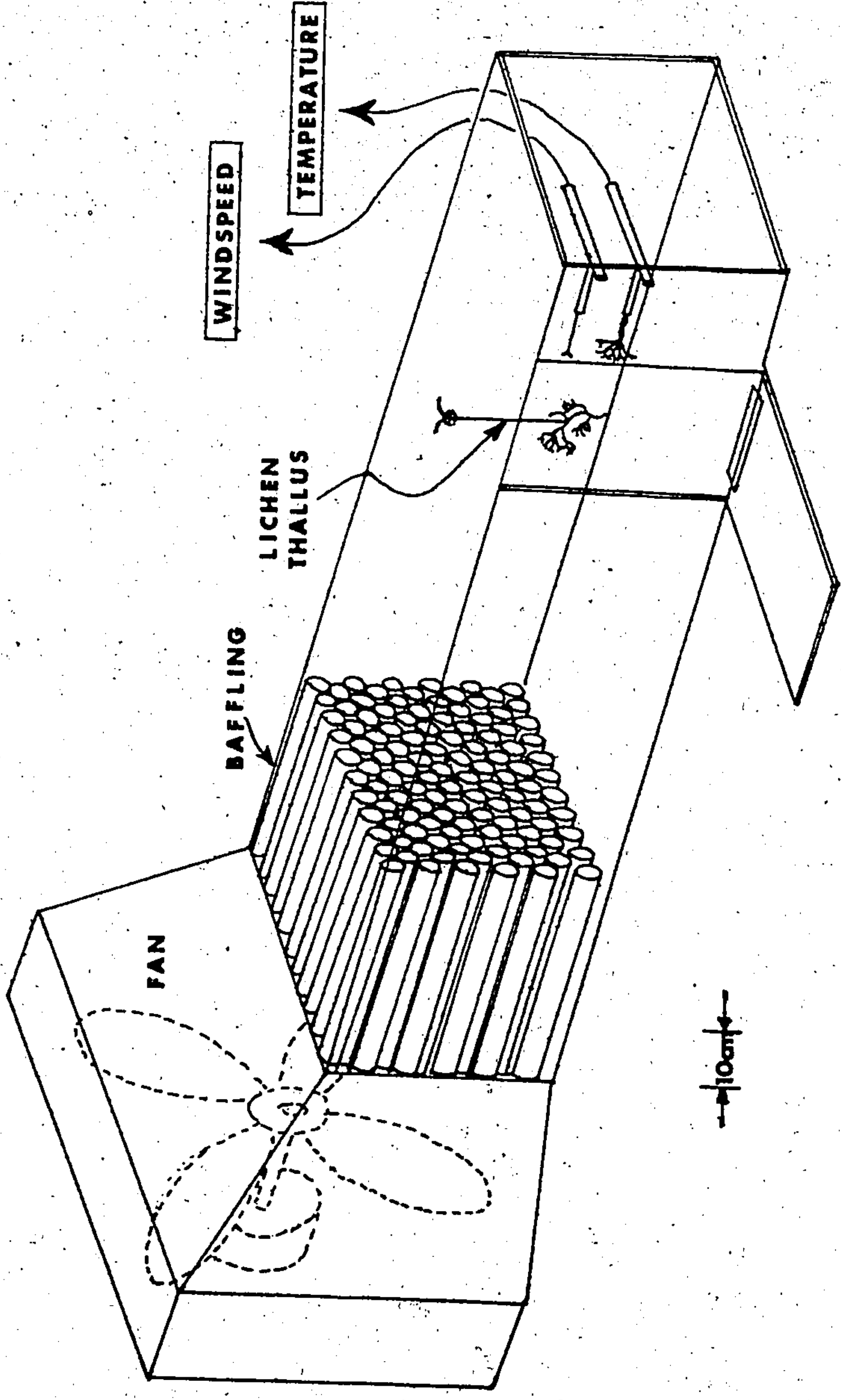
(2.5.3) Evaporation Rates Under Controlled Conditions

In order to measure evaporation rates of lichen material, a wind tunnel was constructed as shown in Figure 17 using twelve inch tubular baffles in front of an 18 inch box fan which provided non-turbulent flow of 1.6 $m \cdot sec^{-1}$ as measured using hot-film anemometry. Air and thallus temperatures were measured using thermocouples as described previously. Ordinary laboratory lighting was used (7 μ einsteins $\cdot m^{-2} \cdot sec^{-1}$) because of its zero infrared component. Thallus drying was thus due to the saturation deficit in the air which showed a relative humidity of 40% at 23°C.

Average thalli (see Figure 16) were soaked for sufficient time to achieve maximum levels of saturation. Light monofilament fishing line was then looped around the wet thallus so that the material could be suspended in the centre of the tunnel. The lichen material was placed inside the tunnel at time t_o. At two minute intervals the thallus moisture content was determined by weight; this interval was increased to five minutes as thallus moisture contents approached 30% by weight. Six to eight determinations were done for each sample. Single thalli and clumps of ten thalli were measured for A. ochroleuca and C. nivalis from Pen Island. Determinations were also made for single thalli of A. ochroleuca collected from the palsa mound and from Melville Island. Evaporation rates were then calculated using known surface area

Figure 17.

Diagrammatic representation of the wind tunnel used in this study . Windspeeds , air and thallus temperatures were measured in the centre of the tunnel.


WINDSPEED
TEMPERATURE
LICHEN THALLUS
BAFFLING
FAN
10cm

to weight ratios, and this was plotted against thallus moisture content.

Since the change in evaporation rate with thallus moisture contents is a function of a change in the potential for water vapour flux from the thallus, an estimation of total resistances to evaporation can be calculated. These resistances were calculated using equation (1) below, from Monteith (1965).

$$r_a + r_i = \frac{\rho c}{\lambda \gamma} \quad \frac{(Es(T_o) - E_a)}{\text{Evaporation}} \tag{1}$$

where:

$r_a + r_i$ = total resistances to evaporation

ρ = 1.2×10^{-3} g · cm^{-3}

c = 0.24 cal · g^{-1} · ^{o}C^{-1}

λ = 584 cal · g^{-1}

γ = 0.66 mb · ^{o}C^{-1}

$E_{s(T_o)}$ = saturation cap pressure at wet bulb temperature

E_a = saturation cap pressure at dry bulb temperature

Evaporation = grams water lost · cm^{-2}·sec^{-1}

Section 3.

RESULTS

(3.1) Relationships Between the General Lichen Heath and Edaphic Factors

(3.1.1) Distribution Patterns of the Most Abundant Species

The patterns of distribution of the nine most abundant species in this raised beach ridge system, *Dryas integrifolia* Vahl., *Equisetum variegatum* Schleich., *Rhododendron lapponicum* (L.) Wahl., *Cetraria islandica* (L.) Ach., *C. cucullata* (Bell.) Ach., *C. nivalis* (L.) Ach., *Cladina mitis* (Sandst.), *Cornicularia divergens* Ach., and *Alectoria ochroleuca* (Hoffm.) Massal., are shown in Appendix A.

Although both *Equisetum variegatum* and *Rhododendron lapponicum* do not show variations in abundance related to the developmental sequence of ridges found in area I, each of the other species shows considerable variation in abundance strongly influenced by both the inland developmental sequence and by the topographic profiles of individual beach ridges. For example, the lichen *Cetraria nivalis* (Figure 18) has higher biomass on the older ridges although it maintains a relatively high biomass throughout the ridge system. Superimposed on this pattern, however, is considerable intraridge variation in abundance related to the topographic characteristics of beach ridge surfaces. This subjective interpretation is substantiated by the regression and ordination results. (Table IX , Figure 57 in Appendix A). While this species tends to be found in wetter areas, a contrasting pattern is shown by *Alectoria ochroleuca* (Figure 19). This species is found to be most abundant on ridges 1 and 2, and to be least abundant on ridge 12. Again however, there is greater variation in the biomass of this species as a function of the topographic profiles of individual beach ridges (Table VIII and Figure 62, Appendix A). While all species examined show such effects due to either the inland developmental sequence or

Figure 18.

Variation in biomass of Cetraria nivalis within and between the ridges of the system. Note the general increase in biomass on progressively older ridges of the system, and the higher levels of biomass on the edges of most ridges regardless of their position in the inland developmental sequence. Transect numbers 1-6, ridge 1; 7-12, ridge 2; 13-18, ridge 7; 19-24, ridge 9; 25-30, ridge 12. Ridge 1 is closest to Hudson Bay while ridge 12 is 1.5 km inland.

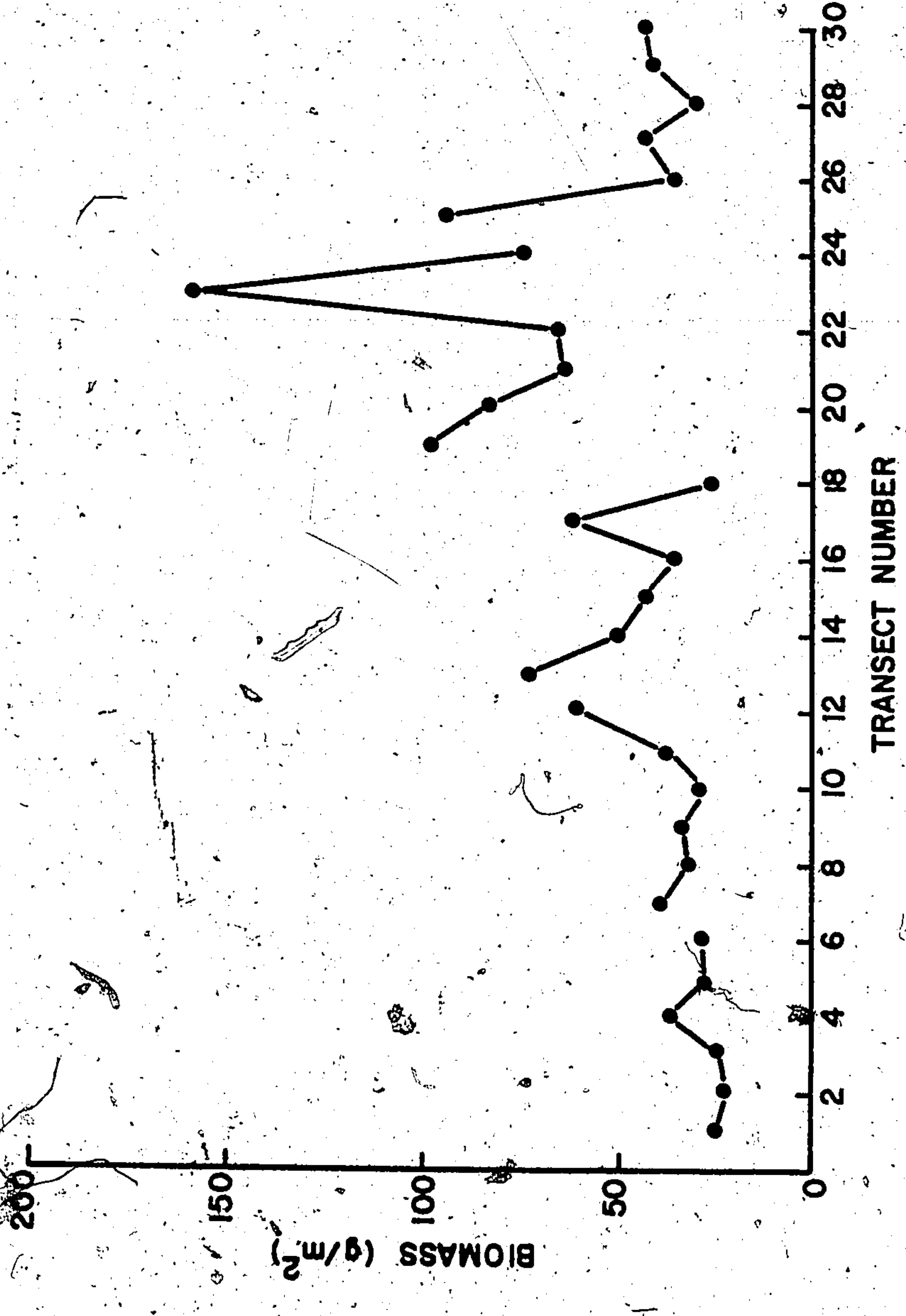
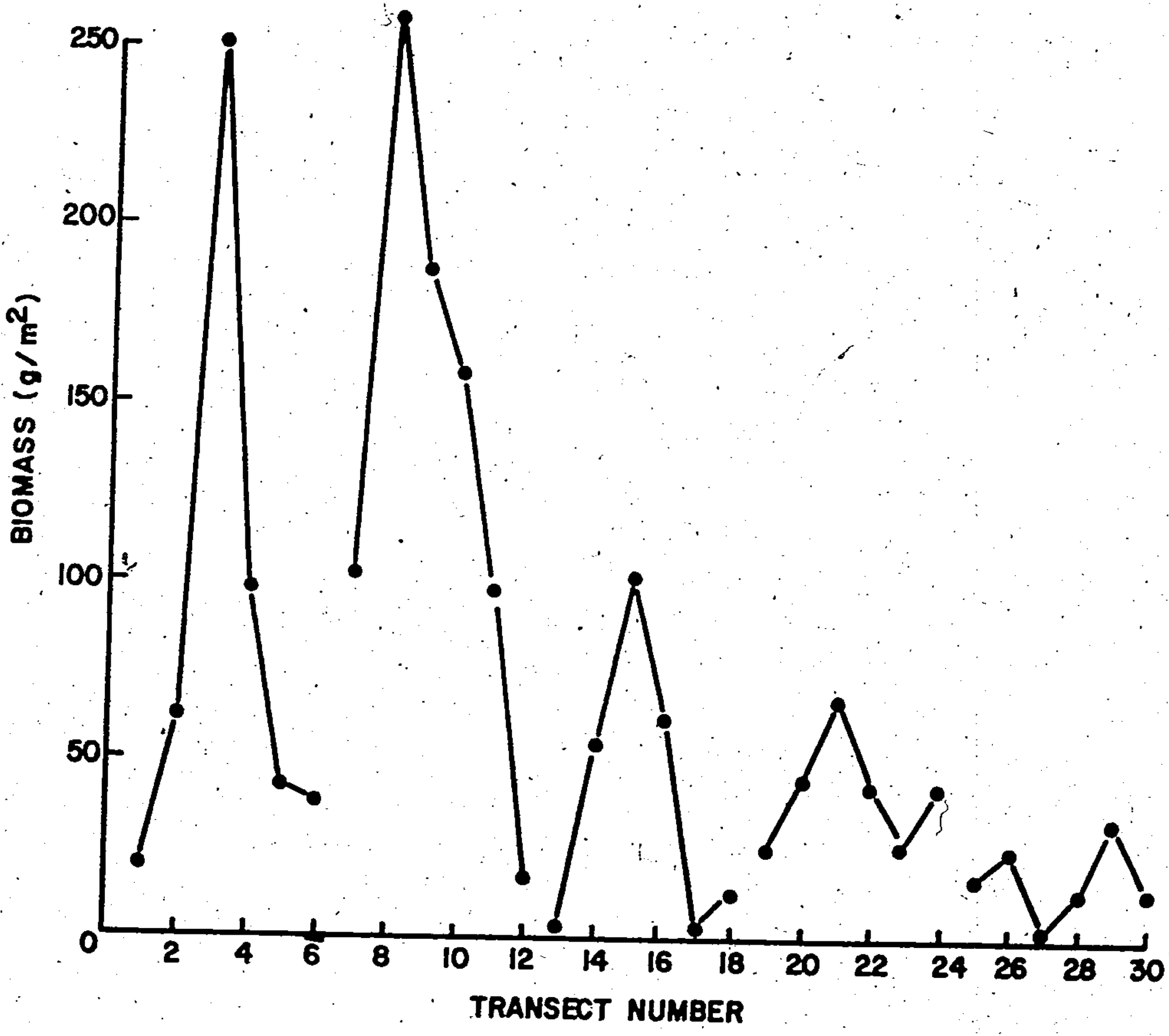

BIOMASS (g/m^2)
0
50
100
150
200
TRANSECT NUMBER
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Figure 19.

Alectoria ochroleuca has high levels of standing biomass on the most recently formed ridges of the system. Highest accumulations of biomass appear on the ridge top postions of ridges 1,2,7 and 9, and indicates the considerable importance of factors independant of any age sequence in controlling the structure of this vegetation. See Figure 20 for details of transect positions.


BIOMASS (g/m^2)
250
200
150
100
50
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
TRANSECT NUMBER

to the effects of individual ridge topography, these two lichen species, because of their mutually exclusive patterns and high abundance were considered to offer the best possibilities for future study (see below).

(3.1.2) Topography

The formula for isostatic uplift given by Webber et al, (1970 provides an estimated uplift rate of 0.9 meters/century for the Pen Island area, based on the evidence that 11 meters of uplift has occurred in the past 1,000 years. The ridges shown in Figure 20 are thus separated temporally; ridge 12 is the oldest at approximately 800 years, while ridge 1 is the youngest at about 250 years. Local topographical variation makes these ages approximations only.

(3.1.3) Peat Layer Development

The development of peat in the ridge system (Figure 21) is a function of time, soil moisture, and vegetation type. A highly significant correlation (r=+.82) between water content and peat thickness was found. Despite the fact that ridge 12 is about 800 years old, the peak thickness of the dry ridge crest is only about 5 cm. This rate of accumulation is much lower than the 100 cm/600 years given by Hustich (1957) for wet sedge meadows. Greater variation in peak thickness is found on an intraridge basis than between individual ridges in the sequence.

(3.1.4) Surface Soil Moisture

Measurement of surface soil moisture by percent weight shows (Figure 22) a gradual increase throughout the system from ridge 1 which is dry to ridge 9 which has higher levels of surface soil moisture. The substantial decreases found on ridge 12 may be a function of more rapid

Figure 20.

Cross sectional profile of absolute elevation within the raised beach system at the points marked on Figure 3. Ridge numbers appear below the profile, while transect numbers appear above the profile. Areas between the ridges are sedge meadow.

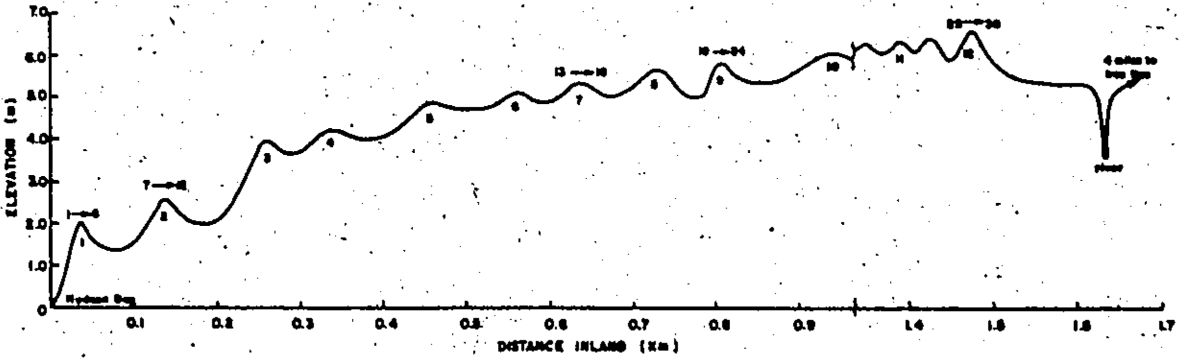
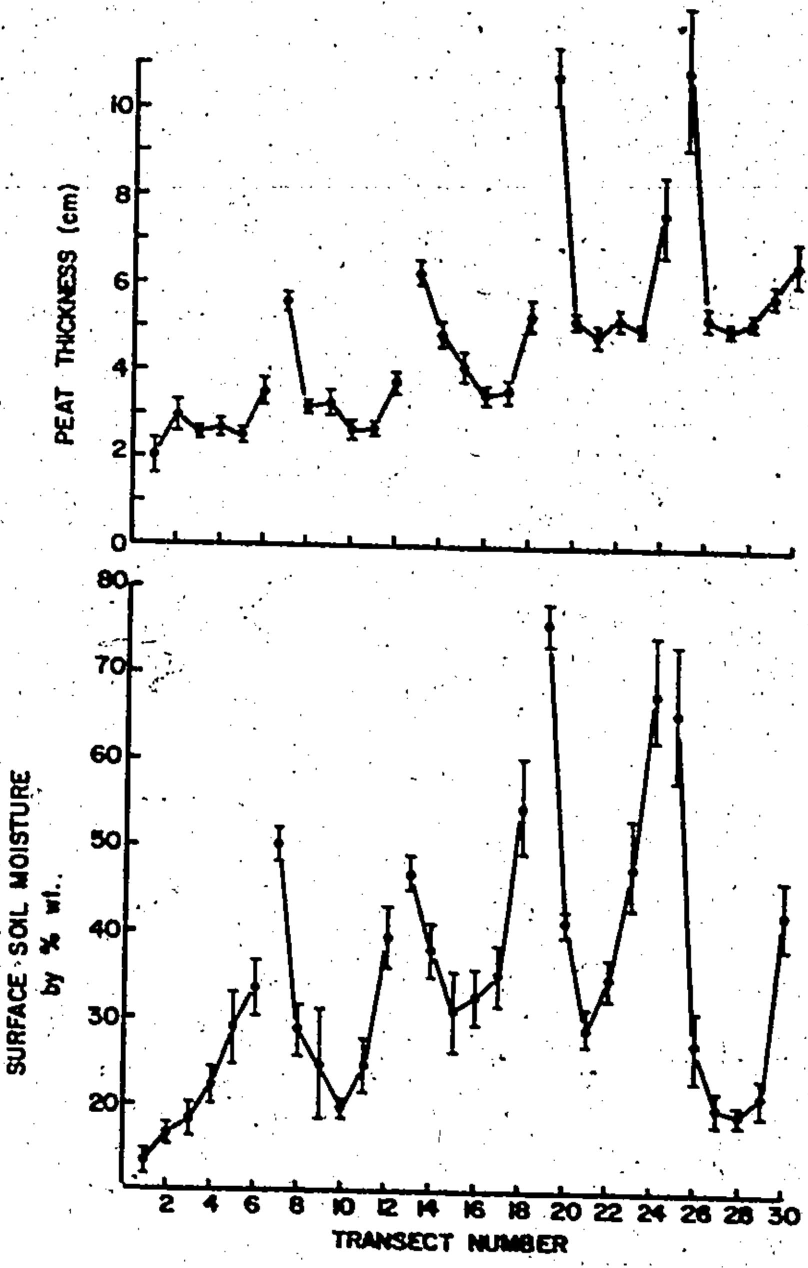

ELEVATION (m)
DISTANCE INLAND (Km)
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.4
1.5
1.6
1.7
Hudson Bay
1
2
3
4
5
6
7
8
9
10
11
12
river

Figure 21.

Accumulation of peat (in cm) across ridge profiles and throughout the ridge system. Transect numbers refer to those in Figure 20. Standard error of the mean given.

Figure 22.

The build up of surface soil moisture as % by weight across ridge profiles , and throughout the ridge system. Note the reduction in values on ridge 12 (transects 25-30) . Standard error of the mean given.


PEAT THICKNESS (cm)
0
2
4
6
8
10
SURFACE SOIL MOISTURE by % wt.
20
30
40
50
60
70
80
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
TRANSECT NUMBER

drainage into the nearby river. In all ridges (except ridge 1), both front and back slopes near the sedge meadows have a surface soil moisture greater than 40% by weight. The marked lack of moisture at the front of ridge 1 probably reflects the more rapid drainage, thin peat cover, and greater exposure to the prevailing winds (c.f. Figures 20-22). The greatest variation in surface soil moisture is related to topographic profiles of individual beach ridges.

(3.1.5) Principle Components Ordination

The ordination diagrams with overlayed environmental data on the transect numbers, shown in Figure 23 have hand fitted isopleths drawn through arbitrary values to best show the relationships present. Neal and Kershaw (1973b) have used trend surface analysis to achieve the same results, but the increased objectivity is of limited value relative to the excessive computing time required as well as the lack of an exact significance test of the surface fitted.

There is a clear relationship between both water content and transect position with the first ordination axis (Figures 24,25) which has extracted 42% of the total variance. The marked sequence of ridges along axis 2 of the ordination (Figure 23), which extracts 20% of the total variance, is not correlated with soil moisture, peat development, or topography. As shown in Figure 26, Axis 3 which extracts 15% of the total variance, shows a marked relationship with peat depth for those transects on the ridge bottoms and tops where the water content is low (c.f. Figures 24,25). Conversely this relationship is lost for those transects with higher water contents at ridge edges.

Figure 23.

Plot ordination of individual transects, showing the marked sequence of ridges along axis 2. Ridge numbers in roman numerals.

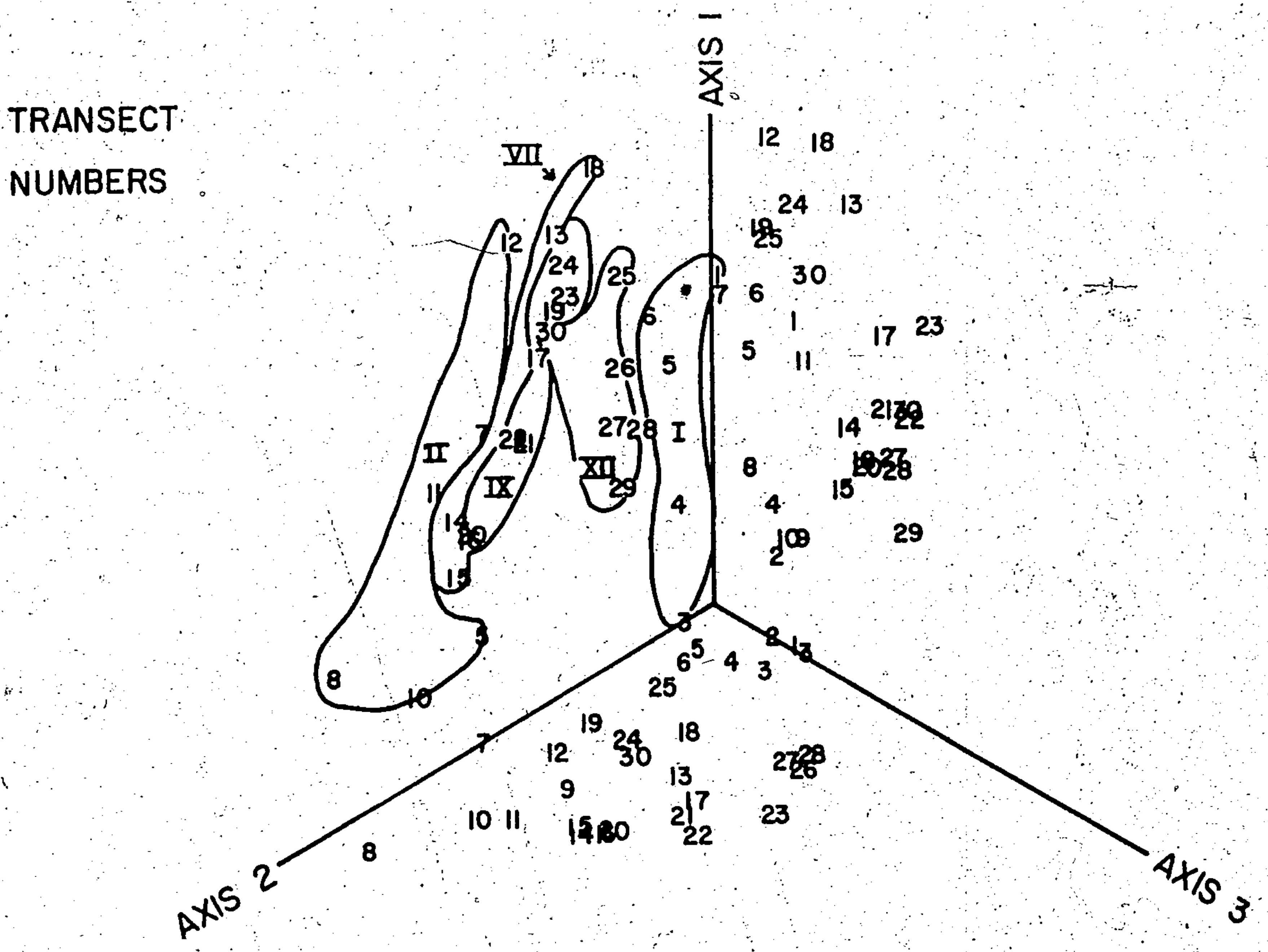

TRANSECT
NUMBERS
AXIS 1
AXIS 2
AXIS 3
I
II
VII
IX
XII

Figure 24.

Overlay of transect position numbers on each transect number shown in Figure 20. Numbers 1&6 are at ridges edges, numbers 2&5 are in the ridge slope positions, while numbers 3&4 are on the ridge top positions.

POSITION
ON RIDGE

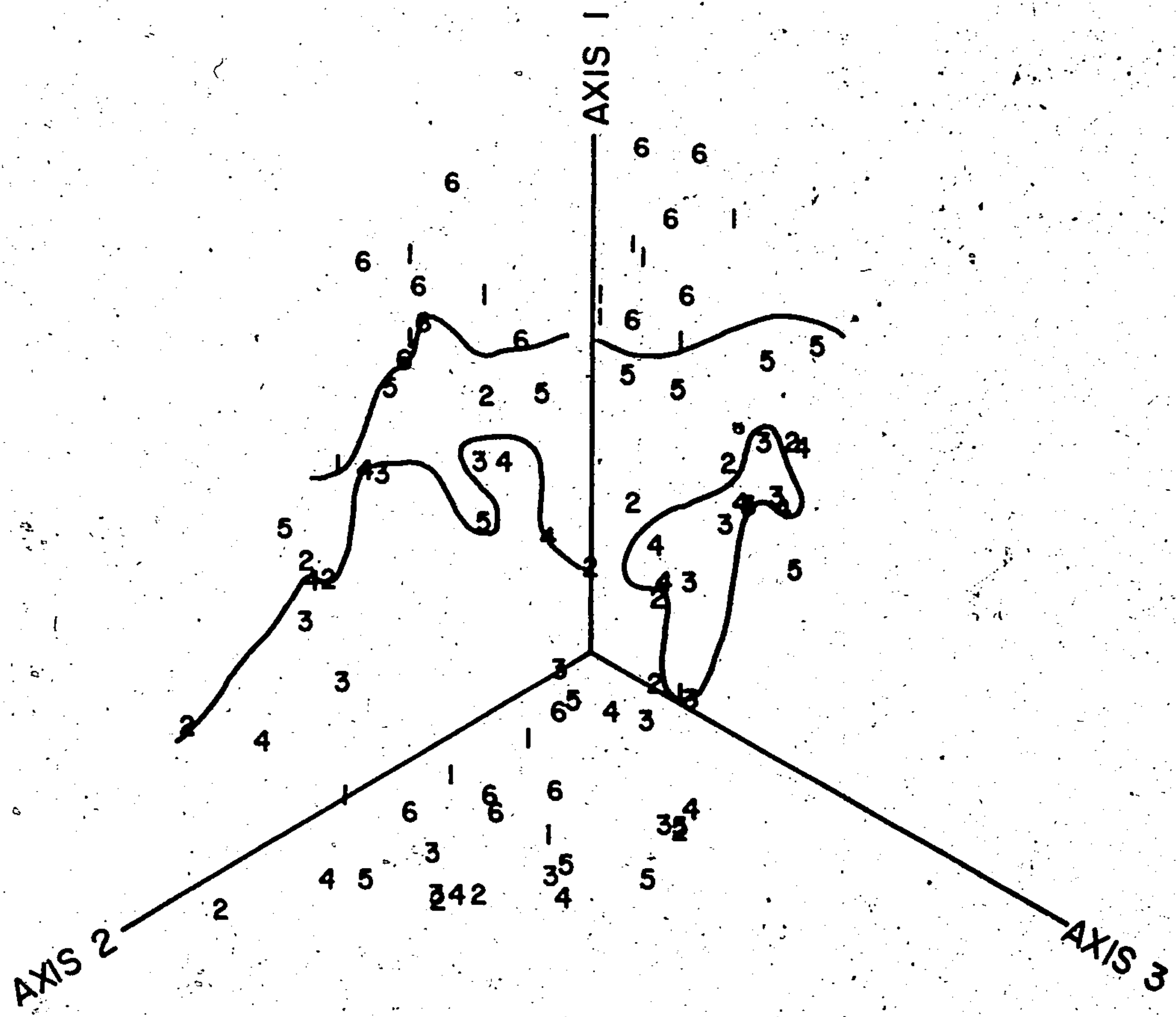


Figure 25.

Overlay of surface soil moisture (% by weight) . The correlation with axis 1 is seen. Classes :I,0-25% ; II, 25-35% ; III , >35%.

% SOIL MOISTURE
BY WEIGHT

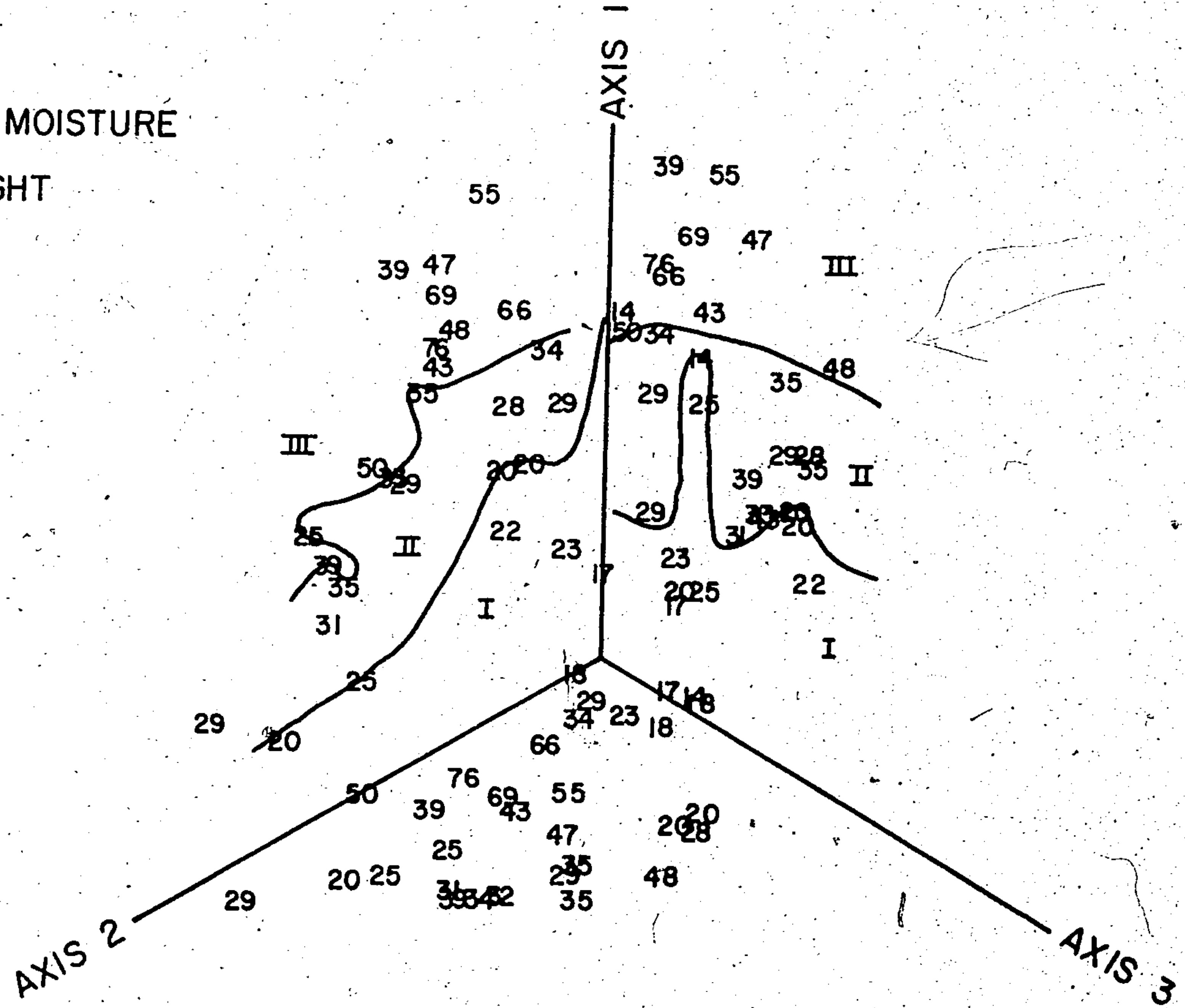
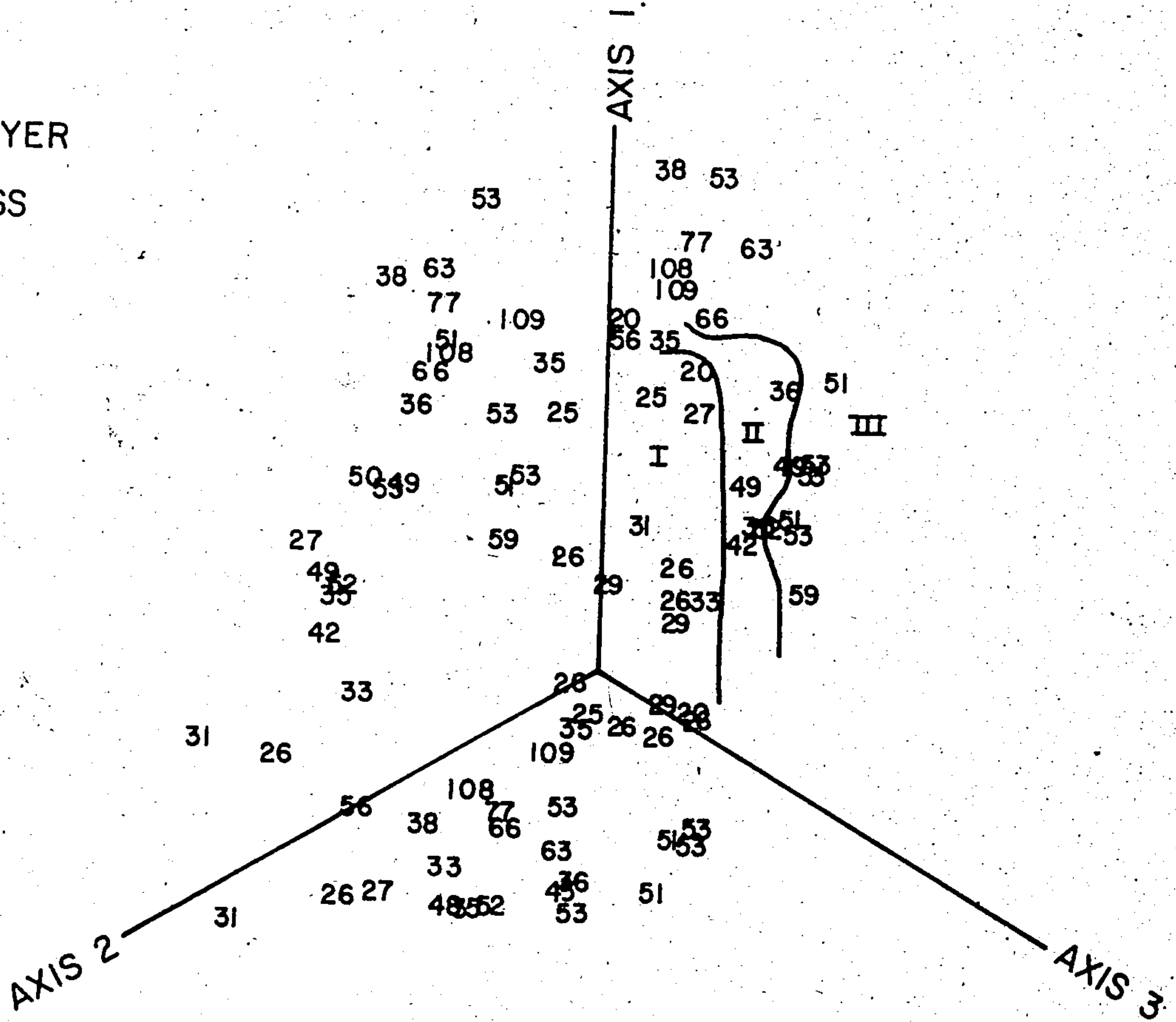


Figure 26.

Overlay of peat layer depths (in mm) showing the relationship with axis 3 for dry transects at ridge slopes and summits. Classes : I - <35mm ; II - 35-50 mm. ; III >50mm.

PEAT LAYER
THICKNESS
(in mm)



This section of results pointed to the importance of ridge topography in determining the structure of vegetation within the general lichen heath. Although the inland developmental sequence is associated with changes in the physical environment, these changes are not as well defined as those associated with topographic influences of individual beach ridges. Thus further study was restricted to an examination of other physical characteristics of raised beach ridges.

(3.2) Other Aspects of the Physical Environment of Raised Beach Ridges

(3.2.1) General Lichen Heath and Winter Snow Cover

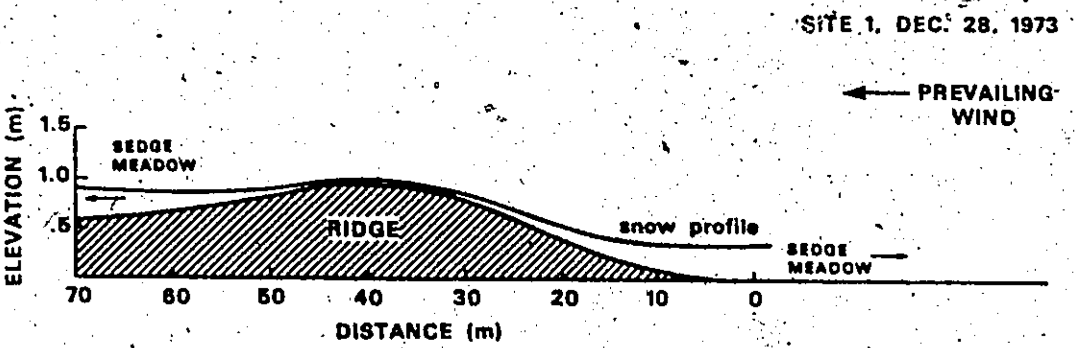
To supplement the data given above, winter snow conditions over raised beach ridges were examined. The profiles of ground elevations and snow depths for sites 1 and 2 at Fort Severn in December, 1973 are shown in Figure 27. Strong prevailing NNW winds strike these ridges diagonally from the front edge. Both ridges studied show a marked reduction in snow depth from the sedge meadow areas (30 cm) to the windward ridge edge (15 cm). A greater reduction is seen from this point to the front and top of the ridge crest where only 2-5 cm of snow is present. Site 2 has an overall greater snow depth than site 1 which may reflect its more inland location rather than its greater relief. Alectoria nitidula (Th.Fr.) Vain A. ochroleuca, and Dryas integrifolia, characteristic of ridge tops, were found exposed to abrasive winds on these and many other ridges in the area.

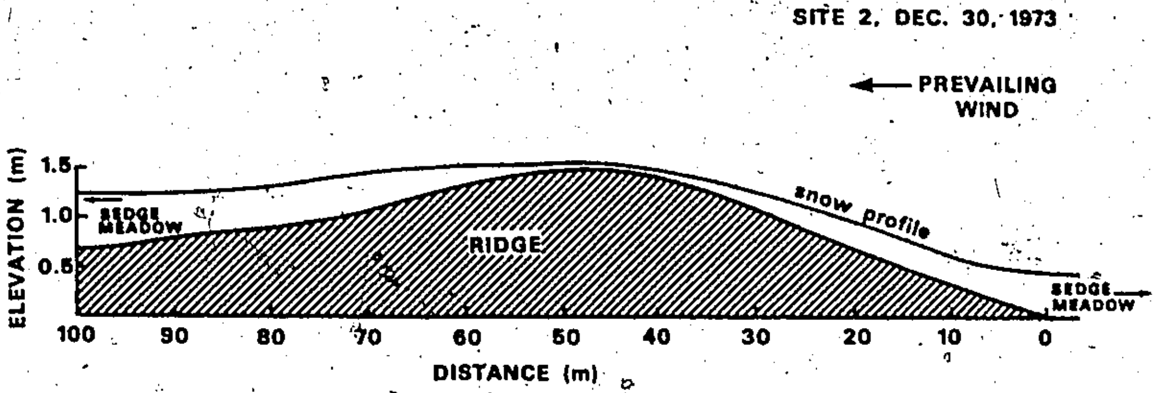
In contrast with the raised beach ridges, the snow cover of the sedge meadows and forested areas, (Table I, sites 3a-3e) was extremely thick. Sedge meadows typically had greater than 30 cm while all forest areas examined had approximately 150 cm of snow.

The observed changes in average snow depth between December 1973 and

Figure 27.

The profiles of snow cover over two raised beach ridges at Fort Severn in December 1973. Site 1 is 1 km. inland ; site 2 is 5 km. inland.


SITE 1, DEC. 28, 1973
PREVAILING WIND
ELEVATION (m)
1.5
1.0
.5
SEDGE MEADOW
RIDGE
snow profile
SEDGE MEADOW
70
60
50
40
30
20
10
0
DISTANCE (m)


SITE 2, DEC. 30, 1973
PREVAILING WIND
ELEVATION (m)
1.5
1.0
0.5
SEDGE MEADOW
RIDGE
snow profile
SEDGE MEADOW
100
90
80
70
60
50
40
30
20
10
0
DISTANCE (m)

March, 1974 are shown in Figure 28. The tops of raised beach ridges experience no increase in snow depth during this three month period. Conversely, the sedge meadows and forested areas showed a 20% increase in snow cover thickness.

The profiles of ground elevation and snow cover for site 4, area II, and site 5, area III, at Pen Island in April, 1974 during the early spring melt are shown in Figure 29. The exposed ridge top at site 4, which forms the basis for the study described below, is dominated by _Alectoria ochroleuca_, _Dryas integrifolia_, and _Cornicularia divergens_. In contrast, the front slope of this beach ridge has a snow cover of several cm and is dominated by _Cetraria nivalis_. A greater contrast between ridge top and bottom positions was found at site 5. The snow-free zone at the ridge top, dominated by _Alectoria ochroleuca_ and _A. nitidula_, contrasts markedly with the ridge bottom zone, dominated by _Cladina alpestris_ (L.) Harm. which had a snow cover thickness of 200 cm.

(3.2.2) Microclimatic Factors over the Raised Beach Ridge Profile

Peat thickness, surface soil moisture, and topography are aspects of the physical environment of raised beach ridge surfaces which either do not fluctuate or which fluctuate rather slowly throughout the year and are thus relatively simple to measure. In contrast, atmospheric factors such as windspeed, temperature, and drying rates, which fluctuate rapidly during the day, are more difficult to measure.

Windspeeds and Temperatures

Measurements of these two variables were obtained under conditions of diffuse radiation usually following mist or rainfall. As shown in Figure 30

Figure 28.

Observed snow depths over the three surfaces examined in December 1973 (unshaded histogram) . Shaded areas show increases in snow depth fron December 1973 to March 1974.

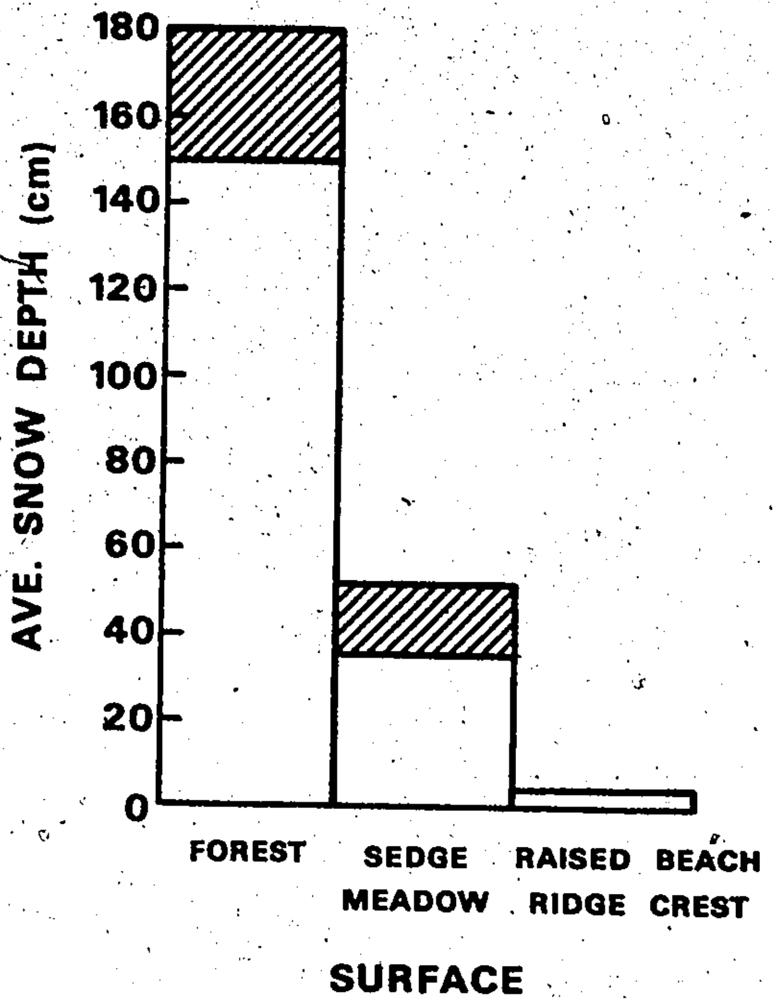
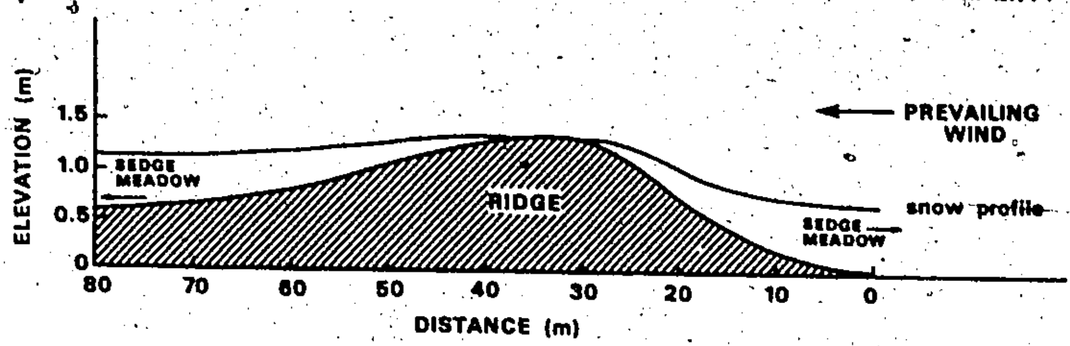

180
160
140
120
100
80
60
40
20
0
AVE. SNOW DEPTH (cm)
FOREST
SEDGE MEADOW
RAISED RIDGE
BEACH CREST
SURFACE

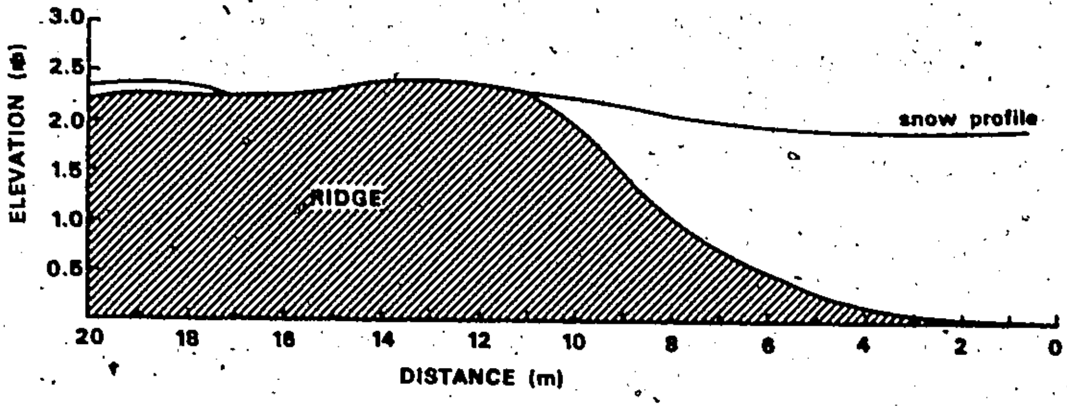
Figure 29.

Profiles of snow cover on raised beach ridges at the Pen Island research site in April 1974. Site 4 is 1 km. inland ; site 5 is 5 km. inland.

SITE 4. APR. 27/74



SITE 5. APR. 27/74



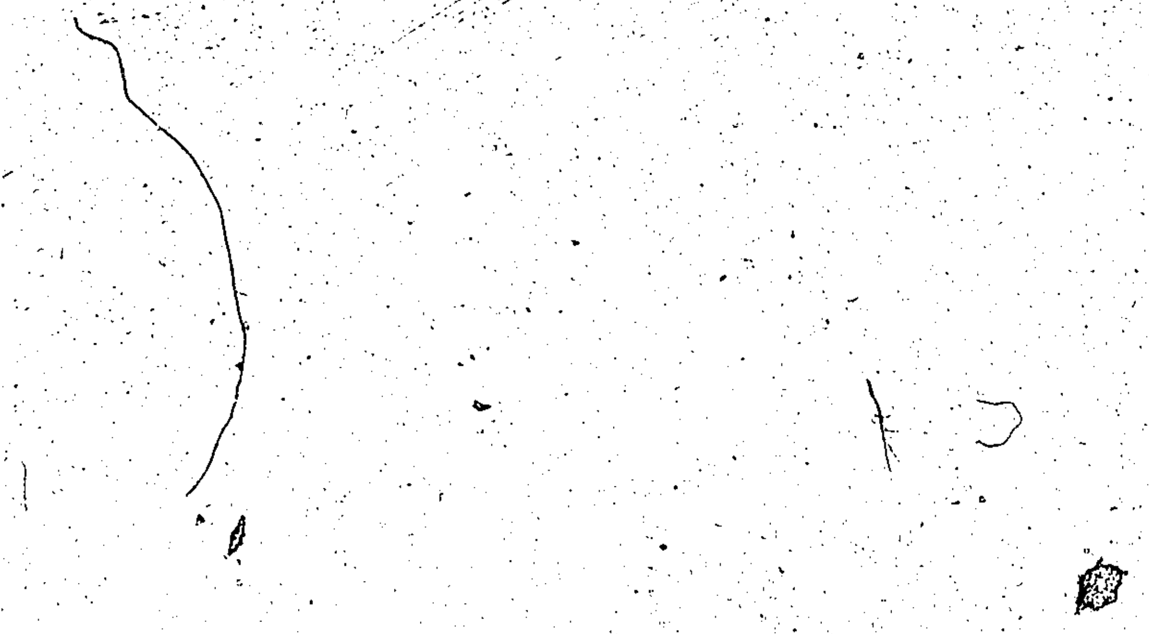
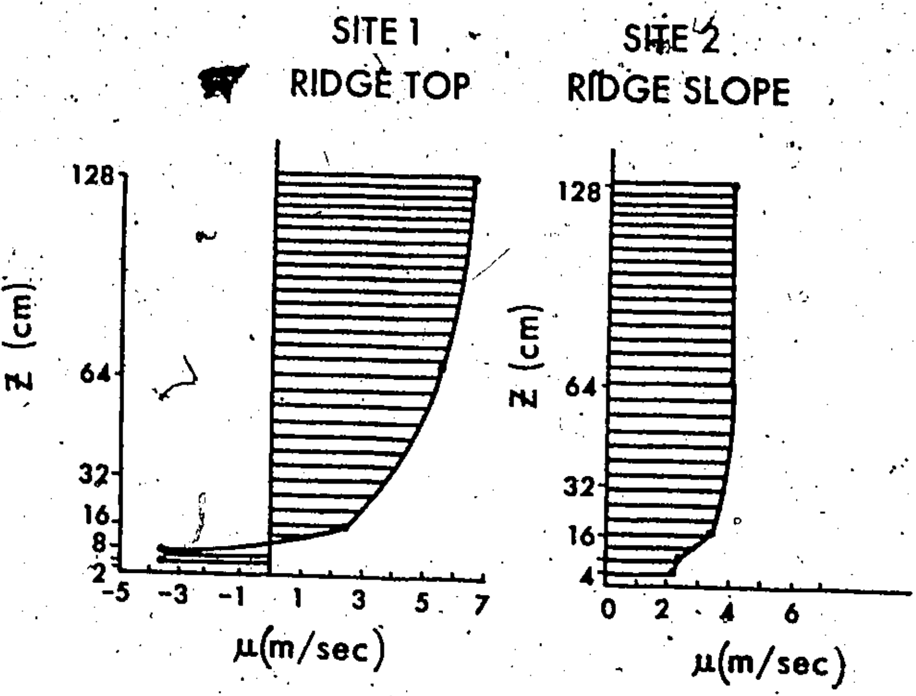


Figure 30.

The contrasting wind profiles for ridge top and bottom positions of the ridge in area III. Data are averaged from three days data. Z (cm.) denotes height above the ground surface; μ(m/sec) denotes mean windspeed at given height. A small degree of flow separation appeared at the top of the ridge. Whether this is characteristic of all beach ridges or not is not known. In any event the ridge top position has a much higher windspeed than the ridge bottom position.


SITE 1
RIDGE TOP
SITE 2
RIDGE SLOPE
128
64
32
16
8
2
Z (cm)
-5
-3
-1
1
3
5
7
μ(m/sec)
128
64
32
16
4
Z (cm)
0
2
4
6
μ(m/sec)

higher windspeeds are found at the top of the raised beach ridge than at the bottom.

Air and thallus temperatures are lower on the ridge top by 1-2°C than on the ridge bottom (Figure 31). Recent evidence (see Kershaw, 1975) indicates that the actual temperatures found on ridge top material coloured yellow may be an additional 1-2°C colder than black thalli placed under the same conditions. Thus yellow thalli at the ridge top could be consistently 4°C colder than similarly pigmented material from the ridge bottom.

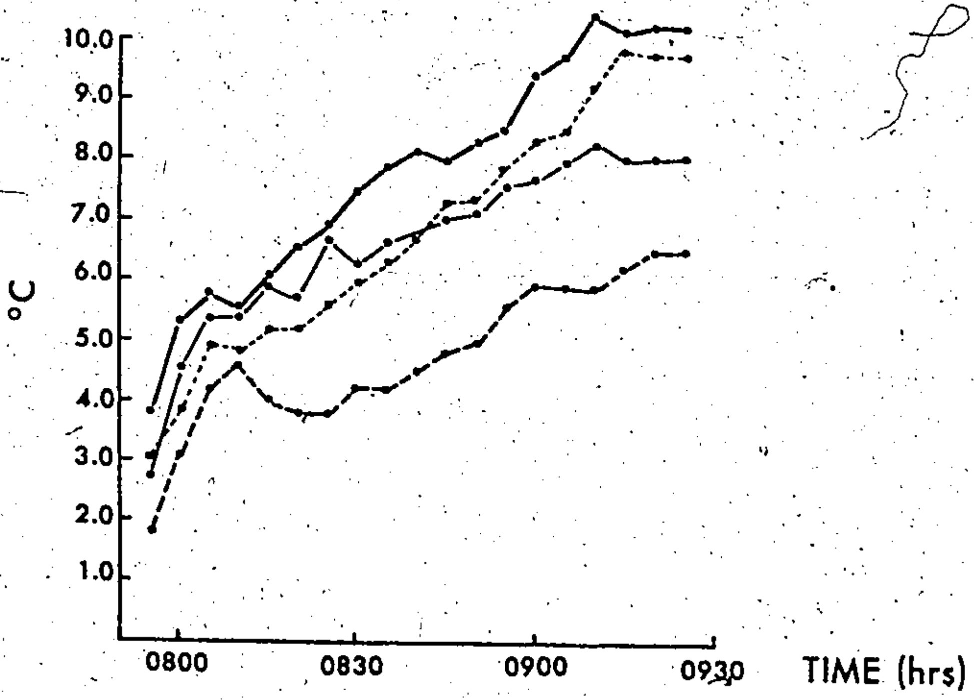
Drying Rates

The relative saturation levels found in the resistance grids at top and bottom position of the ridge in area III are shown in Figure 32a-e In each case the ridge bottom remained at a higher saturation level longer than the ridge top. Figure 32d-e shows the amount of drying that occurs during the night which reduces saturation levels in the grids on ridge top positions to a greater extent than those on the ridge bottom.

On the young ridge in area II the slight relief around *Dryas* hummocks and *Alectoria ochroleuca* dominated hollows greatly influences drying rates. Faster drying rates from the more exposed positions were consistently found (Figure 33a-d). These results are particularly significant in relation to the scale of the hummocks, which are only 0.5 meters centre to centre, with the hollow only 0.1 meters below the level of the *Dryas* mat (Figure 10a,b,c). Topography thus influences the drying rates under diffuse radiation, whether one considers small (hummock/hollow features) or large

Figure 31.

The change in thallus and air temperature for contrasting ridge top and bottom positions on two separate days. Top panel, Aug. 16, 1973, bottom panel, Aug. 18 , 1973. Symbols used : ●━━━●, thallus temperature on the ridge bottom; ●- - -● , thallus temperature on the ridge top ; ●——● , air temperature on the ridge bottom; ●━ ━●, air temperature on the ridge top.


10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
°C
0800
0830
0900
0930
TIME (hrs)

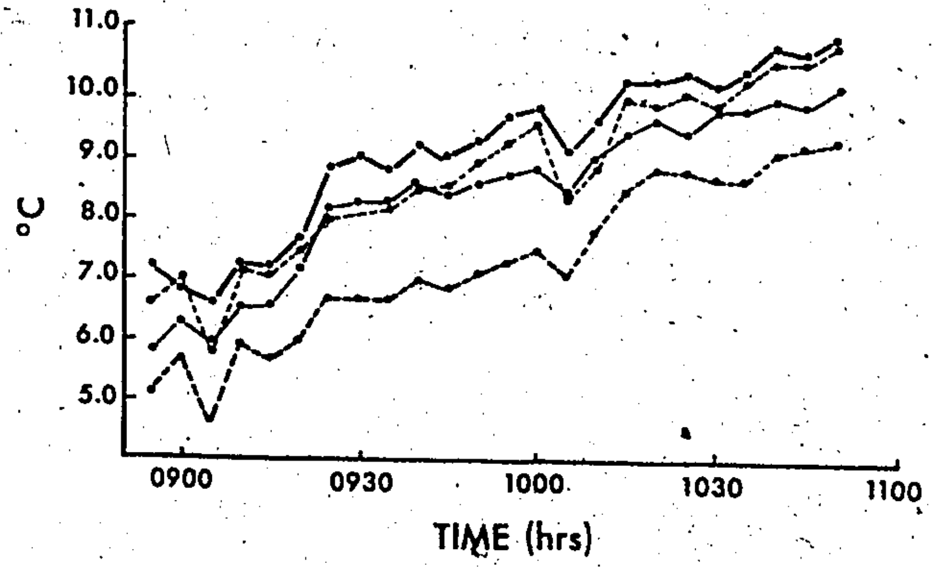
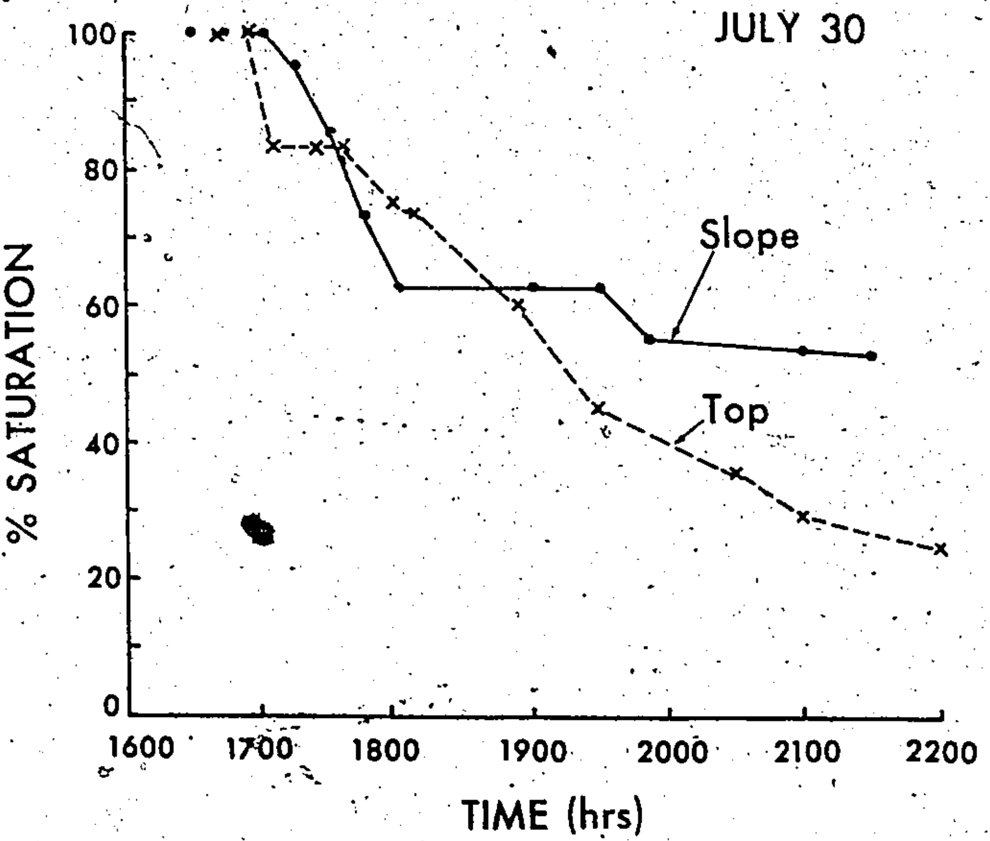

11.0
10.0
9.0
8.0
7.0
6.0
5.0
°C
0900
0930
1000
1030
1100
TIME (hrs)

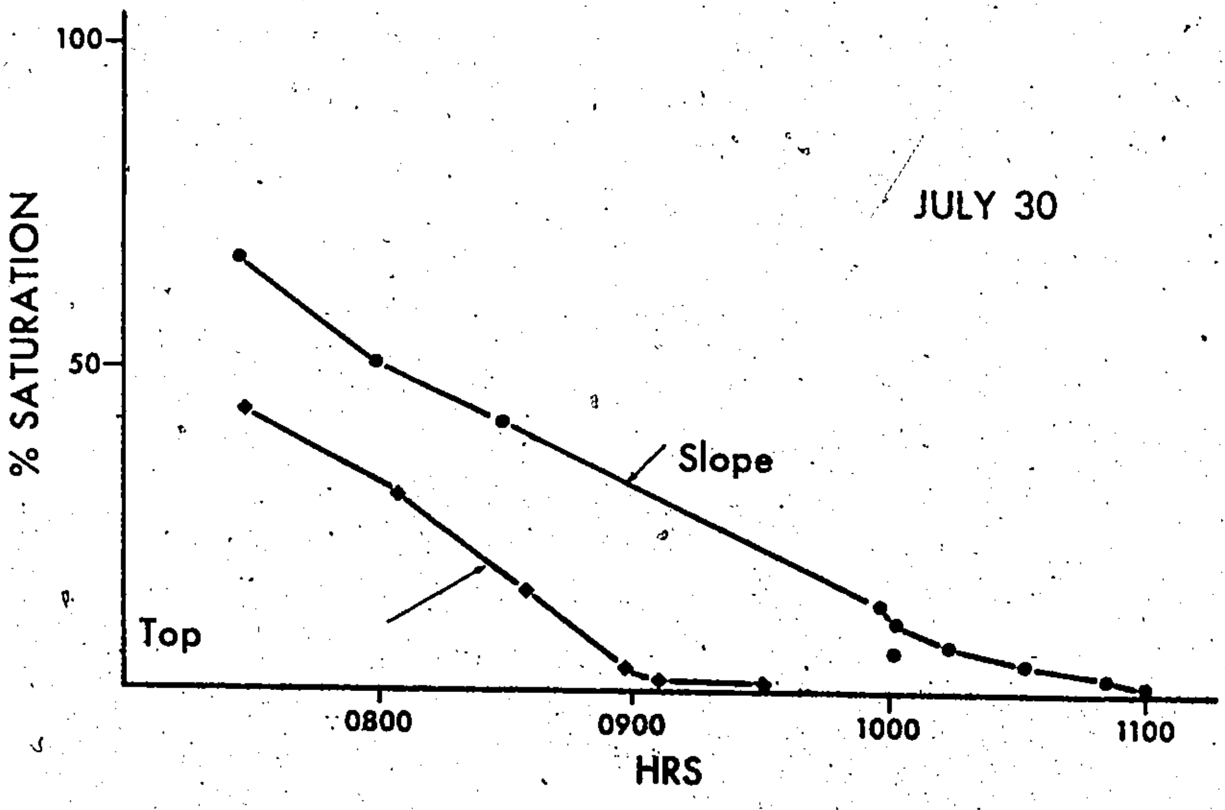
Figure 32.

Five separate drying runs during conditions of diffuse radiation over the ridge surface in area III. The data show that resistance grid moisture probes placed on the exposed ridge tops dry out more rapidly than probes placed on the bottom of the ridge. The percent saturation refers to the saturation levels found in the resistance grid moisture probes which had been placed on the vegetated surface.

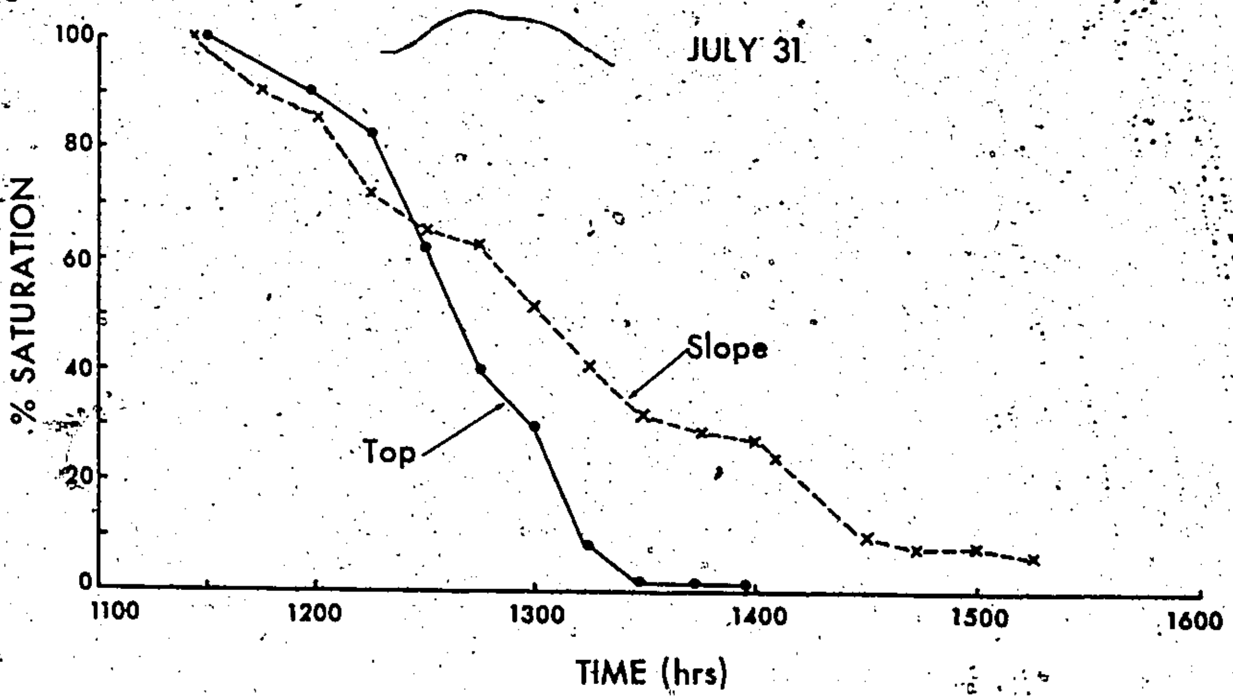
A


JULY 30
100
80
60
40
20
0
% SATURATION
Slope
Top
1600
1700
1800
1900
2000
2100
2200
TIME (hrs)

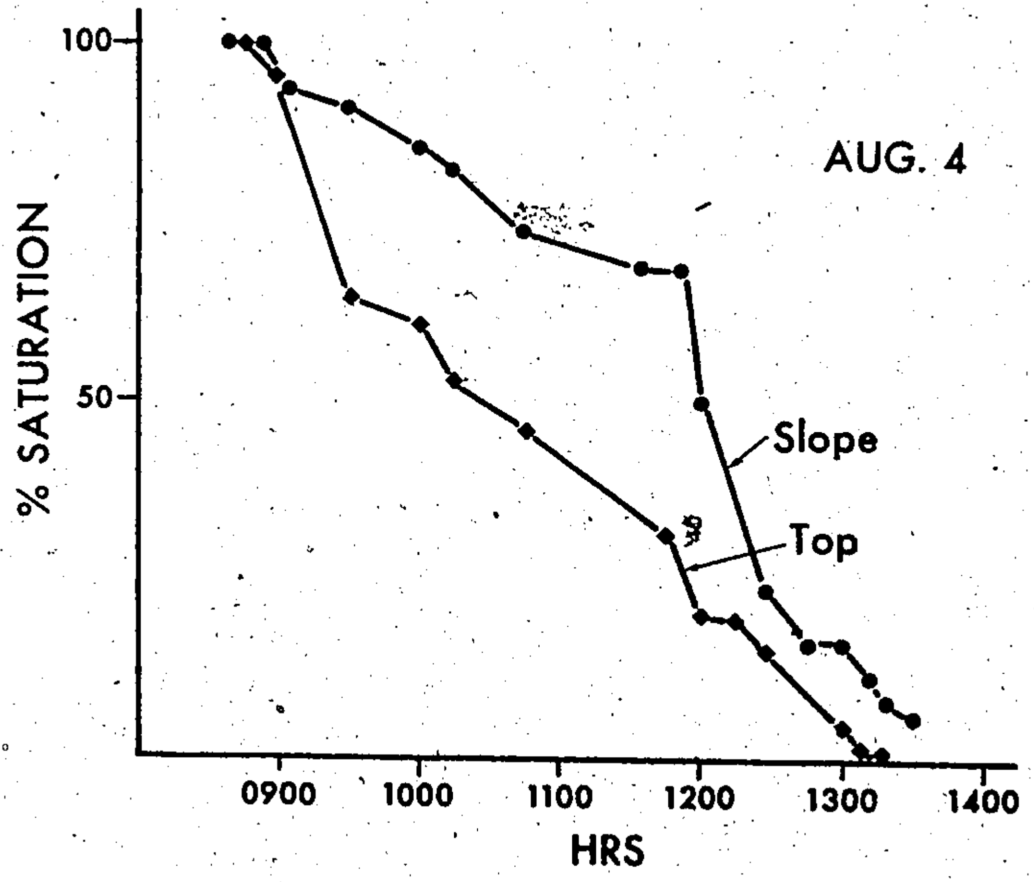
B


100
50
% SATURATION
JULY 30
Slope
Top
0800
0900
1000
1100
HRS

C


JULY 31
% SATURATION
100
80
60
40
20
0
1100
1200
1300
1400
1500
1600
TIME (hrs)
Slope
Top

D


AUG. 4
% SATURATION
100
50
0900
1000
1100
1200
1300
1400
HRS
Slope
Top

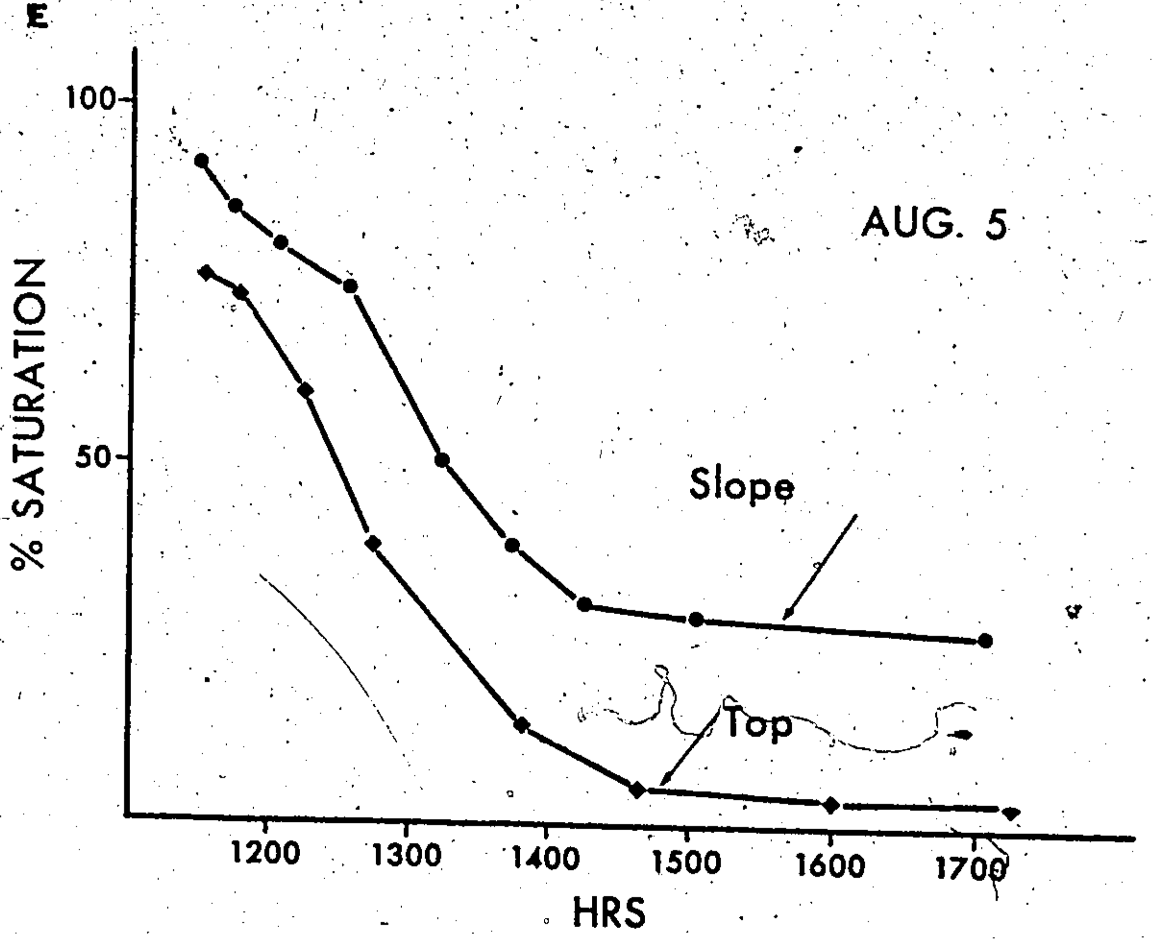
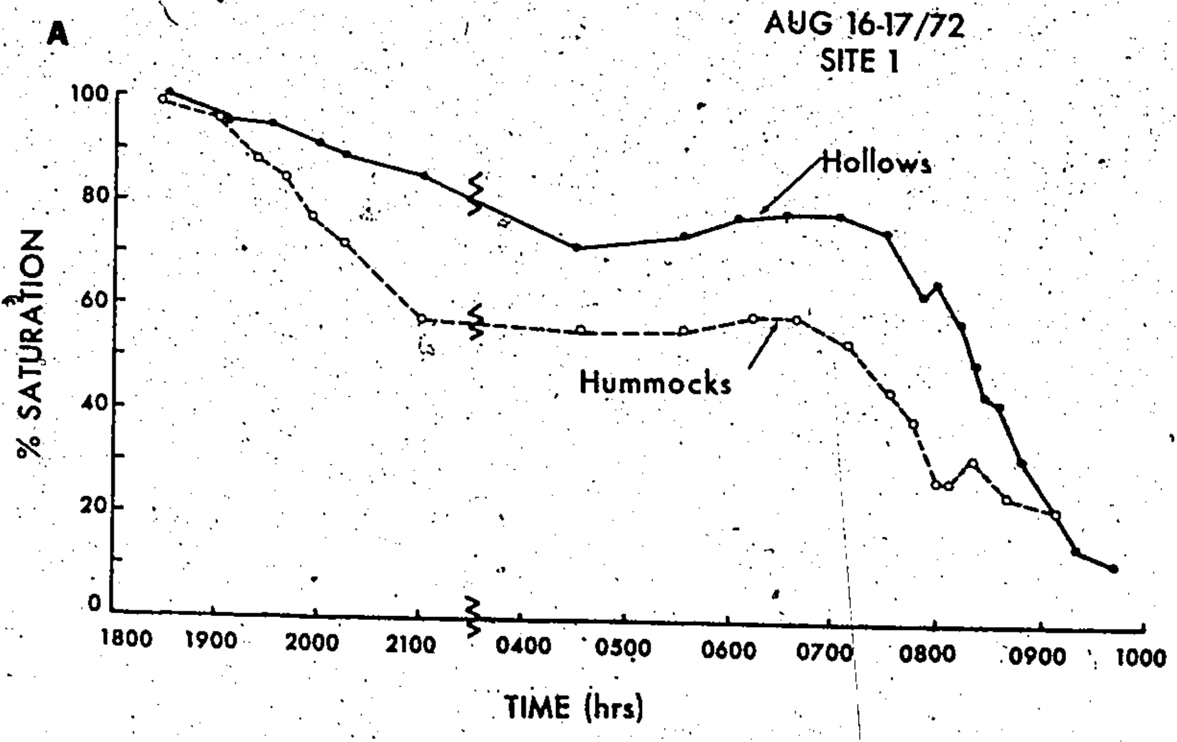

E
100
50
% SATURATION
1200
1300
1400
1500
1600
1700
HRS
AUG. 5
Slope
Top

Figure 33.

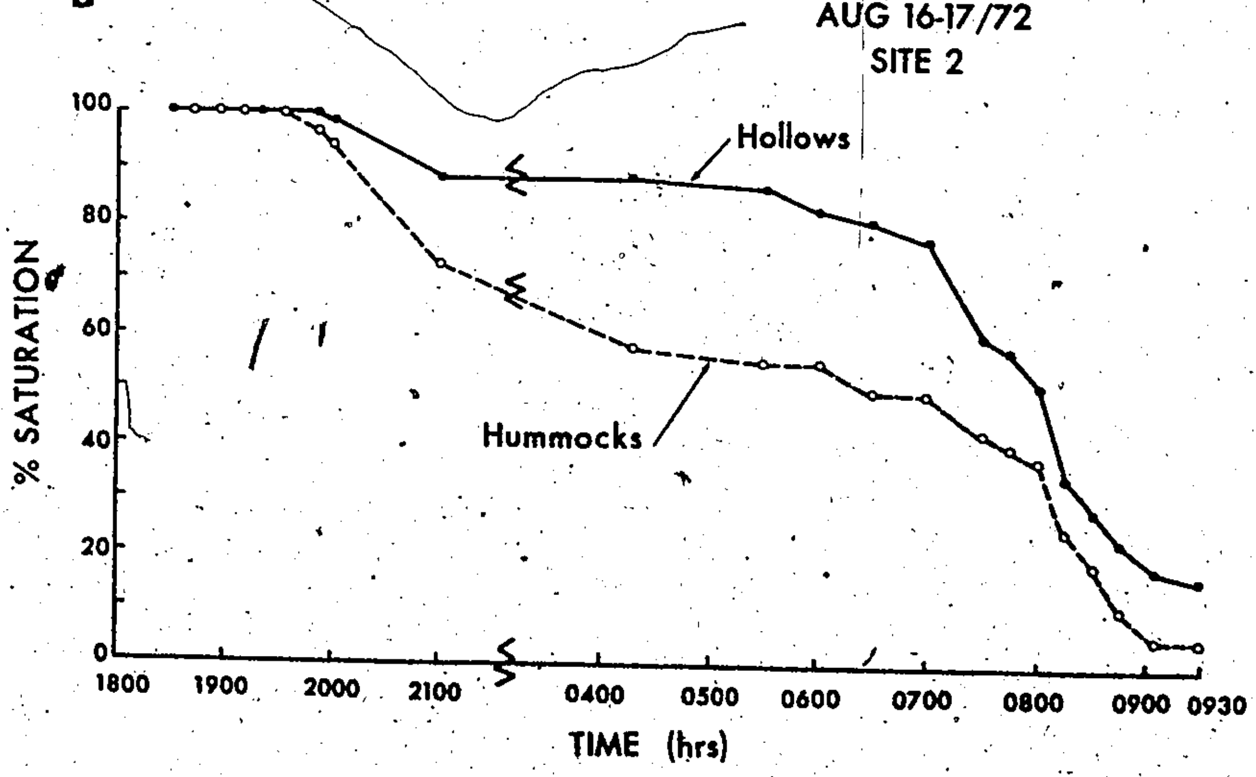
Drying runs over the hummock/hollow features in area I.

a,b - a long run extending through the night; c,d - a shorter run starting late in the morning. Winds from the north. Note that very little evaporation occurs at night.

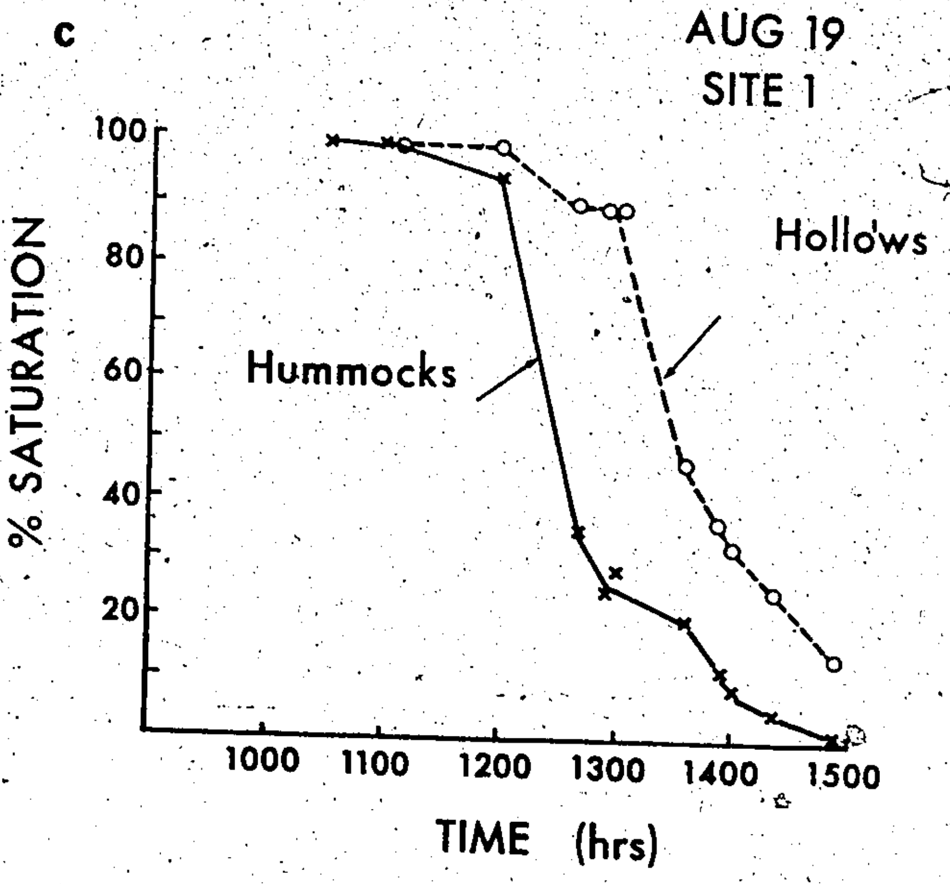
A


AUG 16-17/72
SITE 1
Hollows
Hummocks
% SATURATION
100
80
60
40
20
0
1800
1900
2000
2100
0400
0500
0600
0700
0800
0900
1000
TIME (hrs)

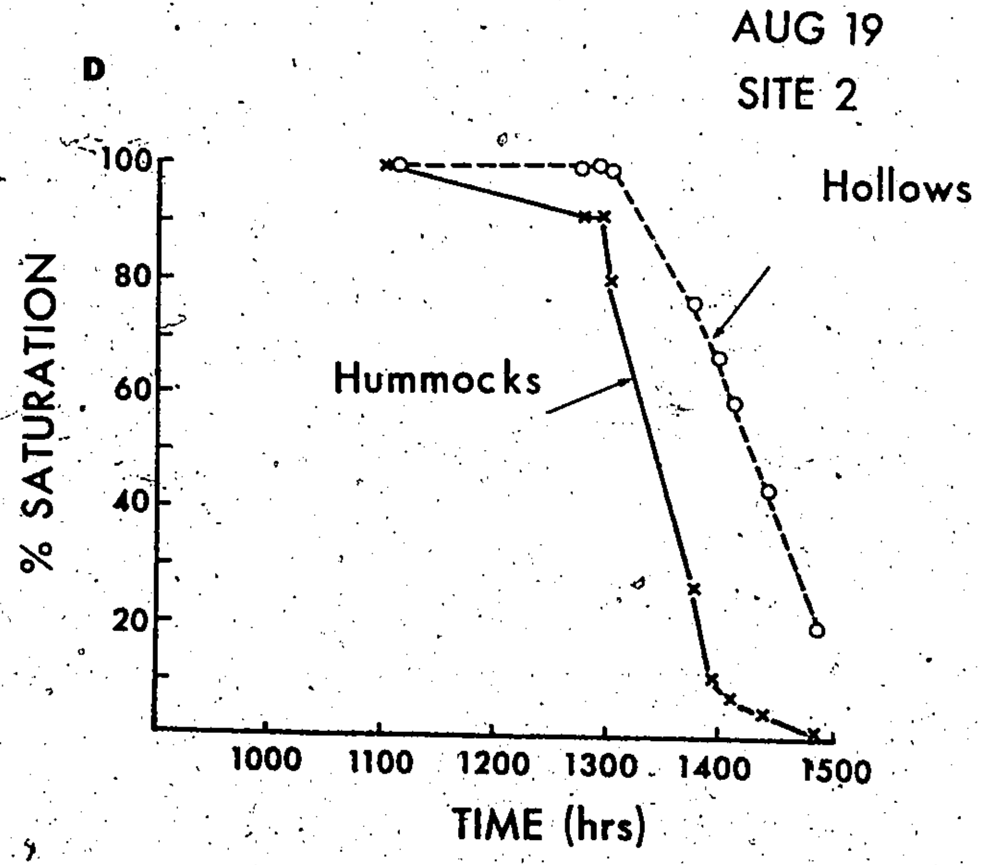
B


AUG 16-17/72
SITE 2
Hollows
Hummocks
% SATURATION
100
80
60
40
20
0
1800
1900
2000
2100
0400
0500
0600
0700
0800
0900
0930
TIME (hrs)

C


AUG 19
SITE 1
Hollows
Hummocks
% SATURATION
100
80
60
40
20
1000
1100
1200
1300
1400
1500
TIME (hrs)

D


AUG 19
SITE 2
Hollows
Hummocks
% SATURATION
100
80
60
40
20
1000
1100
1200
1300
1400
1500
TIME (hrs)

(raised beach) topographic irregularities.

(3.3) Physiological Adaptation to Contrasting Ridge Environments

A simple study designed to relate differences in distribution to patterns of net CO_2 exchange in lichens must account for at least three variables which control net photosynthetic rates. These are thallus moisture content, thallus temperature, and light intensity. In this particular study it was also necessary to repeatedly examine these interactions over a growing season and to compare the patterns seen interspecifically with those observed intraspecifically for samples collected from the two contrasting ridge positions. Alectoria ochroleuca and Cetraria nivalis were the species best suited to this approach because of their abundance and contrasting patterns of distribution (Figure 15), which permitted the collection of samples of both species from both the top and bottom positions of the raised beach ridge in area II.

(3.3.1) Responses Shown by Alectoria ochroleuca Collections from the Ridge Top (April and June)

The physiological data matrix for A. ochroleuca (ridge top) is shown in Figure 34. The response of dark respiration to thallus moisture content is linear at 1°C. As the temperature is raised from 1 to 28°C the rates of dark respiration at 200% moisture content increase from 0.07 to 0.70 mg $CO_2 \cdot h^{-1} \cdot /g^{-1}$. The respiration rates at 28°C show a marked second order interaction with thallus moisture content.

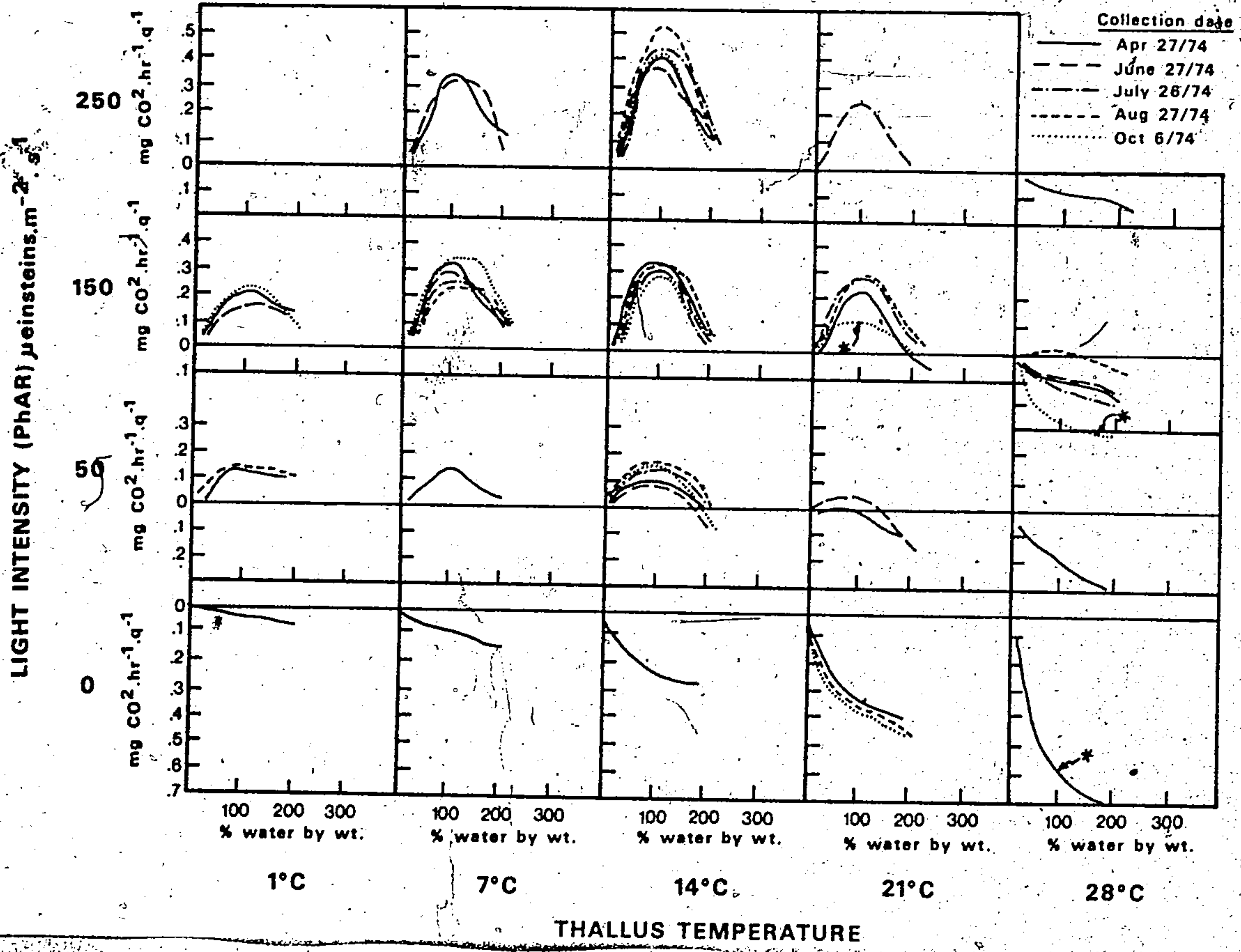
At low light intensities of 50 μ einsteins $\cdot$ $m^{-2} \cdot sec^{-1}$ the

Figure 34.

The physiological data matrix for <u>Alectoria</u> <u>ochroleuca</u> collected from the top of the raised beach ridge shown in Figure 15. The matrix is formed by repeated measurement of the response of net photosynthesis to thallus moisture content, at a variety of experimental conditions. Curves shown are averages of four to ten replicates. Any two points separated by more than 0.05 mg $CO_2 \cdot hr^{-1} \cdot g^{-1}$ are significantly different at the 5% level, with the exception of three experiments (shown by asterisks) which require a difference of 0.07 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ to establish significance. Net photosynthesis is positive above the zero line and negative (respiratory dominated) below the zero line. 1 einstein = Avagadro's number of photons.

Alectoria ochroleuca

from raised beach ridge top



response of net photosynthesis to thallus moisture content between 200 and 70% is constant. Between 70 and 10% however, rates are reduced sharply. Although an increase in the temperature from 1 to 7 and 14°C does not change the maximum rates of fixation at 85% thallus moisture content, rates at 200% decrease steadily from the cooler to the warmer temperatures.

At 150 μ einsteins · m^{-2} · sec^{-1} the response of net photosynthesis to thallus moisture content shows an increase in maximum rates (at 85% thallus moisture content) to an optimum at 7-14°C, followed by reductions at 21 and 28°C. At 200% thallus moisture content an increase in thallus temperature continuously decreases the net photosynthesis until a negative carbon balance appears at 28°C. A further increase in light intensity to 250 μ einsteins · m^{-2} · sec^{-1} at 7-14 and 28°C increases the maximum levels of fixation about 15%.

Although insufficient points beyond 250 μ einsteins · m^{-2} · sec^{-1} have been obtained it would appear that light saturation is close to this level in the material collected in April.

<u>Seasonal Acclimation</u>

The responses of net photosynthesis to light and temperature change seasonally and appear to continuously track the seasonal climatic patterns found at the research site (c.f. Figure 4). In contrast dark respiration rates at 21°C do not change seasonally, these results confirming those given by Stålfelt (1939) for a variety of lichen species.

At a low light intensity of 50 μ einsteins · m^{-2} · sec^{-1} there was an increase of net photosynthesis from April to August at 14°C. From April to June at 21°C and from April to August at 1°C similar changes were evident. There was some evidence that the trend had started to reverse by October at 14°C. In April at 150 μ einsteins · m^{-2} · sec^{-1} the optimal temperature for net photosynthesis at 85% thallus moisture content is between

7° and 14°C. This changes to 14-21°C in August and back to 7°C in October. The pattern seen at 28°C also shows this seasonal change in levels of net photosynthesis. Although the optimum temperature for net photosynthesis changes seasonally, the absolute rates of fixation are the same at these different temperatures.

The changes in response to light intensity at 14°C show that while maximum levels of fixation achieved at 85% thallus moisture content and at 250 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} in April are 0.38 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1}, levels of 0.53 appear by August and fall again to 0.40 in October. This change in response can also be seen by comparing levels of fixation at 150 vs. 250 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} seasonally. While there was only 15% increase in April, a 40% increase in the August collection was found, indicating that the light saturated level had shifted seasonally. This feature was not found by Lechowicz and Adams (1974) examining boreal lichen species.

Collections from the ridge bottom

Intraspecific comparisons were made between ridge top and bottom collections of Alectoria ochroleuca across all experimental conditions. The physiological data matrix is shown in Figure 35; the ridge top-ridge bottom comparison is summarized in Figure 36 and Table IV. Over all conditions and all seasons (grouped) the ridge top and bottom collections were not significantly different in terms of responses to temperature, light, thallus moisture content, and time of year. Comparisons throughout the various seasons did show some small differences. At 50 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} and 14°C, the ridge bottom material collected in June shows a higher net photosynthetic rate than the ridge top material. A similar difference is found by comparing the April response for the ridge top material with the

Figure 35.

The physiological data matrix for Alectoria ochroleuca from the bottom of the beach ridge shown in Figure 15.

Alectoria ochroleuca

from raised beach ridge bottom

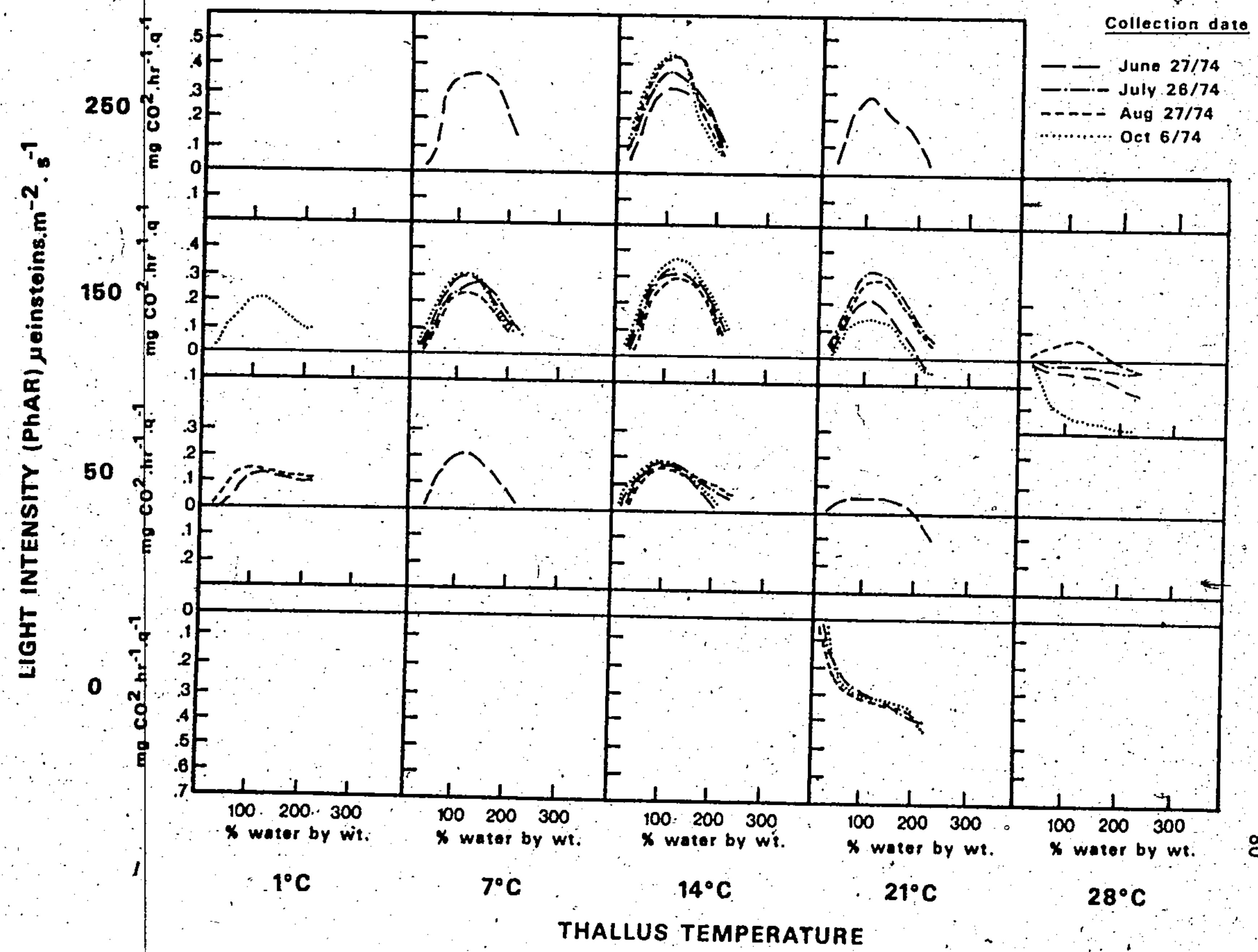


Table IV

Results of intraspecific comparison of net photosynthetic rates at both 100 and 50% relative water content. Shown are deviations away from the simultaneous confidence interval (0.05 mg $CO_2 \cdot h^{-1} \cdot g^{-1}$); + if ridge top material has higher levels, - if ridge bottom material has higher levels. No significant differences favouring one collection over the other appear in the total accumulated comparison.

Alectoria ochroleuca (T) vs. A. ochroleuca (B) 100% BWC

Light intensity (μ einsteins · $m^{-2} \cdot s^{-1}$)	50			150		250	
Thallus temperature (°C)	14	7	14	21	28	14	Average
June	0	0	00	0	0	0	.00
July	0	0	0	0	-.10	0	-.02
August	0	0	0	0	0	0	.00
October	0	0	-.06	0	0	0	-.01
Average	.00	.00	-.02	.00	.00	.00	

Sign Totals over all Conditions

0 = 22
+ = 0 N.S.
- = 2 N.S.

Alectoria ochroleuca (T) vs. A. ochroleuca (B) at 50% RWC

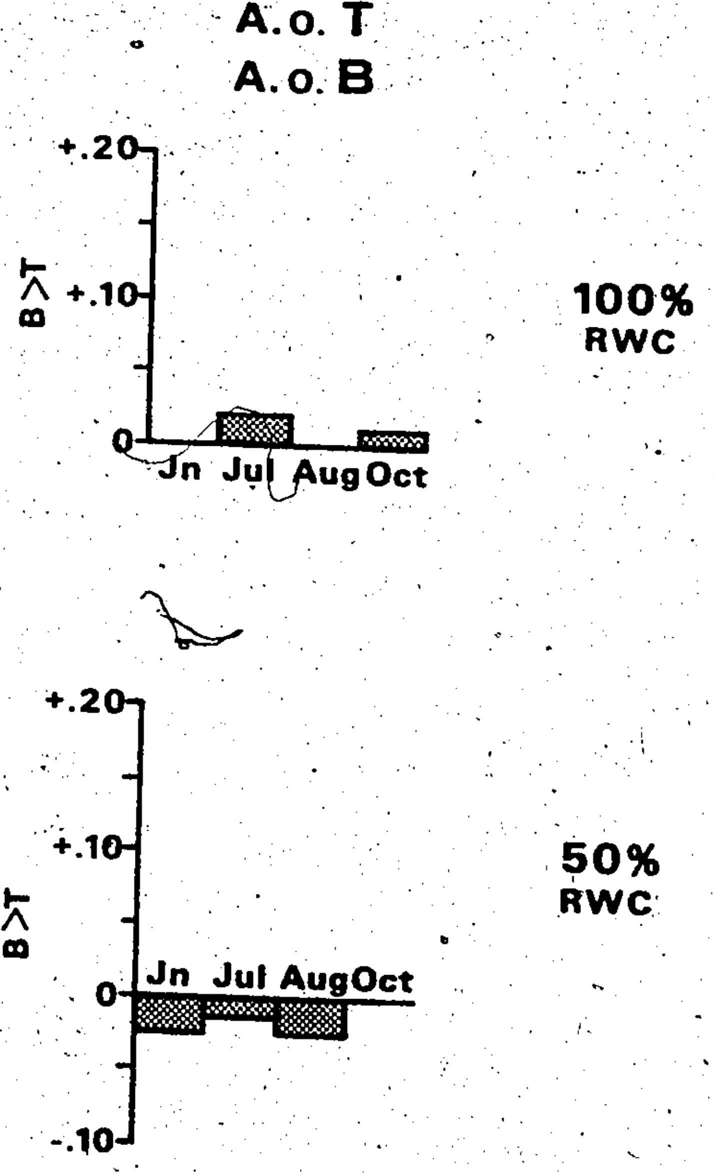
Light intensity (μ einsteins · $m^{-2} \cdot s^{-1}$)	50			150		250	
Thallus temperature (°C)	14	7	14	21	28	14	Average
June	-.07	0	0	0	0	+.05	.00
July	0	0	0	0	-.10	+.07	+.01
August	0	0	0	0	0	+.11	+.02
October	0	+.05	+.06	-.00	0	0	.00
Average	-.02	+.01	-.02	.00	-.03	+.06	

Sign Totals over all Conditions

0 = 17
+ = 4 N.S.
- = 3 N.S.

Figure 36.

The seasonal variation of accumulated intraspecific difference in net photosynthetic rates (data from Table 1V) at both 100 % and 50 % relative water content (RWC) , for *A. ochroleuca* . Values above the zero line show average amounts by which the ridge bottom collections significantly exceed the ridge top collections in terms of net photosynthetic rates at identical experimental conditions. Symbols: A.o., *A. ochroleuca* ; T, collection from the ridge top; B, collection from the ridge bottom.


A.o. T
A.o. B
+.20
+.10
0
B>T
Jn
Jul
Aug
Oct
100%
RWC
+.20
+.10
0
-.10
B>T
Jn
Jul
Aug
Oct
50%
RWC

June material by the ridge bottom material. From June to August at 250 µ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}, 100% thallus moisture content and 14°C, the ridge top material shows higher rates of fixation than the ridge bottom material. In October this advantage is lost as the ridge top material acclimates back towards 7°C where its rates are higher than for ridge bottom material. At the same time, the ridge bottom material still shows an optimum near 14°C, significantly higher than the ridge top material. These differences must be interpreted carefully because the majority of experiments show no significant differences.

(3.3.2) Responses shown by Cetraria nivalis Collections from the Ridge Top (April and June)

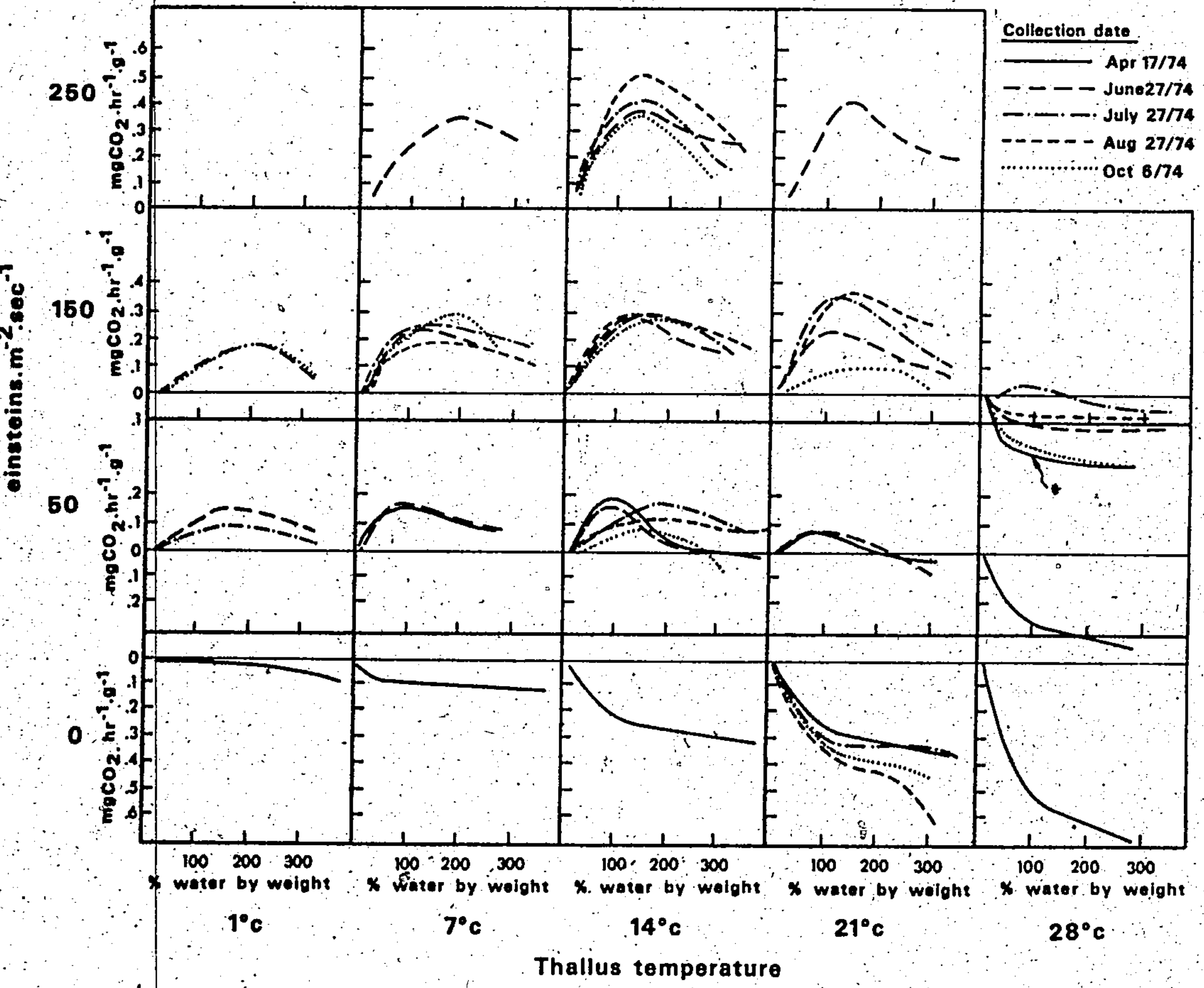
The physiological matrix for C. nivalis (ridge top) is shown in Figure 37. The maximum level of thallus saturation found was 400%, although average values were near to 300-350% of dry weight. The response of dark respiration to temperature and moisture shows second order interactions between these variables. At 1°C respiration is a linear function of thallus moisture content, except at full saturation where the rate is increased. The maximum CO_2 evolved is near 0.10 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1}. Conversely, at 7°C respiration at lower levels of thallus saturation is elevated to a much greater degree than at full maximum thallus saturation. Further increase in temperature serves to move this inflection point to higher thallus moisture contents. The Q_{10} of dark respiration varies from 1.2 at 1-7°C to 3.0 at 21-28°C. These results are consistant with those of Stålfelt (1939) who found considerable variability of Q_{10} under different conditions of temperature and thallus moisture content.

Figure 37.

The physiological data matrix for <u>Cetraria nivalis</u> collected from the top of the beach ridge shown in Figure 15. Note that this species holds up to 350 % thallus moisture content by weight as compared with <u>A. ochroleuca</u> which holds up to 200 % . Any two points separated by more more than 0.05 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ are significantly different at the 5% level, with the exception of one experiment (shown by an asterisk) which requires 0.07 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ to establish significance.

Cetraria nivalis

from raised beach ridge top



At 50 μ einsteins · m^{-2} · sec^{-1} the response of net photosynthesis to thallus moisture contents at low temperatures show an optimum at 100% thallus water content. As the temperature is increased, the increases in dark respiration at full thallus saturation produces a more negative carbon balance until the entire system is respiration dominated at 28°C, regardless of the light intensity. As the light intensity is increased to 150 from 50 μ einsteins · m^{-2} · sec^{-1}, a similar maximum net photosynthesis is obtained at 1°C suggesting that temperature is limiting to the system at these light intensities. As the temperature is increased, the net photosynthetic rate also increases having an optimum at 14°C. Further temperature elevations result in a decrease in net photosynthesis such that at 28°C a negative carbon balance is observed. A further increase in the light intensity from 150 to 250 μ einsteins · m^{-2} · sec^{-1} results in a slight increase in net photosynthetic rate at 7 and 14°C. However significant increases of 0.10 mg CO_2 · h^{-1} · g^{-1} are observed at 21°C.

Seasonal Acclimation

Rates of dark respiration at 21°C are similar from June to July; in August, however, rates increase significantly especially at 350% thallus moisture content. In October, the levels of respiration return to the spring and early summer levels.

At low light levels, 50 μ einsteins · m^{-2} · sec^{-1}, and 1°C, *C. nivalis* shows lower rates of fixation in July than in June. At 14°C a marked sequence of curves indicates requirements for low thallus moisture contents (60-110%) early in the year, followed by a broadening of the response from July to August. This response is followed in October by a tightening of the curve suggesting a return to the April response. This evidence for acclimation to thallus moisture content is of interest when these curves are compared to the response shown by C. nivalis collected from the ridge bottom (see below). Briefly, the ridge bottom material shows little seasonal change in response for this cell of the matrix.

Acclimation to temperature is seen at a light intensity of 150 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}. The optimum temperature for maximal net photosynthetic rate at optimal thallus moisture content is 14°C in the April – June collections, with slightly lower levels at both 7° and 21°C. By July and August, however, net photosynthesis has dropped both at 50 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} at 1°C and at 150 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} at 7°C. Conversely, at 21°C rates have increased to levels above those found at 14°C. A similar pattern appears at 28°C; by August a negative carbon balance appears at high thallus moisture contents. By October, a month showing average temperatures below 0°C (c.f. Figure 4), the ridge top collection acclimates back to show a maximum net photosynthesis at 7°C.

A seasonal change in response to light intensity is found in this species as well. A light saturated net photosynthesis of 0.32 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1} is achieved near 150 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}, in June. By August, the data suggest that the light saturated point is well above 250 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}. By October, this pattern has started to reverse itself.

Collections from the ridge bottom

C. nivalis is most abundant at ridge bottom positions (Figure 15). Only four collections (June, July, August, October) were compared because, this ridge position is not snow free until the end of May. The physiological data matrix for this material is shown in Figure 38 while Table V shows the total intraspecific comparison for all seasons and all conditions.

Figure 38.

The physiological data matrix for Cetraria nivalis collected from the bottom of the beach ridge shown in Figure 15. Any two points separated by more than 0.05 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ are significantly different, with the exception of one experiment (shown by an asterisk) which requires a difference of 0.07 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ to establish significance.

Cetraria nivalis

from raised beach ridge bottom

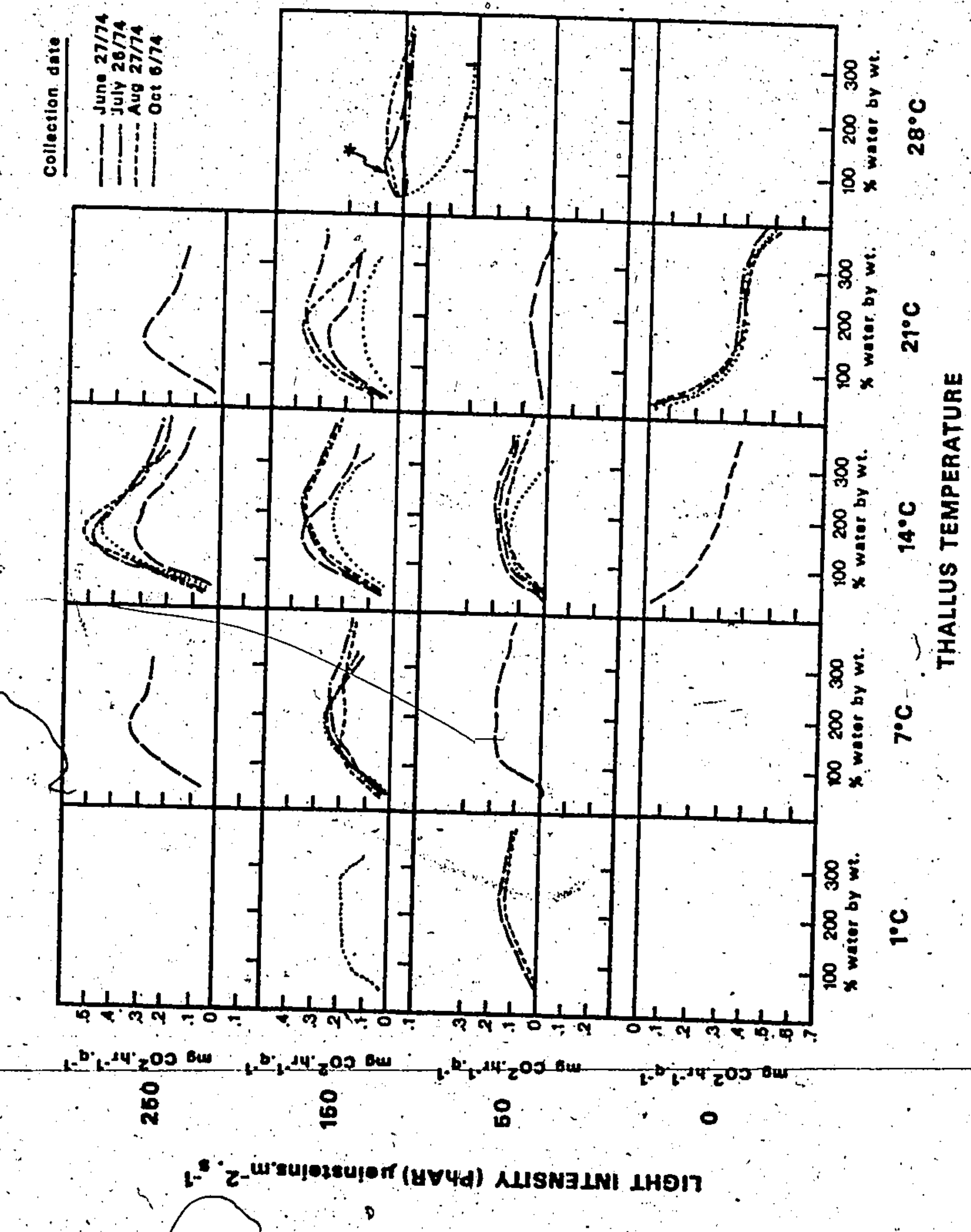


Table V

Results of intraspecific comparison of net photosynthetic rates at both 100 and 50% relative water content. Shown are deviations away from the simultaneous confidence interval (0.05 mg $CO_2 \cdot h^{-1} \cdot g^{-1}$); + if ridge top material has higher levels, – if ridge bottom material has higher levels. Asterisks indicate differences significant at the 5% level.

C. nivalis (T) vs. C. nivalis(B) at 100% RWC

Light intensity	50			150		250		
Thallus temperature	14	7	14	21	28	14	Average	
June	-.15	0	0	0	-.10	+.10	-.01	
July	0	0	-.10	-1.5	0	-.10	-.06	*
August	0	0	-.05	-1.5	-1.5	0	-.06	
October	0	0	0	0	0	-1.5	-.03	
Average	-.04	.00	-.05	-.08	-.06	-.04		

Sign Totals over all Conditions

0 = 14
+ = 1*
– = 9*

C. nivalis (T) vs. C. nivalis (B) at 50% RWC

Light intensity	50			150		250	
Thallus temperature	14	7	14	21	28	14	Average
June	0	0	-.12	0	-.10	0	-.04
July	0	0	-.10	0	0	-.10	-.03
August	0	0	-.05	0	-.15	0	-.03
October	-.05	0	0	0	0	-.15	-.03
Average	-.01	.00	-.07	.00	-.06	-.06	

Sign Totals over all conditions

0 = 16
+ = 0*
– = 8*

When identical experiments are compared, material collected from the ridge bottom does significantly better in terms of net photosynthetic production than material collected from the ridge top. This is true for thallus saturation levels of 160% and 350%. Figure 39 shows that these significant differences favoring higher CO_2 fixation in the ridge bottom collection at 350% thallus moisture content are not equally distributed seasonally. The amount by which the ridge bottom material exceeds the ridge top material is greater in July and August than in June and October.

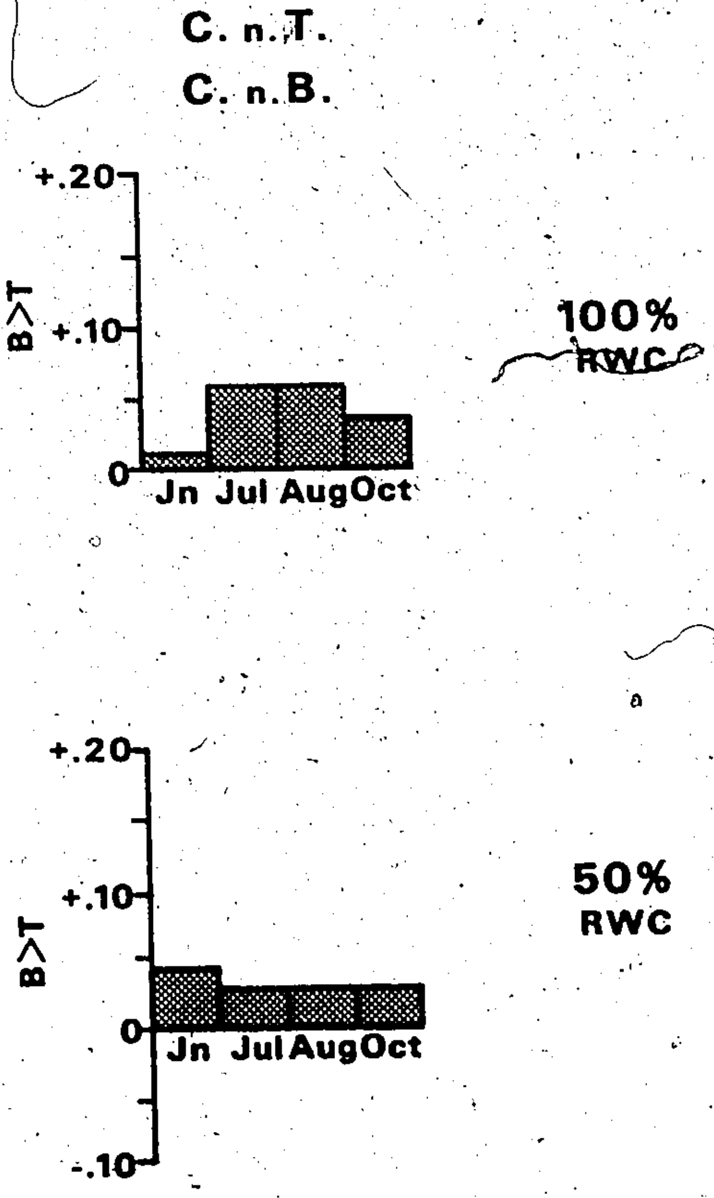
Some of the more significant differences between these two collections are as follows. Rates of dark respiration at 21°C found in the ridge bottom material are constant throughout the year, unlike the ridge top material which changes in August. Net photosynthesis is much higher in the ridge bottom material at low light intensities (50 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}), 350% thallus moisture content, and at 7°, 14°, and 21°C than in ridge top material. At 150 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}, 14°, 21° and 28°C and 350% thallus moisture content, ridge bottom material has higher net photosynthesis than the ridge top material in July and August. Such differences effectively disappear by October. At high light intensities (250 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}) in June, the net photosynthesis of the ridge bottom material is lower than the ridge top material. By July both samples have acclimated so that the ridge bottom exceeds the ridge top material.

(3.3.3) Collections of *A. ochroleuca* from Other Geographical Locations

The lack of intraspecific variation observed in *A. ochroleuca* stimulated interest in the potential geographical variations in net photosynthetic rates in this species. *A. ochroleuca* collected from a palsa mound, forty miles south of the tree line at Pen Island and from Little Point,

Figure 39.

The seasonal variation of accumulated intraspecific difference in net photosynthetic rates (data from Table V) at both 100 % and 50 % relative water content (RWC) for *Cetraria nivalis* . Values above the zero line show average amounts by which ridge bottom material significantly exceeds ridge top material. At 100 % RWC the amounts by which the ridge bottom material exceed the ridge top material is significant in July and August but not so in June and October. An asterisk indicates differences significant at the 5 % level. Symbols : C.n., *C. nivalis* ; T, collection from the ridge top ; B, collection from the ridge bottom.


C. n. T.
C. n. B.
B>T
+.20
+.10
0
Jn
Jul
Aug
Oct
100%
RWC
B>T
+.20
+.10
0
-.10
Jn
Jul
Aug
Oct
50%
RWC

Melville Island, Northwest Territories are shown in Figures 16 d and e, respectivley. Figure 40 shows that rates of dark respiration at 21°C are very much lower for the Melville Island material, although the shape of the curve is similar to the Pen Island material. The respiration rates found in the very robust palsa mound material are lower too, but are not significantly different from the Pen Island material.

At 150 μ einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} and 1°C the Melville material fixed only 0.045 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1} at its maximum, as compared to the palsa mound and Pen Island materials, both fixing 0.15 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1}. A slightly negative carbon balance appears at full saturation (200%), but these levels of saturation are only rarely found in the field. At 7°C, the rates of net photosynthesis in the Melville Island material are not significantly increased above those levels at 1°C. This contrasts with the palsa mound and Pen Island materials which increase to about 0.225 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1} at 100% thallus moisture content. At 200% thallus moisture content, the palsa mound material nears the compensation point, whereas the Pen Island material is fixing about 0.10 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1}. At 14°C, no significant increase in levels of fixation appears for the Melville Island material although a more negative carbon balance appears at 200% thallus moisture content. Conversely, the Pen Island material reaches its optimum near this temperature giving levels of 0.325 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1}. These patterns contrast markedly with the palsa mound material whose levels of fixation between 7° and 14°C drop from 0.225 to 0.150 mg CO_2 $\cdot$ h^{-1} $\cdot$ g^{-1}. This pattern is made more apparent by the results at 21°C which show the separation of these three varieties.

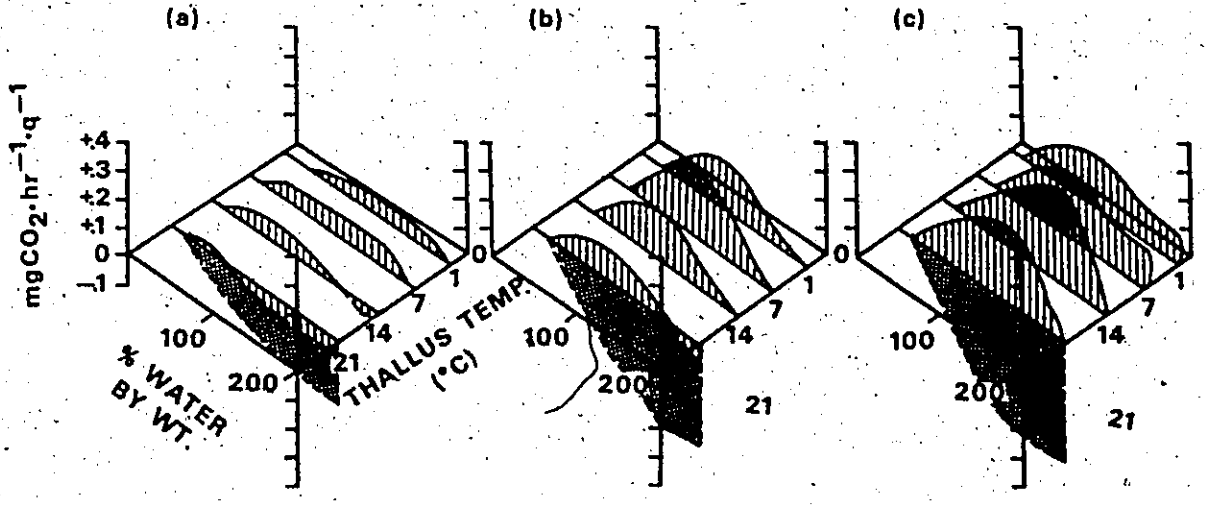
Figure 40.

The responses of net photosynthesis to thallus moisture content and thallus temperature at 150 μ einsteins $\cdot m^{-2} \cdot sec^{-1}$ (vertical shading) for a) A. ochroleuca collected from Melville Island, Northwest Territories.

b) A. ochroleuca collected from a palsa mound 40 miles south of the tree line near the Pen Island research site.

c) A. ochroleuca collected from the beach ridge top (area II) East Pen Island.

The responses of dark respiration to thallus moisture content at 21 °C are shown as stippled shading. All collections July 26, 1974.


(a)
(b)
(c)
mgCO$_2$·hr^{-1}·g^{-1}
+4
+3
+2
+1
0
-1
0
0
100
200
% WATER BY WT.
THALLUS TEMP. (°C)
1
7
14
21

An increase in the light intensity to 250 μ einsteins · m^{-2} · sec^{-1} does not increase rates of fixation at 14°C for the Melville Island and palsa mound materials, in contrast to the Pen Island material (Figure 41). Thus, the palsa mound and Melville Island collections are light saturated at 150 μ einsteins · m^{-2} · sec^{-1} while the Pen Island material is not.

(3.34) Comparison of the Physiological Data Matrices for A. ochroleuca and C. nivalis from East Pen Island

A. ochroleuca and C. nivalis have very different maximum water holding capacities due to morphological dissimilarities. These differences result in different responses of net photosynthetic rate to thallus moisture content (Figures 34, 35, 37, 38). The maximum net photosynthetic rate in A. ochroleuca is near 85% thallus moisture content by weight whereas it is near 160% in C. nivalis. Thus at relatively high levels of thallus saturation, net photosynthesis in C. nivalis is greater than in A. ochroleuca, since the former is near its optimal moisture content for net photosynthesis. Conversely, at 100% thallus moisture content, A. ochroleuca exceeds C. nivalis since the former is at its optimum thallus moisture content for net photosynthesis, while C. nivalis is showing limitation of net photosynthesis by low thallus moisture contents.

While it appears that C. nivalis is adapted to utilize high levels of thallus saturation, the effect observed is predominantly morphologically derived. The physiological comparison that is necessary can only be made when the data for both species are converted to relative water content (RWC). This process effectively removes that component of variation in net photosynthetic rates which morphologically derived. Thus the data in Figures 34, 35, 37, 38

Figure 41.

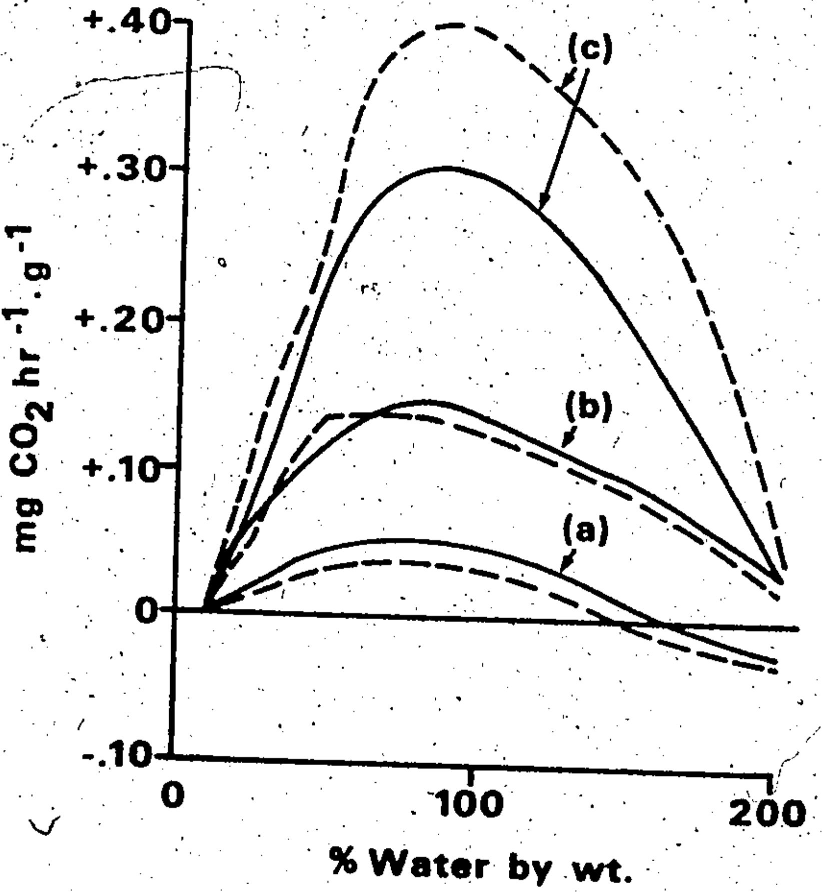
Patterns of net photosynthesis shown by the three varieties of A. ochroleuca when the light intensity is increased from 150 to 250 μeinsteins $\cdot m^{-2} \cdot sec^{-1}$ .Solid lines represent responses at 150 μeinsteins$\cdot m^{-2} \cdot sec^{-1}$, dotted lines are for 250 μeinsteins $\cdot m^{-2} \cdot sec^{-1}$.

a) collection from Melville Island

b) collection from the palsa mound

c) collection from the beach ridge at East Pen Island.

All collections July 26 1974. Curves are the mean of four to ten replicates . Points separated by more than 0.05 $mgCO_2 \cdot hr^{-1} \cdot g^{-1}$ are significantly different.


+.40
+.30
+.20
+.10
0
-.10
mg CO_2 hr^{-1}.g^{-1}
0
100
200
% Water by wt.
(c)
(b)
(a)

were converted to a percentage of the maximum thallus moisture content and interspecific comparisons were then made using these data. The results of interspecific comparisons between *A. ochroleuca* and *C. nivalis* are shown in Table VI. The two points examined on each curve were the net photosynthetic rates both at 50 and 100% relative water content. Only experiments done at all conditions for all collections were included in this comparison.

An examination of the accumulated totals through all comparisons shows that *C. nivalis* significantly exceeds *A. ochroleuca* at 100% RWC. At 50% RWC the situation tends to reverse, although the total amount by which *A. ochroleuca* exceeds *C. nivalis* is insignificant. Since these patterns are accumulated differences over all experimental conditions, it was possible that deviations in one direction were being cancelled out by deviations of equal magnitude in the other direction, thus producing a non-significant total difference. Thus these totals were proportioned to row averages which show the seasonal distribution of the total difference, and to column averages to show the temperature distribution of these differences. These differences are also shown in Table VI and Figure 42. A lack of data prevented a similar approach from being taken to observe the distribution of these differences amongst the different light intensities used.

In Case 1, the comparison of *A. ochroleuca* (ridge top) with *C. nivalis* (ridge top), *C. nivalis* exceeds *A. ochroleuca* by a constant amount between June and July; between August and October, however, these differences decrease. At 50% RWC, *A. ochroleuca* significantly exceeds *C. nivalis* only in October. In Case 2, comparing *A. ochroleuca* (ridge top) with *C. nivalis*

Table VI

Results of interspecific comparisons of net photosynthetic rates at both 100 and 50% relative water content. Shown are deviations away from the simultaneous confidence interval (0.05 mg $CO_2 \cdot h^{-1} \cdot g^{-1}$); + if *A. ochroleuca* has higher levels of net photosynthesis, - if *C. nivalis* has higher net photosynthetic rates. Asterisk indicates differences significant at the 5% level.

Case 1 A. ochroleuca (T) vs. C. nivalis (T) at 100% RWC

Light intensity	50	150				250	
Thallus temperature	14	7	14	21	28	14	Average
June	-.18	-.10	-.15	-.15	0	-.20	-.13*
July	-.18	-.13	-.20	-.08	-.15	-.05	-.13*
August	-.08	0	-.20	-.25	+.05	-.08	-.09
October	0	0	-.15	0	0	0	-.03
Averages	-.11	-.06	-.18	-.12	-.03	-.08	

Sign Totals over all Conditions

0 = 7

+ = 1*

- = 16*

Case 1 A. ochroleuca (T) vs. C. nivalis (T) at 50% RWC

Light intensity	50	150				250	
Thallus temperature	14	7	14	21	28	14	Average
June	-.10	+.06	0	0	0	0	-.01
July	+.08	0	0	-.05	-.10	+.07	.00
August	+.10	+.05	+.05	-.10	+.06	+.07	+.04
October	+.08	+.08	+.07	+.06	0	+.13	.07*
Averages	+.04	+.05	+.03	+.01	-.01	+.07	

Sign Totals over all Conditions

0 = 8

+ = 12

- = 4

Table VI (cont'd)

Case 2 A. ochroleuca (T) vs. C. nivalis (B) at 100% RWC

Light intensity	50			150		250	
Thallus temperature	14	7	14	21	28	14	Average
June	-.20	-.07	-.15	-.15	-.15	0	-.12*
July	-.15	-.10	-.20	-.25	-.15	-.13	-.16*
August	0	0	-.20	-.13	0	-.15	-.08
October	0	0	0	0	0	-.12	-.02
Averages	-.09	-.04	-.14	-.13	-.08	-.10	

Sign Totals over all Conditions

0 = 9

+ = 0*

- = 15*

Case 2 A. ochroleuca (T) vs. C. nivalis (B) at 50% RWC

Light intensity	50			150		250	
Thallus temperature	14	7	14	21	28	14	Average
June	-.10	0	-.06	0	-.15	+.05	-.02
July	0	0	-.05	-.10	-.15	0	-.05
August	0	0	0	-.10	0	0	-.02
October	0	+.15	+.08	0	0	0	+.04
Averages	-.03	+.04	+.01	-.05	-.08	+.01	

Sign Totals over all Conditions

0 = 14

+ = 3

- = 7

Table VI (cont'd)

Case 3 A. ochroleuca (B) vs. C. nivalis (T) at 100% RWC

Light intensity	50			150		250	
Thallus temperature	14	7	14	21	28	14	Average
June	0	-.07	0	-.15	0	-.15	-.06
July	-.12	-.15	-.15	0	0	0	-.07
August	0	0	-.15	-.05	0	0	-.05
October	0	0	-.15	-.05	0	0	-.05
Averages	-.03	-.06	-.11	-.10	0	-.09	

Sign Totals over all Conditions

0 = 13

+ = 0*

– = 11*

Case 3 A. ochroleuca (B) vs. C. nivalis (T) at 50% RWC

Light intensity	50			150		250	
Thallus temperature	14	7	14	21	28	14	Average
June	0	+.0	0	0	0	0	+.01
July	+.08	0	0	0	-.07	0	.00
August	+.08	+.06	0	-.10	+.15	0	+.03
October	+.15	+.05	+.15	+.08	0	+.15	+.10*
Average	+.08	+.05	.04	-.01	+.02	+.04	

Sign Totals over all Conditions

0 = 12

+ = 10

– = 2

Table VI (cont'd)

Case 4 A. ochroleuca (B) vs. C. nivalis (B) at 100% RWC

Light intensity	50	150				250	
Thallus temperature	14	7	14	21	28	14	Average
June	-.18	-.10	-.07	-.20	+.07	0	-.06
July	-.10	-.15	-.18	-.25	0	-.15	-.14*
August	0	-.05	-.18	-.10	0	-.15	-.08
October	0	-.07	0	-.10	0	-.10	-.04
Averages	-.07	-.09	-.11	-.16	+.01	-.10	

Sign Totals over all Conditions

0 = 7

+ = 1*

− = 16*

Case 4 A. ochroleuca (B) vs. C. nivalis (B) at 50% RWC

Light intensity	50	150				250	
Thallus temperature	14	7	14	21	28	14	Average
June	0	+.05	-.05	0	+.07	0	+.01
July	0	0	0	-.05	0	-.15	-.03
August	0	0	0	-.08	0	-.10	-.03
October	0	+.05	+.15	0	0	0	+.03
averages	0	+.03	+.05	-.03	+.02	-.06	

Sign Totals over all Conditions

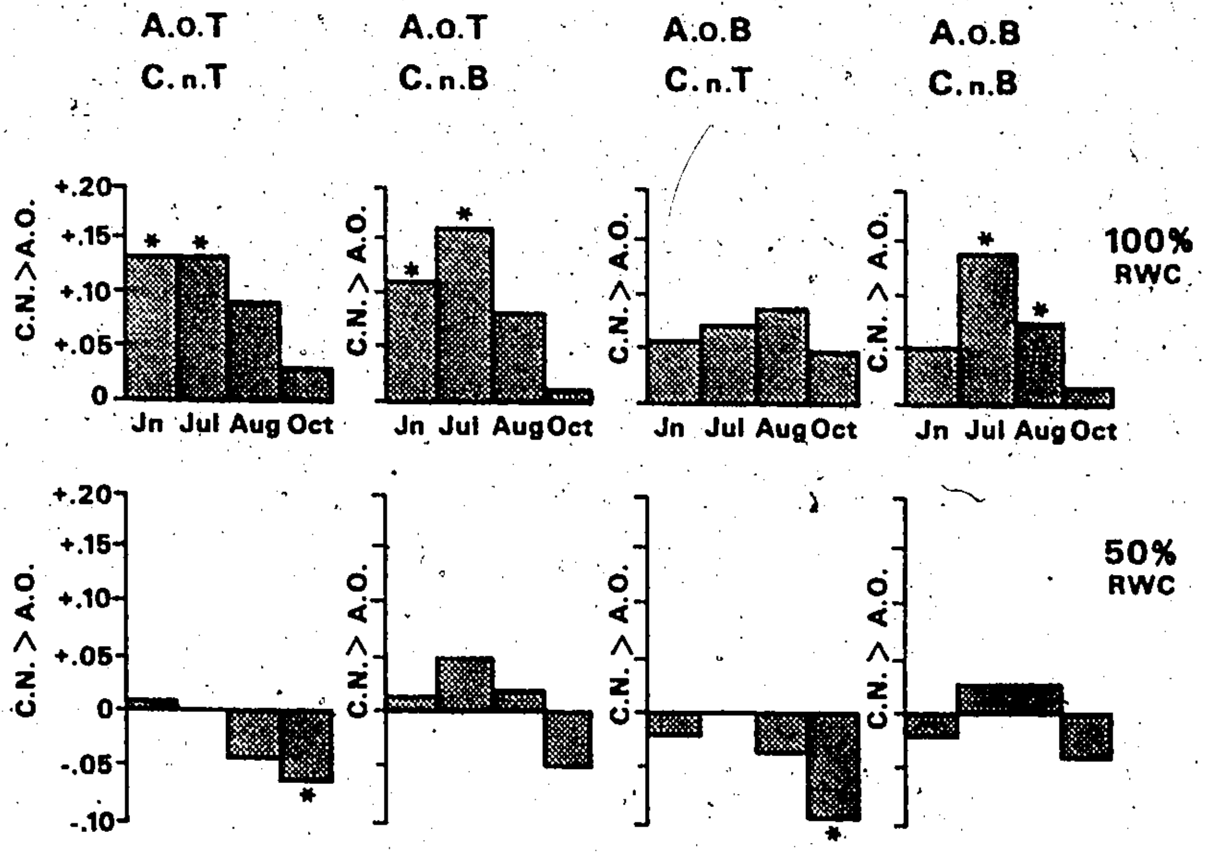
0 = 15

+ = 4

− = 5

Figure 42.

Seasonal variation of accumulated interspecific difference in net photosynthetic rates (data from Table VI) at both 100 % and 50 % relative water content (RWC) for both species collected from the two contrasting ridge top and ridge bottom positions. Values above the zero line indicate average amounts by which net phtosynthesis in *C. nivalis* exceeds *A. ochroleuca* under identical experimental conditions. Values below the zero line show the reverse. An asterisk indicates differences significant at the 5 % level. Symbols used : A.o. , *A. ochroleuca* ; C.n., *C. nivalis* ; T , collections from the ridge top ; B, collections from the ridge bottom.


A.o.T
C.n.T
A.o.T
C.n.B
A.o.B
C.n.T
A.o.B
C.n.B
100%
RWC
50%
RWC
C.N. > A.O.
+.20
+.15
+.10
+.05
0
-.05
-.10
Jn
Jul
Aug
Oct
*

(ridge bottom), slightly different pattern appears at both 100 and 50% RWC. Since the A. ochroleuca material in Case 2 is the same as in Case 1, these differences are due to the intraspecific variation between C. nivalis (ridge top) and C. nivalis (ridge bottom) (see section 3.3.3). The comparison A. ochroleuca (ridge bottom) with C. nivalis (ridge top), Case 3, shows no individual significant differences at 100% RWC but A. ochroleuca significantly exceeds C. nivalis in October at 50% RWC. This suggests that the ridge top collection of C. nivalis is less active than the ridge bottom collection. The final comparison, A. ochroleuca (ridge bottom) with C. nivalis (ridge bottom), Case 4, shows the same pattern as Case 2, again showing the lack of intraspecific variation in A. ochroleuca, but important variation in C. nivalis. These interspecific comparisons can be summarized as follows. The net photosynthetic rate of C. nivalis exceeds that of A. ochroleuca at 100% RWC by a decreasing amount as both species from both topographic positions acclimate seasonally. These patterns are also seen at 50% RWC but at this level of thallus saturation it is the net photosynthesis of A. ochroleuca that exceeds that of C. nivalis by increasing amounts throughout the year. The ridge top collections of A. ochroleuca are the only ones which show significantly higher levels than the C. nivalis, presumeably because of the intraspecific variation within the latter species.

The temperature related variations in interspecific differences were not significant due to a small sample size. It was recognized during the course of these experiments that a consideration of four basic matrices would prevent each matrix from being satisfactorily completed. Future studies should benefit from these findings by concentrating on individual matrices to generate sufficient degrees of freedom, thus permitting effects due to temperature and light intensity to be examined in detail.

(3.4) Morphological Adaptation to Contrasting Beach Ridge Surfaces

The striking morphological dissimilarities between A. ochroleuca and C. nivalis, and between the collections of A. ochroleuca from the other two geographical locations, is shown in Figure 16. It was necessary to examine the potential adaptive significance of this variation in relation to the physiological experiments described above. Determinations of surface area to weight ratios, of thallus moisture contents under differing rainfall intensities, and the interaction of thallus morphology with drying under controlled conditions are useful means of elucidating these patterns.

(3.4.1) Surface area to Weight Ratios

The extremely small finely branched material from Melville Island has the highest surface area to weight ratio of 580 $cm^2 \cdot g^{-1}$ while the robust material from the palsa mound has only 197 $cm^2 \cdot g^{-1}$ (Table VII). The top and bottom forms of A. ochroleuca from Pen Island are intermediate at 350 cm^2/g. When the weights of average thalli of these three types are considered, and used to determine the average surface area per thallus, a progression from smallest of these to largest thalli coincides with an increase in the actual areas of each thallus type. It is interesting to note that C. nivalis has the same area to weight ratio as A. ochroleuca from Pen Island even though the thallus morphology is very different.

There is no significant variation in surface area to weight ratios between ridge top and ridge bottom collections of A. ochroleuca even though the individual thalli from the ridge bottom appear to be slightly larger. In contrast, there is significant difference ($p < 0.05$ using a t-

TABLE VII

Results of surface area to weight ratio determinations for the *A. ochroleuca* and *C. nivalis* material used in this study. Pieces of filter paper were used as controls. Standard error of the mean given.

Sample	Sample size	Area/weight ($cm^2 \cdot g^{-1}$)	Weight/thallus ($g \cdot thallus^{-1}$)	Area/thallus ($cm^2 \cdot thallus^{-1}$)
A. ochroleuca (palsa mound)	6	197 ± 4.7	0.13	27.5
A. ochroleuca (Melville Island)	25	580 ± 2.7	0.011	6.4
A. ochroleuca (Pen , ridge top)	10	352 ± 3.5	0.035	11.8
A. ochroleuca (Pen, ridge bottom)	10	351 ± 4.2	0.045	16.0
C. nivalis (Pen ,ridge top)	10	345 ± 3.1	0.023	7.9
C. nivalis (Pen, ridge bottom)	10	370 ± 5.5	0.031	11.6
Filter paper	2	230	-	-

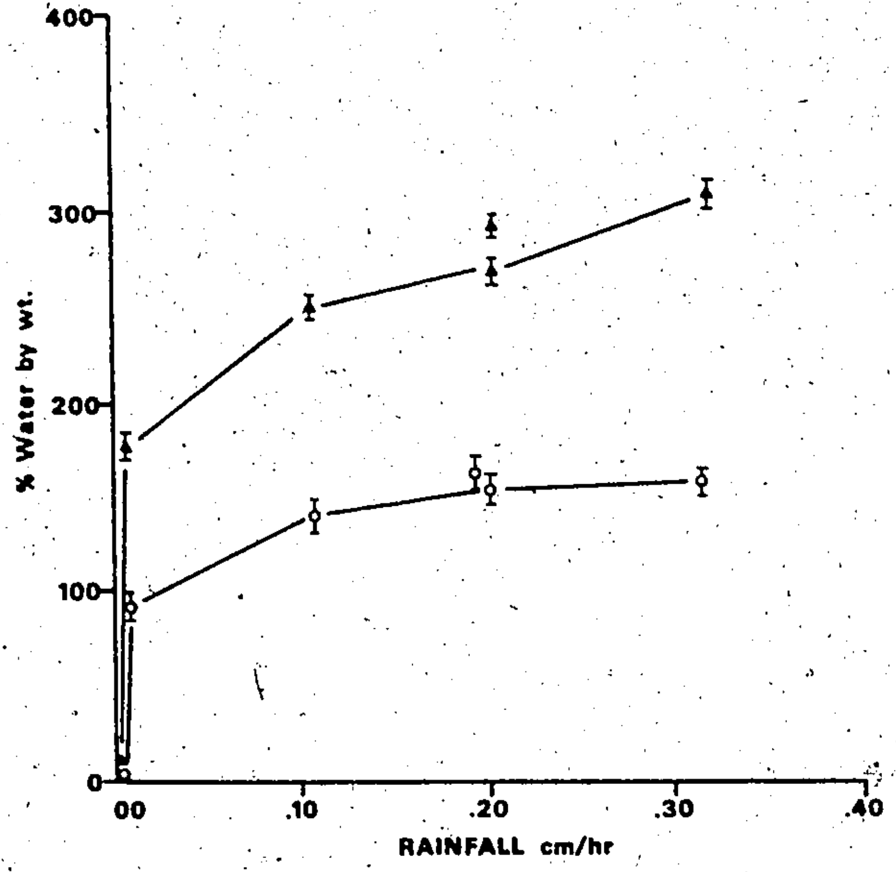
test) between the C. nivalis collections from the ridge top and bottom positions although the magnitude of this difference is small. There is no significant difference between the ridge top collections of C. nivalis and either the ridge top or bottom collections of A. ochroleuca despite the finely branched nature of the A. ochroleuca. It appears that surface rugosities are an important morphological characteristic of the C. nivalis thallus which results in such high surface area to weight ratios. The differences between both ridge top and bottom collections of A. ochroleuca and the ridge bottom collections of C. nivalis are only marginally significant at the $p < 0.05$ level.

(3.4.2) Thallus Moisture Contents under Rainfall of Differing Intensity

Thallus moisture contents for A. ochroleuca and C. nivalis from the ridge surface at Pen Island were determined under identical rainfall conditions (Figure 43). Exposed for five hours under a variety of rainfall intensities, thalli of C. nivalis imbibe much more water than thalli of A. ochroleuca, pointing to the importance of thallus morphology in intercepting and holding water. Under light rain ($0.01 \text{ cm} \cdot \text{h}^{-1}$), similar to those conditions found most frequently at the Pen Island site, both species are saturated to their optimum thallus moisture contents for maximum net photosynthesis. Further increase in rainfall intensity increases thallus moisture contents to 160% for A. ochroleuca, a plateau appearing in the curve at $0.10 \text{ cm} \cdot \text{h}^{-1}$. Conversely for C. nivalis thallus moisture contents continue to rise with each increase in rainfall intensity. At a high rainfall intensity of $0.32 \text{ cm} \cdot \text{h}^{-1}$ the curve shows no plateau suggesting that C. nivalis is only fully saturated under standing water. These higher levels

Figure 43.

Thallus moisture content as a function of rainfall intensity for exposures of approximately five hours. With very light rains (0.01 cm·hr^{-1}) the thallus moisture content of both species rises to their optimum for maximum net photosynthesis. A maximum of 162 % for <u>A. ochroleuca</u> and 315 % for <u>C. nivalis</u> was found under very heavy rain. Under identical rainfall conditions the species maintain very different thallus moisture contents. Open circles – <u>A. ochroleuca</u>; triangles – <u>C. nivalis</u>. Standard error of the mean given.


400
300
200
100
0
% Water by wt.
00
.10
.20
.30
.40
RAINFALL cm/hr

of saturation, however, are likely to involve standing water on the thallus surface, which should not be considered as thallus moisture per se (Blum, 1973). Such levels could only be achieved in the field in the spring when ridge bottom positions are flooded with meltwater.

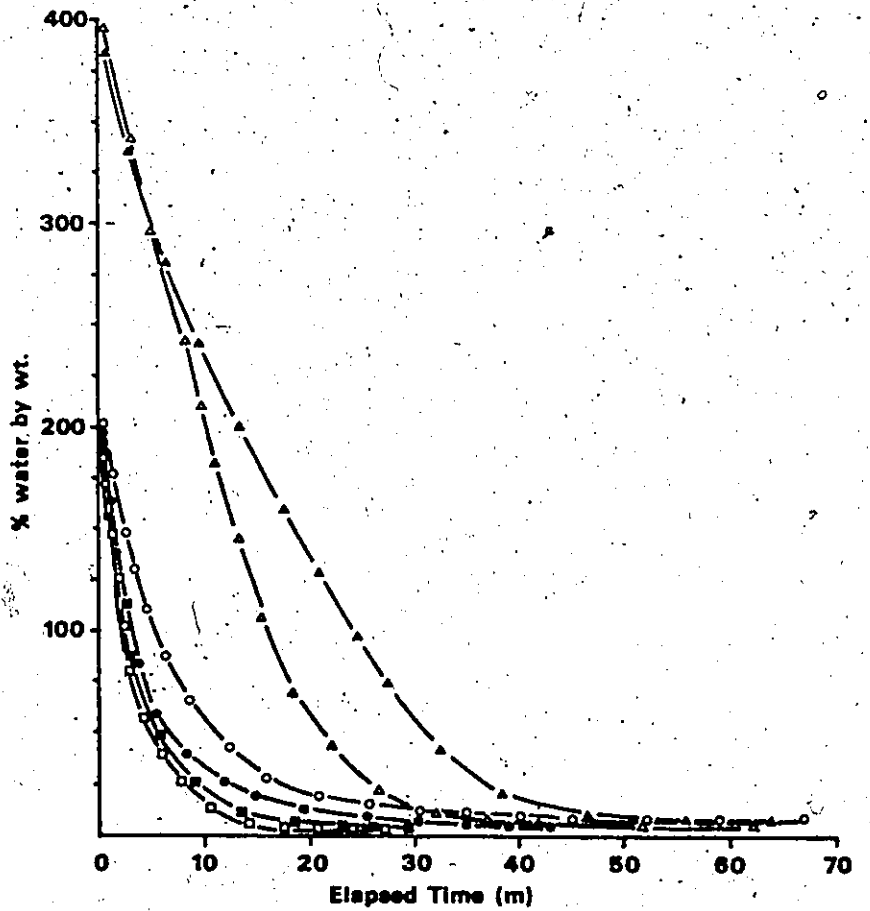
(3.4.3) Interaction of Morphology with Thallus Drying

During physiological experimentation described above, it was noted that at equivalent thallus saturation levels, C. nivalis dried out more slowly than A. ochroleuca. At that time it was speculated that A. ochroleuca had a higher surface area to weight ratio, thus accounting for the observed differences in drying rates. As shown above, however, the two species have similar ratios, thus an alternative explanation of slower drying was required.

The change in thallus moisture content with time is shown in Figure 44 for the various samples used. While the main interest was related to a comparison of A. ochroleuca and C. nivalis, as single or clumped thalli, from Pen Island, an examination of the collections of A. ochroleuca from the palsa mound and Melville Island was useful for comparative purposes. Single thalli of C. nivalis dry out more slowly than those of A. ochroleuca. A similar though more pronounced effect is observed when clumps of ten thalli are used. The clumping arrangement does not alter the surface area to weight ratios but rather it changes the exposure of the thallus surface to the wind. When comparisons are made between materials which show equivalent surface area to weight ratios, the results indicate that the thallus morphology can alter evaporation rates by a change in the exposure of the thallus to the dry air-stream. Equally, when thalli are compared which have the same basic

Figure 44.

The change in thallus moisture content with time ; 1.6 m·sec^{-1} windspeed, 40 % relative himidity , 23 °C . Symbols used : ▲ , *C. nivalis*, clumps of 10 thalli ; △ , *C. nivalis* , single thalli ; 0 , *A. ochroleuca* , clumps of 10 thalli , collected from Pen Island ; ● , *A. ochroleuca* , collected from the palsa mound , single thalli ; □ , *A. ochroleuca* , collected from the beach ridge at Pen Island, single thalli; ■ , *A. ochroleuca* collected from Melville Island, single thalli. Each curve is the mean of 6–8 determinations with a standard error less than 3 % of the mean.


400
300
200
100
0
10
20
30
40
50
60
70
% water by wt.
Elapsed Time (m)

structural features, but show wide variation in surface area to weight ratios, differences in drying patterns are again observed, as shown in Figure 44.

Filter paper controls show similar patterns (Figure 45). A single flat sheet of paper (230 $cm^2 \cdot g^{-1}$) dries out much more rapidly than a double sheet of the same paper with a corresponding surface area to weight ratio of 115 $cm^2 \cdot g^{-1}$. A crumpled piece of paper that is one sheet thick (230 $cm^2 \cdot g^{-1}$) dries out more slowly than the same sheet when flat.

Drying of filter paper is thus influenced by both surface area to weight ratios and by exposure of the surface area to the air - stream in a fashion similar to that found when the lichen materials were examined. (see above).

Evaporation rates from thalli were determined as grams water lost per cm^2 per minute, and plotted against thallus moisture content in Figure 46. Filter paper controls appear in Figure 47. When single thalli of A. ochroleuca and C. nivalis are placed under identical experimental conditions, evaporation rates from C. nivalis are lower than those of A. ochroleuca at equivalent levels of thallus saturation. Evaporation rates are reduced markedly by clumping. In A. ochroleuca, evaporation rates at 200% thallus moisture content drop from 0.0016 to 0.0008 $g \cdot cm^{-2} \cdot min^{-1}$ when thalli are clumped together. Similarly in C. nivalis, evaporation rates drop from 0.008 to 0.0048 $g \cdot cm^{-2} \cdot min^{-1}$. All of these comparisons are for material which has the same surface area to weight ratio. When single thalli of A. ochroleuca collected from Melville Island and the palsa mound are compared with the variety collected from the beach ridge at the Pen Island site, differences in

Figure 45.

Filter paper controls under the same conditions as Figure 44 above. Symbols used : ⊗ , flat piece of filter paper, double sheet ; × , flat piece of filter paper , single sheet ; ⊖ , crumpled single sheet of filter paper. Each curve is the mean of three replicates showing a standard error less than 3 % of the mean.

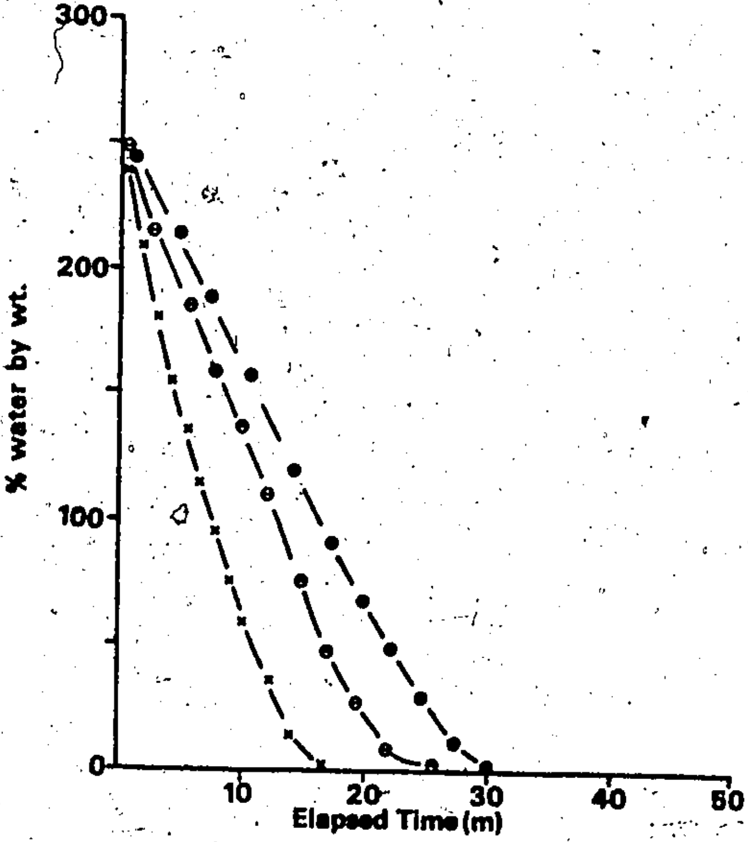
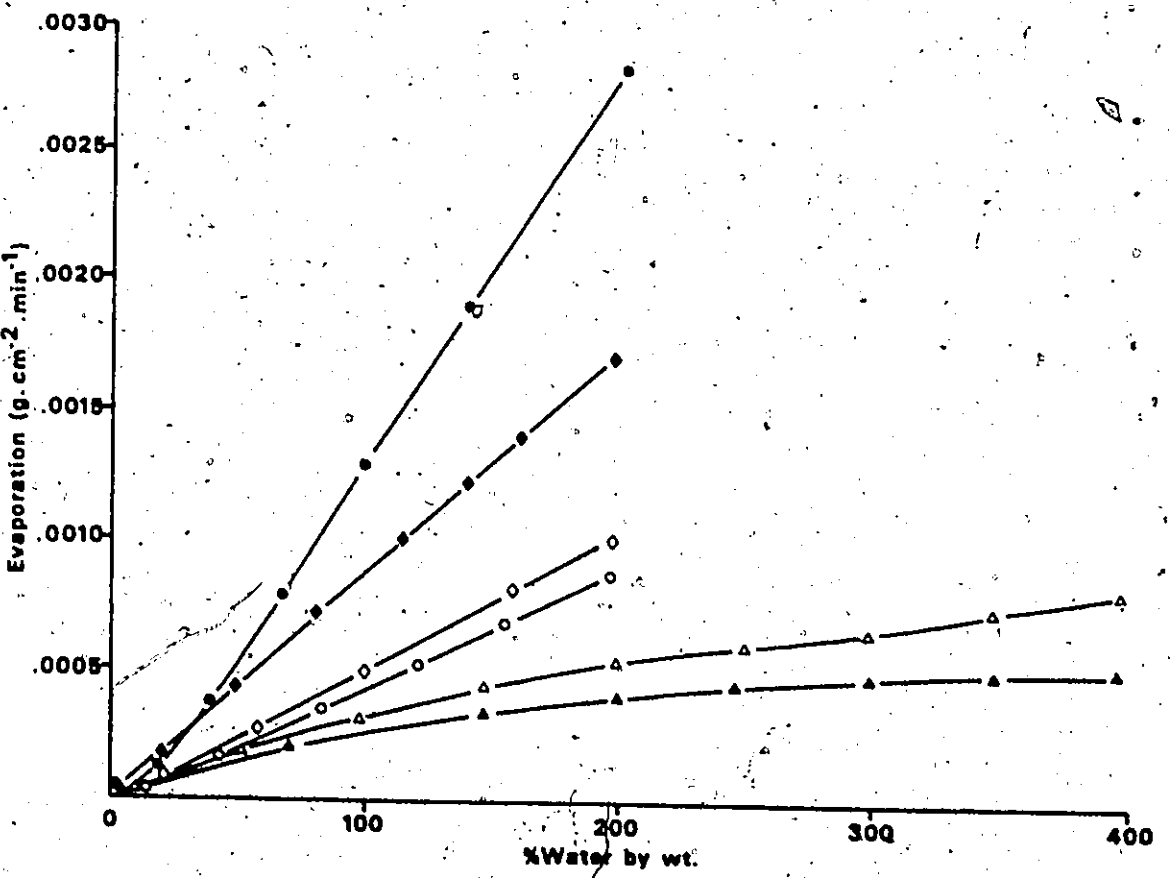

300
200
100
0
% water by wt.
10
20
30
40
50
Elapsed Time (m)

Figure 46.

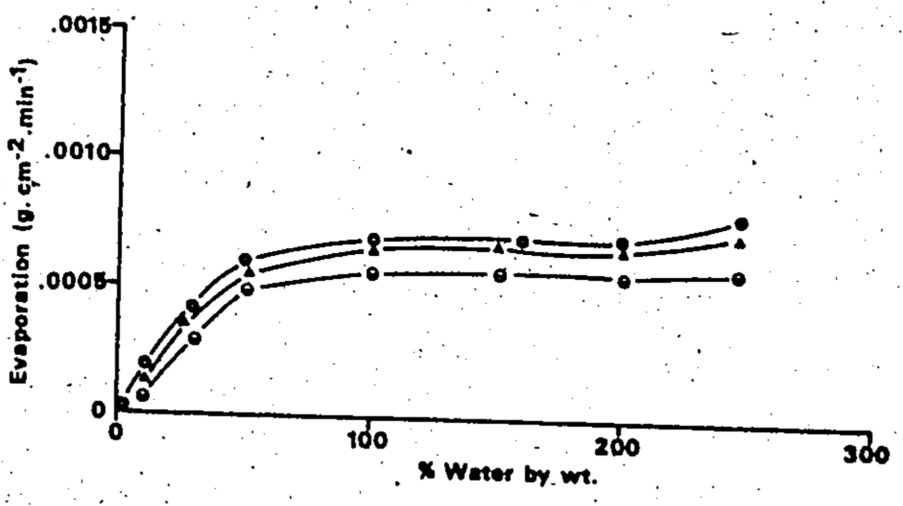
The change in evaporation rate during the wind tunnel experiments. All material starts at maximum thallus saturation at the start of the experiment. Symbols used : ▲ , *C. nivalis* , clumps of 10 thalli ; △ , *C. nivalis*, single thalli; ○ , *A. ochroleuca* , clumps of 10 thalli, collected from Pen Island ; ◇, *A. ochroleuca* , single thalli collected from Melville Island ; ◆ , *A. ochroleuca*, single thalli, collected from Pen Island ; ● , *A. ochroleuca* , single thalli, collected from the palsa mound. Curves are the mean of 6-8 determinations with a standard error consistently less than 3% of the mean.



Evaporation (g.cm^{-2}.min^{-1})
.0030
.0025
.0020
.0015
.0010
.0005
0
100
200
300
400
%Water by wt.

Figure 47.

The change in evaporation rate fron filter paper controls as a function of the paper's water content. Symbols used : △⃝ , flat filter paper, double sheet ; ⊖ , flat filter paper , single sheet ; △ , crumpled filter paper, single sheet.


Evaporation (g.cm-2.min-1)
.0015
.0010
.0005
0
0
100
200
300
% Water by wt.

evaporation rates at equivalent levels of thallus saturation appear. These differences are in proportion to the differing surface area to weight ratios between collections although the basic structural features are similar. A. ochroleuca collected from the palsa mound shows the highest rates of evaporation while the Melville Island material shows the lowest evaporation rates at given levels of thallus moisture content. The A. ochroleuca material from Pen Island shows intermediate rates. Thus evaporation from lichen material is influenced both by surface area to weight ratios and by the characteristic exposure of the lichen surface to the moving air-stream.

The apparent linearity in the curves for both species (Figure 46) implied that the total resistances to evaporation were constant as the thalli dried out since the change in the evaporation rate was constant. This evidence contradicted that given by Harris (1969) and Hoffman and Gates (1971) for a variety of foliose lichens under similar experimental conditions. Total resistances to evaporation were calculated for each sample at a variety of thallus moisture contents. Since the formulation used (Monteith, 1965) requires constant windspeed and radiation, the only measurements required were evaporation rate and thallus temperatures. Changes in thallus temperature as the lichen material dried out are shown in Figure 48. The maximum temperature depression at maximum thallus saturation was about 9.5°C. These values of thallus temperature at known thallus moisture contents were used to determine saturation vapour pressures at both thallus and air temperatures, permitting calculation of total resistances (Table VIII). In each case there was very little fluctuation in total resistance terms as the thalli

Figure 48.

Thallus temperature as a function of thallus moisture content for both *C. nivalis* and *A. ochroleuca*, expressed as a percentage of the maximum temperature difference between maximum thallus moisture content and air-dry under the following conditions : windspeed 1.6 $m \cdot sec^{-1}$, air temperature 23 °C , relative humidity 40 %, laboratory lighting only. The average wet - dry temperature difference was about 9 °C. Three determinations were done for each species as described in the text. Curves are mean values with a standard error of less than 3 % of the mean. Symbols : ● , *A. ochroleuca* ; ▲ , *C. nivalis* .

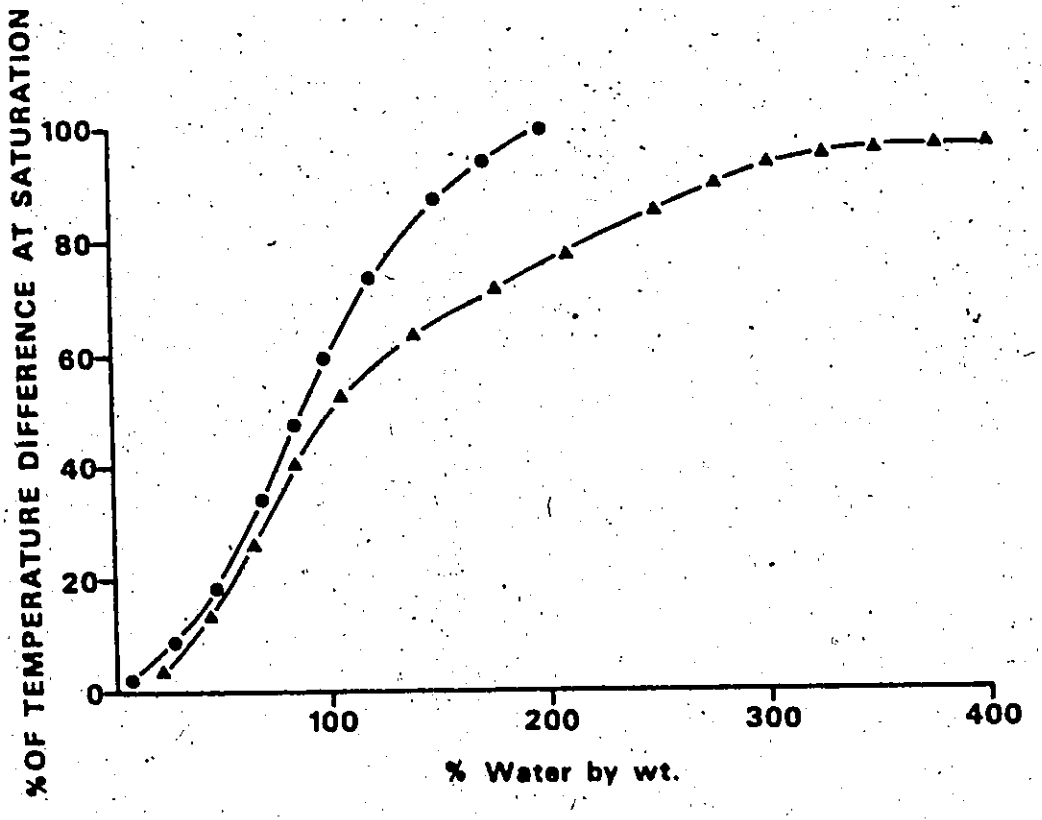

%OF TEMPERATURE DIFFERENCE AT SATURATION
100
80
60
40
20
0
100
200
300
400
% Water by wt.

TABLE VIII

Calculation of the total evaporative resistance shown by different lichen thalli under controlled conditions (see text for description) at different thallus moisture contents. The formulation of Monteith (1965) was used here. (TW) Terms for the Melville Island material are obtained from the Pen Island material. Dittos refer to corresponding values for conditions above.

Sample	% saturation	T_w (^oc)	T_a (^oc)	E_w (mb)	E_a (mb)	E_w-E_a (mb)	Evaporation ($g \cdot cm^{-2} \cdot sec^{-1}$) X 10^{-5}	$r_a + r_i$ ($sec \cdot cm^{-1}$)
A. ochroleuca (Pen Island)	200	13.0	23.0	11.5	20.5	9.0	2.70	.251
	150	15.0	23.0	13.7	20.5	6.8	2.00	.283
	100	17.5	23.0	15.5	20.5	5.0	1.35	.279
	50	21.0	23.0	18.8	20.5	2.7	0.68	.299
	10	22.5	23.0	20.0	20.5	0.5	0.14	.269
A. ochroleuca (Melville Island)	200	"	"	"	"	"	1.70	.399
	150	"	"	"	"	"	1.27	.445
	100	"	"	"	"	"	0.85	.443
	50	"	"	"	"	"	0.43	.478
	10	"	"	"	"	"	0.09	.418
A. ochroleuca (palsa mound)	200	"	"	"	"	"	4.66	.145
	150	"	"	"	"	"	3.41	.166
	100	"	"	"	"	"	2.17	.174
	50	"	"	"	"	"	1.09	.187
	10	"	"	"	"	"	0.17	.221

Cont'd

TABLE VIII (cont'd)

<u>A.</u> <u>ochroleuca</u> (clumps)	200	13.0	23.0	11.5	20.5	9.0	1.50	.452
	150	15.0	23.0	13.7	20.5	6.8	1.13	.499
	100	17.5	23.0	15.5	20.5	5.0	0.75	.502
	50	21.0	23.0	18.8	20.5	2.7	0.38	.535
	10	22.5	23.0	20.0	20.5	0.5	0.08	.471
<u>C.</u> <u>nivalis</u>	400	13.0	23.0	11.5	20.5	9.0	1.30	.521
	300	13.5	23.0	12.3	20.5	8.2	1.05	.609
	200	15.5	23.0	14.2	20.5	6.3	0.92	.614
	100	18.0	23.0	16.0	20.5	4.5	0.50	.753
	50	21.0	23.0	18.8	20.5	1.7	0.28	.673
	10	22.5	23.0	20.0	20.5	0.5	0.05	.801
<u>C.</u> <u>nivalis</u> (clumps)	400	"	"	"	"	"	0.83	.817
	300	"	"	"	"	"	0.76	.842
	200	"	"	"	"	"	0.67	.843
	100	"	"	"	"	"	0.42	.897
	50	"	"	"	"	"	0.20	.942
	10	"	"	"	"	"	0.04	.876

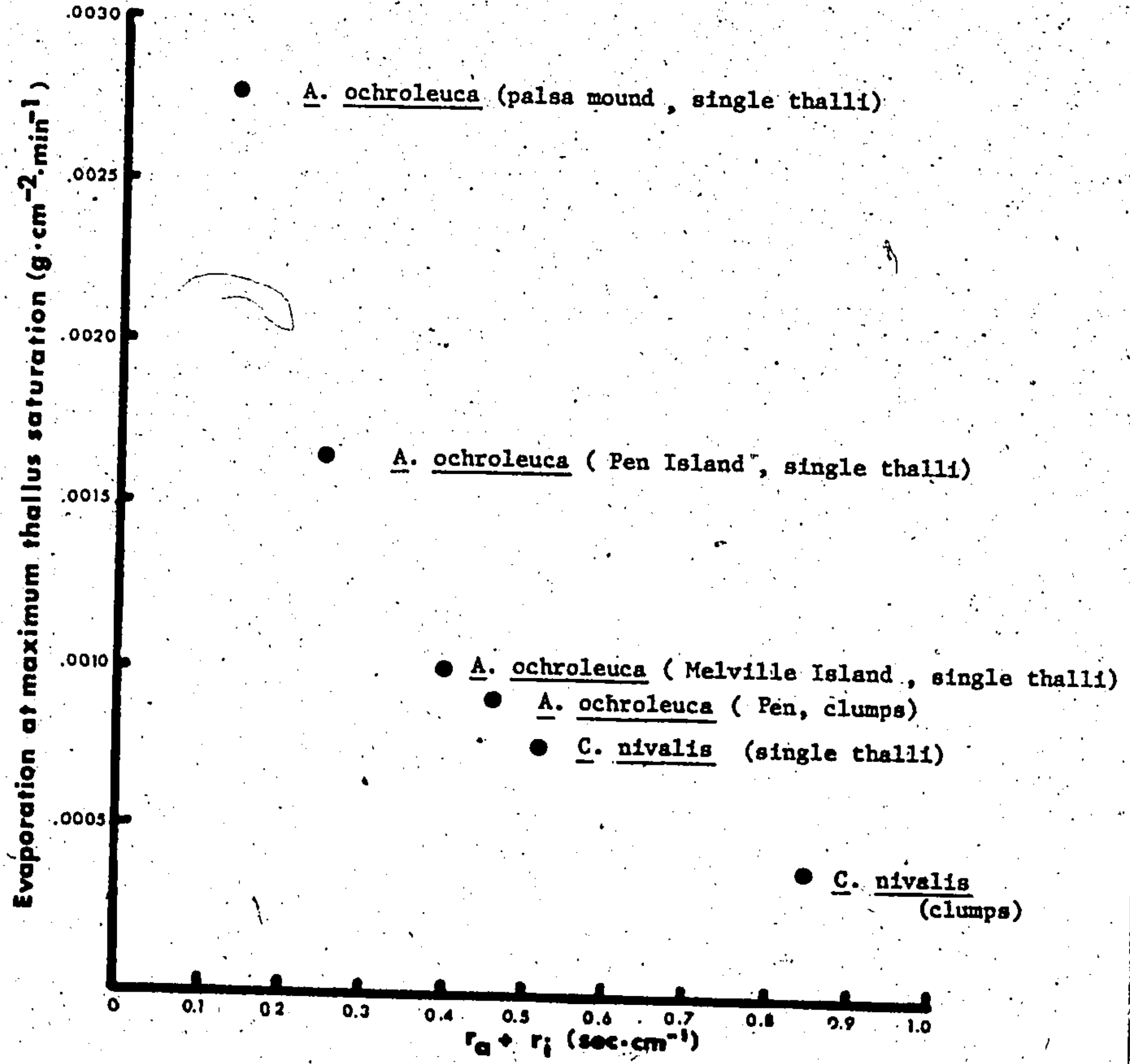
dried, as was predicted of the basis of the linearity observed for the curves in Figure 46.

Each sample appears to have a characteristic resistance value. These terms are a function of both surface area to weight ratios and the manner in which thallus surfaces are exposed to the moving air-stream. Clumping thalli of A. ochroleuca doubles the resistance from about 0.27 to 0.50 sec $\cdot$ cm^{-1} (Table VIII). Similarly, clumping of C. nivalis thalli increases resistance from about 0.65 to 0.85 sec $\cdot$ cm^{-1}. While single thalli of A. ochroleuca from Pen Island have much lower resistances than single thalli of C. nivalis, A. ochroleuca from Melville Island shows very much higher total resistances, almost equal to the levels found for clumps of A. ochroleuca from Pen Island. The lowest resistance terms are found in the A. ochroleuca collected form the palsa mound. Apparently the low resistance to evaporation (0.175 sec $\cdot$ cm^{-1}) accounts for the relatively high evaporation rates found in this collection.

The magnitude of these resistance terms appeared to reflect a simple relationship between total resistances and evaporation rates at constant thallus moisture content. Rates of evaporation at maximum thallus moisture contents were plotted against calculated resistance terms (Table VIII). As shown in Figure 49 this relationship points to the adaptive significance of this morphological variation in lichens. The position of each point shows the combined influence of surface area to weight ratios and the exposure of the thallus surface to the air-stream. For example, C. nivalis collected from more mesic sheltered areas of raised beach ridges shows a very high resistance and very low evaporation rates at maximum thallus saturation. A clumping of thalli exaggerates this pattern. Thus higher

Figure 49.

The relationship between evaporation rate at maximum thallus moisture content and total resistances to evaporation (calculated using formulation of Monteith , 1965) showing the influence of thallus morphology on these two factors. The data points are taken from Table VIII.


A. ochroleuca (palsa mound , single thalli)
A. ochroleuca (Pen Island , single thalli)
A. ochroleuca (Melville Island , single thalli)
A. ochroleuca (Pen, clumps)
C. nivalis (single thalli)
C. nivalis (clumps)
Evaporation at maximum thallus saturation ($g \cdot cm^{-2} \cdot min^{-1}$)
.0030
.0025
.0020
.0015
.0010
.0005
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
$r_a + r_i$ ($sec \cdot cm^{-1}$)

levels of thallus saturation can be maintained for a longer period under which conditions C. nivalis shows high net photosynthetic rates. Conversely, A. ochroleuca from ridge top positions at Pen Island shows much higher evaporation rates and lower resistance terms. The morphology of A. ochroleuca reduces high levels of thallus saturation relatively quickly. This is advantageous to this species which shows very low rates of CO_2 fixation at maximum thallus saturation. The rather wide variation in these evaporative and resistance terms within species indicates that lichens may have the potential to modify their simple morphology in ways that are important physiologically.

Section 4

DISCUSSION

The abundance of lichens in northern regions suggests that these plants are particularly well adapted to these often severe arctic environments. Despite their overall importance in influencing surface microclimate (Rouse and Kershaw, 1971) studies on lichen dominated systems had not adequately demonstrated clear relationships between the distribution of the plants, their physiological characteristics, and the physical parameters of the environments in which they grow. Although studies by Bliss and Hadley (1964), Adams (1971a,b), Rundel(1972), Lange 1969) and Karenlampi (1971) were successful in demonstrating physiological patterns adapted to large scale climatic factors, only one attempt (Harris, 1969) has been made to understand spatial distribution based on physiological patterns and small scale microclimatic differentiation. The majority of studies relating the distribution of lichens to specific environments lack the necessary spatial contrasts to provide reference comparisons, and spatial controls to show that observed patterns are repeating and persistent.

The system used throughout this thesis, consisting of a series of repeating raised beach ridges, included such controls and contrasts to permit a better understanding of the distribution of lichens.

(4.1) The General Lichen Heath and the Importance of Topography

A survey was conducted in order to define the structure of the general lichen heath vegetation and to relate this structure to two different types of environmental gradients. The first gradient was a function of the process of isostatic uplift occurring in the Hudson Bay area (Webber et al, 1970). This uplift, which started about 8,000 years B.P., has produced a series of raised beach ridges marking successive coastlines of what is now Hudson Bay. As a result of continued uplift a temporal sequence of beach ridges has been formed from the coast inland with environmental and vegetational factors responding to this gradient. The second gradient was imposed by the topographic characteristics of individual beach ridges. The relatively constant orientation and morphology of these ridges results in a set of repeating gradients, independant of one another, from the coast inland.

The primary survey (Kershaw and Rouse, 1973) conducted in this same area showed only the first gradient, since the methods used were not designed to test specifically for those influences due to ridge topography. In contrast the secondary survey described above was designed to be sensitive to these influences (for further detail see Larson and Kershaw, 1974).

The survey showed that an inland developmental sequence leading toward spruce-lichen woodland was characterized by changing species composition and abundance and by increases in both soil moisture and peat layer thickness (Figures 20, 21, 22). These changes were not regular, however and showed more variability in the proximity of rivers and mud flats. The vegetation was dominated by a number of species each with a unique pattern of distribution throughout the ridge system. Cetraria nivalis (Figure 18) and Cladina mitis (Figure 59 Appendix A) have higher levels of abundance on progressively older ridges in the system having thicker peat layers and higher levels of surface soil moisture. On an intraridge basis, however, Cetraria nivalis is seen to be more abundant at ridge bottom positions, while Cladina mitis is more abundant on dry ridge tops. Other species such as *Cetraria cucullata*, (Figure 56) *C. islandica* (Figure 55), *Dryas integrifolia* (Figures 50-52), and *Alectoria ochroleuca* (Figure 19, 62) have greater abundance on more recently formed ridges which have lower surface soil moisture contents, although on an intraridge basis each of these species is distributed differently. The percentage cover for other species such as *Equisetum variegatum* (Figure 53) and *Rhododendron lapponicum* (Figure 54) did not fluctuate markedly between ridges but both species showed marked patterns of distribution related to ridge topography.

Although the presence of a developmental sequence within a single raised beach system only 1.6 km wide has been shown and is consistent with the general picture of slow successional development in dry lichen heath tundra leading towards open lichen-woodland (Kershaw and Rouse, 1973), the variation in vegetational structure across the topographic profile of individual ridges indicates the considerable importance of environmental parameters independant of any age sequence. The fact that 40% of the variation in the ordination data was related to the contrasting topographic positions of beach ridges (Figure 24) suggested that further studies should concentrate on the significance of this finding.

(4.2) The Contrasting Physical Environments of Raised Beach Ridges

The experimental system was redefined to permit an examination of the physical characteristics of the contrasting top and bottom positions of individual raised beach ridges and to relate these physical environments to patterns of distribution of common species. Although it was shown in Figures 23, 25 and 26 that the greatest variation in surface soil moisture and peat depth was related to the topographic characteristics of individual beach ridges, the importance of atmospheric factors to a lichen dominated system was not known. Thus, atmospheric factors to which lichen would be continuously exposed such as snow depths, windspeeds, temperatures, and drying rates were examined.

Patterns of snow accumulation in these northern regions are directly influenced by the shelter afforded by topographic irregularities on the ground (Hare, 1972). The exposed crests of lichen dominated beach ridges, although only 1-2 m above the neighbouring sedge meadows, are directly exposed to these strong winds and accordingly only a thin snow cover is seen (Figure 27). Further snowfall between December and March (Figure 28) is also accompanied by strong winds preventing further snow accumulation (Longley, 1960). Conversely, the more sheltered sedge meadows lying between the ridges which are dominated by taller willows and sedges (Kershaw, 1974) exhibit a relatively thick snow cover which, unlike the ridge crests, increases with further snowfall between December and March (Figure 28). The extremely thick snow cover found on forested raised beaches several km inland, reflects the shelter provided by trees and this same influence results in large seasonal increases in snow cover thickness from December to March (Larson and Kershaw, 1975a) (Figure 28).

Many of the physical properties of a snow cover relate directly to the underlying vegetation. In late June all sedge meadows have considerable amounts of standing water derived primarily from snowmelt. Closely underlying permafrost, present all summer, prevents drainage from these areas thus extending the influence of snowload throughout the summer. Conversely, the tops of raised beach ridges which have a very thin snow cover and rapidly lowering permafrost table are extremely dry at all times of the year (Rouse and Kershaw, 1973). In addition, this thin snow cover would expose the vegetation of these surfaces (*Alectoria ochroleuca*, *A. nitidula*, *Dryas integrifolia*) to cold temperature and surface erosional stresses (Warren-Wilson, 1959) not experienced by the vegetation at the ridge bottom positions (*Cetraria nivalis*, *Cladina alpestris*). A snow depth greater than 20 cm effectively damps cold temperature fluctuations experienced at the snow-air interface (Bergen, 1968). Thus, sedge meadows and forested areas will also be protected from these stresses. Since the depth of snow relates directly to the rapidity with which the ground surface is exposed in the spring, areas such as the tops of raised beach ridges have a much longer effective growing season than more sheltered areas. This fact may be of considerable importance to the ecology of species characteristic of these exposed habitats.

The measurement of the microclimatic factors was thought to be difficult because of the rather low energy conditions present. Thus, a well defined ridge of elevation 2.0 m in area III was selected in order to demonstrate more pronounced topographically related differences. To provide a situation in which these differences should be less marked, the hummock / hollow features in area II were examined. The results showed that ridge top positions are characteristically more windy, cooler and drier than corresponding ridge bottom positions. These results, combined with those for the hummock / hollow features and with data presented by Warren and Wilson (1959) and Geiger (1971), suggest that for any scale of observation, sheltered topographic features show reduced windspeeds, higher temperature, and lower rates of evaporation under conditions of diffuse radiation (Figures 30-33). The distribution of winter snow would substantiate this conclusion (Figure 27). When solar radiation predominates, evaporation is directly related to incoming radiant energy supply (Rouse and Stewart, 1972) and the topographically induced differences in windspeed are not likely to produce differential evaporation over the ridge surfaces.

Although the level of topographically related microclimatic differentiation is small, the direction of the differences is very consistent and when integrated over time periods of several years may be appreciable. These results suggest, though, that if any species distribution is related to microclimatic edaphic or winter factors, as influenced by ridge topography physiological differences may also be very small thus demanding very sensitive measurements over an exceptionally wide range of environmental conditions.

(4.3) Physiological Adaptations to Contrasting Beach Ridge Surfaces

The selection of the appropriate experimental system to demonstrate these adaptations was extremely important as discussed in Section 1. *Alectoria ochroleuca* and *Cetraria nivalis* were the species best suited to this system. It was necessary to examine the responses of net photosynthesis in both species, collected from both the top and bottom positions of the raised beach ridge in area II, as a function of thallus moisture content, thallus temperature, light intensity, and time of year, with the experiments arranged factorially. The methods available to examine the response of net photosynthetic rate to environmental factors were found to be too slow to permit an examination of this type. Thus a new experimental system was developed. This new system produced data in the form of physiological data matrices for each collection. Complete matrices for each collection of each species were produced using materials collected in April and June. Further testing of the matrices was restricted to those experimental conditions thought to be of greater importance. In the end the lack of complete and symmetrical matrices limited the usefulness of the data, and pointed to the importance of restricting the number of matrices under examination so that only complete arrays are produced. Despite this limitation in this study, a large volume of ecologically interpretable data was obtained.

Two important features characteristic of the lichens used in this study allowed the use on non-ventilated gas exchange cells. In contrast to higher plants (Jarvis et al, 1971) net photosynthetic rates in these lichens was not influenced by ventilation (Table III). It was also found that net photosynethesis was constant between 350 and 150 ppm CO_2, thus the CO_2 limitation point was low relative to higher plants (Figure 13). These findings are best explained by the low rates of CO_2 fixation in lichens which would produce only small potential graddents for CO_2 exchange. Further evidence (Section 3.4.3) showing that total resistance terms for water vapour exchange are low relative to higher plants substantiates this interpretation. Although Smyth (1934) showed that Peltigera polydactyla was CO_2 limited up to 10% CO_2 in air, the influence of these high concentrations on the fungal respiration was not shown.

Seasonal acclimation

The responses of net photosynthesis in the collections of A. ochroleuca and C. nivalis from the ridge top and bottom positions showed seasonal acclimation to thallus temperature and a change in response to light intensity (Figure 34, 35, 37, 38). Under low light intensities C. nivalis from the ridge top position also showed a change in the response to thallus moisture content (Figure 37). This change in response to thallus moisture content appears to track the seasonal availability of water under low energy conditions. However, this observation was restricted to one set of conditions and thus a general interpretation of these changes is not possible. Conversely, the seasonal change in response to light intensity can be explained on the basis of evidence presented in the literature that algal numbers (Harris, 1972) or chlorophyll contents (Grace and Woolhouse, 1973) fluctuate seasonally in patterns which track the availability of solar radiation. Lechowicz and Adams (1974) examining *Cladina mitis* did not find this feature. The temperature acclimation found in this study maintains levels of net photosynthetic rate although the temperature optimum for maximum fixation changes from season to season. These changes correlate with the observed yearly temperature fluctuations found at the research site (Figure 4).

The temperature acclimation in this study is characterized by a shift in the optimum temperature for maximum net photosynthesis, but without any apparent change in the absolute levels of fixation at the various temperature optima. A stability in rates of dark respiration at $21^{\circ}C$ is also seen in these two species. The term acclimation is defined as a physiological mechanism which permits the maintenance of vital metabolic processes under differing optimal conditions (Prosser, 1958). As applied to higher plants, acclimation is characterized by a shift in the optimum temperature for net photosynthesis which coincides with a decrease in photosynthetic capacity when cold acclimation occurs and an increase in this capacity when warm treatments are given. Cold treatments also show increases in dark respiration while warm treatments reverse this pattern. Acclimation of the photosynthetic mechanism has been described for a variety of species in both field and laboratory situations. Many studies (Mooney and West, 1964; Strain and Chase, 1966; Billings et al, 1971; Smith and Hadley, 1974; Sawada and Miyachi, 1971; Chatterton et al, 1970; Mooney and Harrison, 1970; and Steponkus and Lanphear, 1968) have described acclimation in higher plant systems, however as DePuit et al (1973) caution, it is virtually impossible to control a higher plant system to such a degree that the acclimation phenomenon can be demonstrated independant of other processes. In most cases phenological or senescent events significantly alter responses of net photosynthesis to a greater degree than acclimation. In addition to these problems, may of the experiments were uncontrolled in the rooting environment (Smith and Hadley, 1974). The importance of soil temperature in controlling leaf or shoot net photosynthetic rates is great enough to make difficult any interpretation of such uncontrolled experiments (Pieters, 1974).

An additional problem present in these studies is that acclimation of the photosynthetic mechanism is discussed, although only data for net photosynthesis and dark respiration are given. In many cases the addition of dark respiration to net photosynthesis shows that gross photosynthesis itself does not experience a net change when the plants are cold acclimated, but rather the shifts in net photosynthesis are derived simply from increases in dark respiration. Discussions of the adaptability of the photosynthetic mechanism from one population to the next based on such data (Billings et al, 1971; Smith and Hadley, 1974) are not valid. The evidence reported by Sawada and Miyachi (1971) suggested that in cold acclimation situations which reduce the maximum net photosynthesis at the new temperature optimum, the shifts in gas exchange responses cannot be interpreted as an ecological advantage to the plant since these decreases can be explained on the basis of the inactivation of important enzymes involved with carboxylation reactions in the dark fixation of CO_2 and not due to any adaptation of the plant's photosynthetic mechanism to low temperature. The only systems in which acclimation can be properly demonstrated are those which use organisms which can show only an acclimation of the photosynthetic mechanism, uncomplicated by metabolic changes due to other processes. It would appear that lichens such as *A. ochroleuca* and *C. nivalis* have these characteristics. Based on the experiments described above (see section 3.3) there is an apparent distinction between acclimation phenomena and the patterns observed in higher plants. An examination of the effect of cold pretreatments on higher plants provides an alternative explanation for these seasonally changing responses. A wide variety of higher plants including rice (Kishitani and Tsunoda, 1974) pine (Rook, 1969) and wheat (Sawada and Miyachi, 1974) show seasonal changes in a number of important characteristics which coincide with seasonal fluctuations in frost hardiness (Levitt, 1956, 1972). The literature on frost hardiness suggests that the acclimation of the photosynthetic mechanism as reported in ecological literature is a typical characteristic of plants undergoing cold temperature hardening, and thus is not adaptive in itself.

The Importance of Acclimation to Patterns of Distribution

The ability to acclimate permits an organism, which has little opportunity for growth in stressful environments, to maximize its production by continually adjusting its physiological patterns to suit the environment to which it is exposed. Since the extent of acclimation shown in this study was not constant, this variation may be important to the problem of species distribution over these raised beach ridge surfaces.

Although considerable variability in net photosynthetic rates was found among the collections of _A_. _ochroleuca_ collected from other geographical locations, an intraspecific comparison of _A_. _ochroleuca_ from the ridge top and bottom positions did not demonstrate either consistent or significant seasonal trends (Figure 36) suggesting that the extent of acclimation was similar although the two collections were from contrasting physical environments. In contrast, an intraspecific comparison of _C_. _nivalis_ from the raised beach ridge surfaces demonstrated consistent seasonal trends maintaining higher level of CO_2 fixation in _C_. _nivalis_ from the ridge bottom position (Figure 39). The amounts by which ridge bottom exceeds ridge top samples are significant in July and August, but not in June and October (Table VII). If acclimation was not present, there would not be seasonal changes in the amounts by which one sample exceeded another. Thus acclimation serves to differentiate between these two collections of _C_. _nivalis_.

Different patterns of acclimation on an interspecific basis can also be shown to provide further information regarding the patterns of species distribution over the ridge profile. Acclimation results in changing amounts by which _C_. _nivalis_ exceeds _A_. _ochroleuca_ at 100% relative water content on a seasonal basis (Figure 42). These differences are maximized in July and minimized in October. Conversely at 50% relative water content, acclimation changes the amounts by which *A. ochroleuca* (ridge bottom and top) exceeds *C. nivalis* (ridge top) so that while the responses are similar in June, *A. ochroleuca* exceeds *C. nivalis* by significant amounts in October. That the net photosynthetic rates of *A. ochroleuca* significantly exceed those of *C. nivalis*, ridge top but not ridge bottom, in October can be accounted for by the intraspecific variation within *C. nivalis* (see cases 1 and 3, Figure 42). Considering these effects observed at both water contents, the amounts by which the two species are different in terms of net photosynthesis show higher rates in *C. nivalis* early in the year, and higher rates on *A. ochroleuca* later in the year.

On the basis of these experiments and the assumptions that factors influencing patterns of CO_2 exchange will influence patterns of distribution; *C. nivalis* should be much more abundant than *A. ochroleuca* in a characteristically mesic ridge bottom position. Conversely, the abundance of *A. ochroleuca* should be only slightly higher than *C. nivalis* on the more exposed, xeric ridge positions. The patterns of species distribution over the ridge profile in area II (Figure 15) is similar to this prediction. *C. nivalis* is much more abundant at the ridge bottom position (40% vs. 5% for *A. ochroleuca*) whereas *A. ochroleuca* is only slightly more abundant than *C. nivalis* (23% vs. 18% for *C. nivalis*) on the ridge top position. The patterns of distribution cannot be completely explained on this basis although some of the factors controlling growth rates and hence distribution of plants can clearly be related to requirements of net photosynthetic production. As shown in Figure 1, other factors such as stress and erosional tolerances, browsing pressures and water relations are also involved . . The degree to which these distributional patterns are predictable on the basis of patterns of net photosynthesis alone, as opposed to the amounts predictable on the basis of other measurements cannot yet be made.

(4.4) Morphological Adaptation to Contrasting Beach Ridge Surfaces

The apparent involvement of thallus morphology with water relations in the physiological experiments described above (Section 3.4) necessitated an examination of these factors to assess their importance in controlling species distribution.

Measurements of thallus moisture contents under a variety of rainfall intensities showed that when *A. ochroleuca* and *C. nivalis* were placed under identical conditions, they differentially imbibed water. Under light mists (Figure 34) each is elevated to the thallus moisture content which is optimal for its maximum net photosynthesis. Heavier rain intensity results in saturated *A. ochroleuca* thalli but not *C. nivalis*. It was found that the two species have different maximum water holding capacities and different thallus shapes which resulted in a differential interception of rainfall. The fact that *A. ochroleuca* and *C. nivalis* have similar surface area to weight ratios, however, (Table VII) demonstrates the significance of thallus shape alone in controlling water uptake.

Hilitzer (1927) quoted in Blum (1973) conducted experiments showing that for individual lichen species, characteristic relationships appeared between the evaporation rate, thallus moisture content and the saturation deficit of the air. These relationships were tested by Blum (1965) who did not find any useful relationships between these factors, in differentiating species ecologically. Harris (1969), conducting wind tunnel experiments, did not show significant differences between evaporative resistance terms in three *Parmelia* species, when exposed to identical environments. Equally, Hoffman and Gates (1970) working with both a lichen and a liverwort found that although internal resistances to evaporation were very different between the two forms, the total resistances were about the same, although in general these levels were much lower than in higher plants. Their results are consistant with general conclusions found in the literature which are that lichens do not show mechanisms for the control of water loss.

The results of experiments conducted using the wind tunnel (see section 3.4 above) did not substantiate these general statements. Lichen material exhibits at least three different mechanisms for the control of thallus moisture as shown in Figures 44-49. The first mechanism, differences in surface area to weight ratio, provided at least a three fold increase in evaporative resistance within A. ochroleuca. A change in the growth habit from single thalli to clumps of several thalli resulted in equally large increases in total resistance terms for both species. The third mechanism, differences in thallus shape with constant surface area to weight ratios demonstrated at least a two fold increase in resistances of C. nivalis over A. ochroleuca. The collections of A. ochroleuca from other geographical locations demonstrated that morphological differences coincided with marked physiological differences (c.f. Figures 16,40, 41)

The stability of resistance terms at various thallus moisture contents and the marked relationship between evaporation and total resistances suggest that evaporative and resistance characteristics of thalli are ecologically significant (Figure 49). Although Blum's (1965) criticism of Hilitzer's work was based on the fact that xerotic and mesotic species could have the same evaporative characteristic, Blum did not recognize that the range of these terms within species was itself ecologically significant. The high resistance to evaporation shown by single thalli of A. ochroleuca from Melville Island is probably related to the extremely dry polar desert environment at that site. The low rates of net photosynthesis (Figures 40, 41) would also result in very slow growth rates maintaining the size of these thalli small and thus resistance terms large. The large size of the A. ochroleuca collected from the palsa mound would seem to contrast markedly with the Melville Island collection, except that the growth form of this material in the field is cushion-like. Thus although the evaporation rates from individual thalli are high and resistance terms are low, the growth habit of this material would maintain high resistance to evaporation.

The morphological characteristics of A. ochroleuca and C. nivalis can be correlated with the physical parameters of the environment in which they are most abundant. Thalli of A. ochroleuca are adapted to maintain low levels of thallus moisture content relative to C. nivalis. A. ochroleuca is most abundant on the ridge top positions showing higher windspeeds, lower temperatures and higher rates of evaporation under conditions of diffuse radiation. In contrast, C. nivalis is most abundant on the ridge bottom positions, where windspeeds are reduced, temperatures are slightly higher, and evaporation rates are lower. Thalli of C. nivalis show characteristics which maintain thallus saturation at high levels for extended periods of time, thus affording this species greater photosynthetic production.

Section 5

SUMMARY

1) A raised beach system supporting a general lichen heath vegetation was studied to determine the relationships between the distribution of the important species and environmental gradients. Although an inland developmental sequence was present from the coast of Hudson Bay going inland, the largest proportion of variation in the sample was related to the topographic characteristics of individual beach ridges.

2) The significance of this variation in relation to the contrasting top and bottom positions of raised beaches was tested by measurement of peat depth, surface soil moisture, aspect, snow cover thickness, windspeeds, temperatures and drying rates over a variety of raised beach ridge surfaces. Ridge tops were found to be more windy, cooler, dryer, and had reduced snow cover and peat layer thickness relative to ridge bottom positions. Since some of these differences were small, it was important to realize the potentially subtle physiological adaptation in plants to these environments.

3) A simple system was selected to study adaptation of organisms to these contrasting ridge environments. The system used two lichens, which showed mutually exclusive patterns of distribution, as experimental material and examined i) responses of net photosynthesis of Alectoria ochroleuca and Cetraria nivalis from ridge top and bottom positions, on a seasonal basis, ii) morphological adaptation of these two species to these contrasting ridge environments.

4) The physiological study involved the development of a new method for the measurement of gas exchange in lichens which permits the generation of

physiological data matrices containing factorially arranged experiments.

5) Both lichens examined showed rapid seasonal acclimation which did not follow the patterns of acclimation commonly found in higher plants. It is concluded that the phenomenon shown by these plants is acclimation while the responses shown by higher plants are likely responses shown by plants undergoing hardening. The ability to acclimate and the fact that the four collections acclimate differently, points to the importance of acclimation in contributing to the patterns of distribution found for these two species lichens over the ridge profile. The patterns of distribution of these 2 species can be predicted qualitatively, on the basis of the physiological data presented, although the interaction of a variety of other processes is probable.

6) The two species show marked morphological adaptation to their physiological requirements and to the physical characteristics of the ridge environments from which they were collected.

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Section 7

APPENDIX "A"

Distribution Patterns of the Most Abundant Species

Dryas integrifolia

There is a highly significant correlation coefficient between Dryas performance and surface soil moisture (Figure 50 and Table IX) which is reflected in its consistently high cover and performance values on dry ridge tops and in its higher cover value on the drier ridges of the system (Figures 51, 52).

Equisteum variegatum

The lack of interridge pattern for this species (Figure 53) contrasts markedly with the consistently high cover values which appear at ridge edges where soil moisture contents are high. Low cover values appear on dry ridge tops (c.f. Figure 22). The correlation coefficient substantiates this result (Table IX).

Rhododendron lapponicum

This species shows small interridge variations in abundance although substantial increases in its cover are found on the leeward slopes of ridges 1, 2, 7, and 9 (Figure 54). This is reflected in the correlation coefficient results (Table IX). This type of intraridge pattern suggests a relationship between species distribution and some atmospheric factor such as windspeed.

Figure 50.

The linear regression of Dryas performance index against surface soil moisture as % by weight. (r=-0.86)

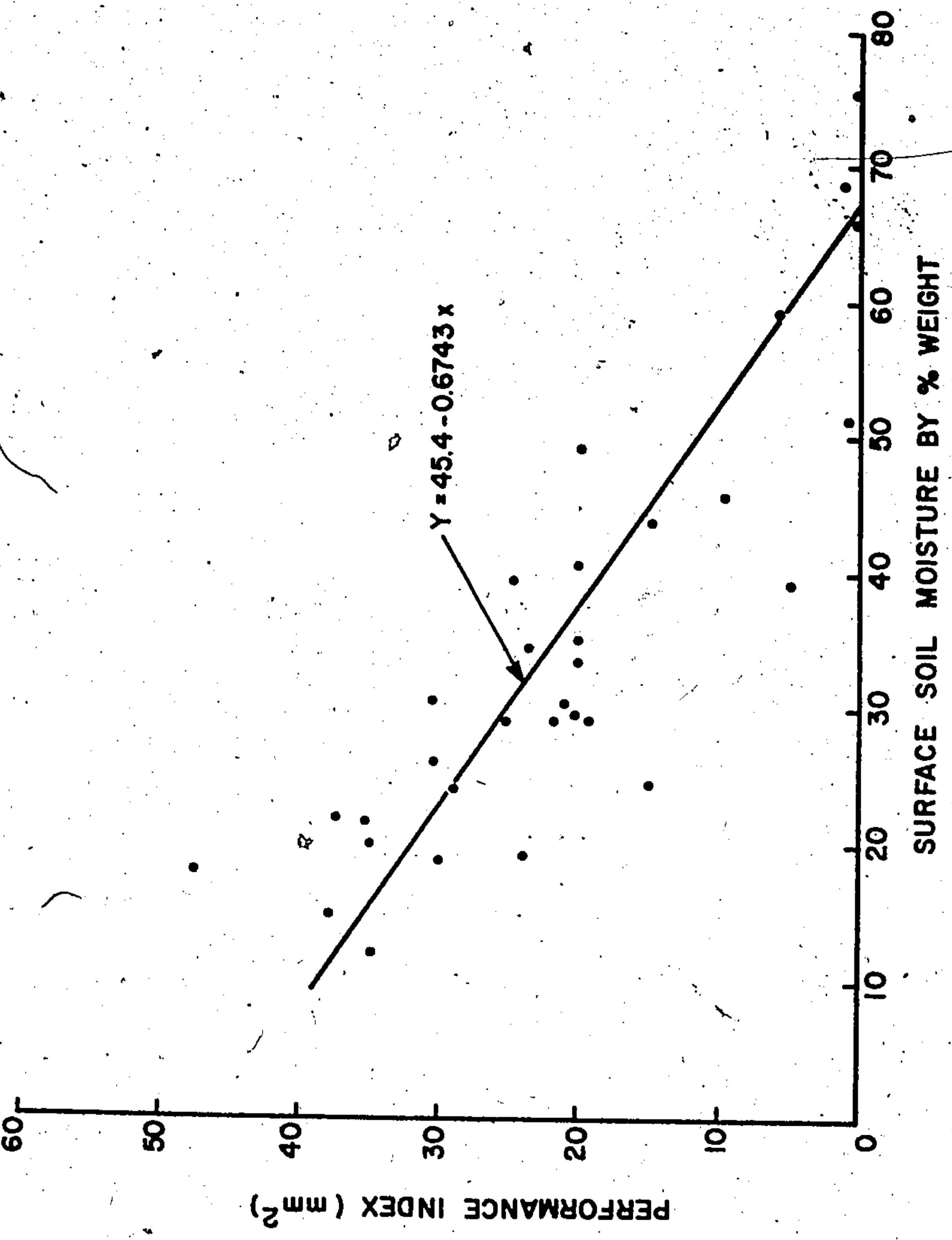

Y = 45.4 - 0.6743 x
PERFORMANCE INDEX (mm²)
SURFACE SOIL MOISTURE BY % WEIGHT
0
10
20
30
40
50
60
10
20
30
40
50
60
70
80

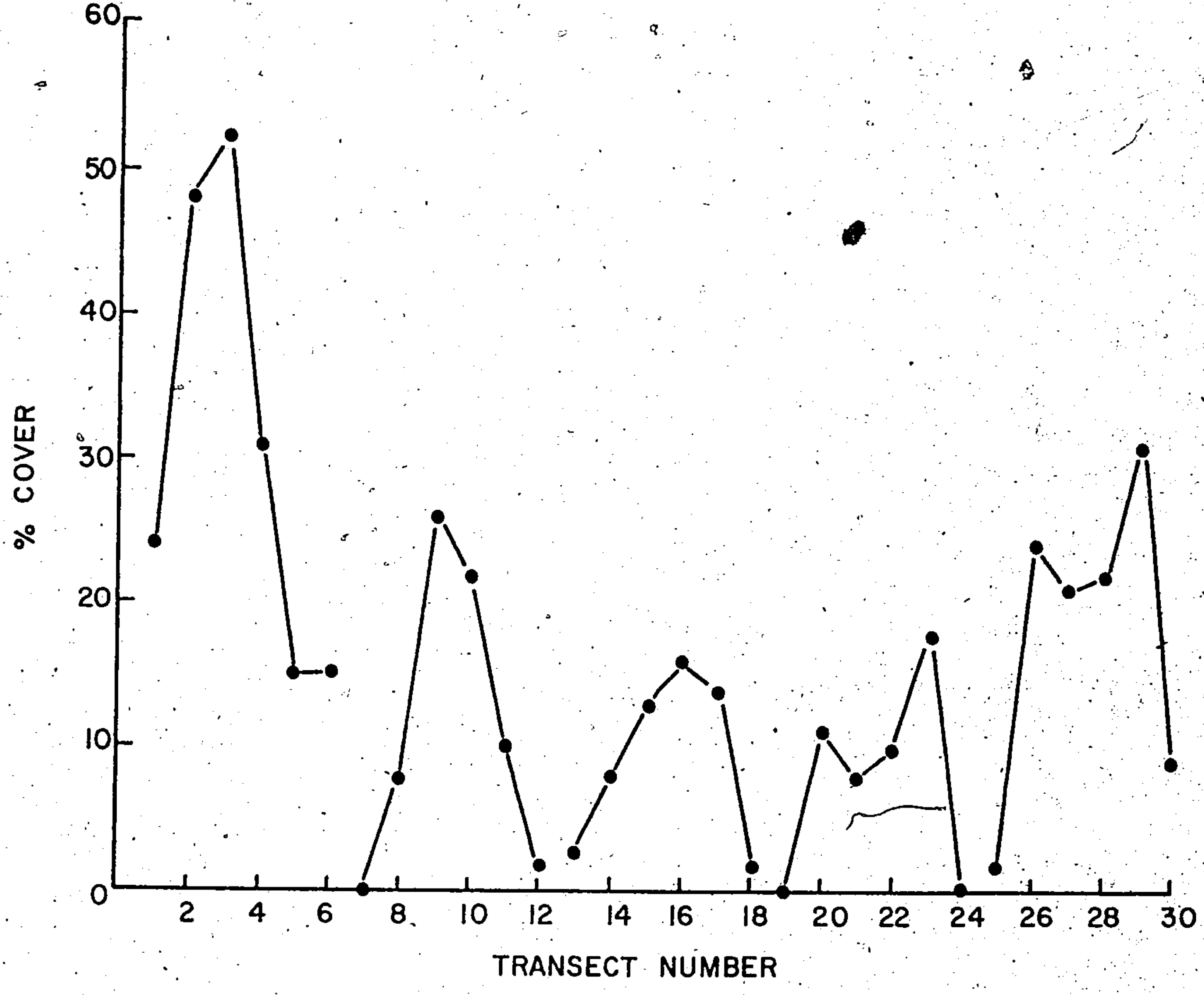
TABLE IX

Results of linear regression analysis between percent cover (or biomass) of species and environmental variables which are significant at the p = .05 level.

Species	Abundance Measure	Variable	r	Y-intercept	Slope
Cetraria islandica	cover	position on ridge	-0.38	20.05	-1.57
C. nivalis	cover	peat	0.58	12.00	8.80
	biomass	peat	0.57	13.83	7.71
	cover	water	0.43	12.90	0.23
	biomass	water	0.62	9.74	1.16
	cover	total lichen biomass	-0.39	29.93	-0.03
Dryas integrifolia	cover	peat	-0.53	30.70	-3.12
	performance	peat	-0.62	28.75	-3.56
	cover	water	-0.74	36.85	-0.60
	performance	water	-0.86	45.40	-0.67
Equisetum variegatum	cover	water	0.57	-5.28	0.34
Alectoria ochroleuca	biomass	peat	-0.51	150.90	-16.72
		water	-0.43	138.70	-1.91
		total lichen biomass	0.67	-61.61	0.45
	cover	total lichen biomass	0.72	-5.15	0.09
Rhododendron lapponicum	cover	position on ridge	0.54	1.38	1.56
Cetraria cucullata	cover	peat	-0.45	14.53	-1.20

Figure 51.

Variations of percent cover of Dryas integrifolia across ridge profiles , and throughout the ridge system as a whole. Higher abundances are found on ridge summits and on the drier ridges of system .



% COVER
60
50
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
TRANSECT NUMBER

Figure 52.

Performance index of Dryas is correlated to the first ordination axis in the same way as surface soil moisture. Classes : I- 0-10 mm^2 ; II- 10-35 mm^2 ; III - >35 mm^2.

DRYAS

PERFORMANCE

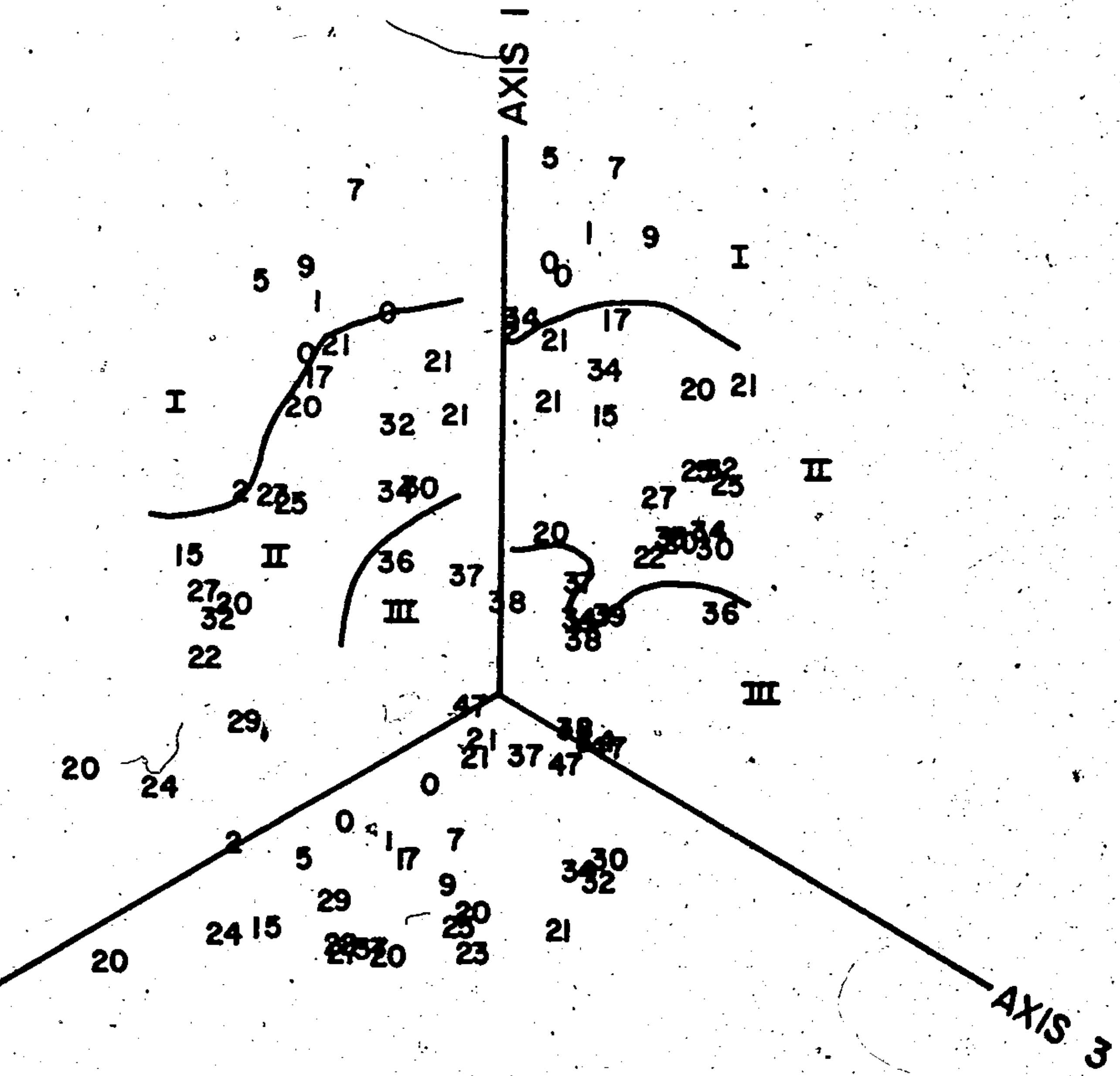


Figure 53.

The amount of interridge pattern in Equisetum variegatum is seen to be very much less marked than the considerable intraridge variation.

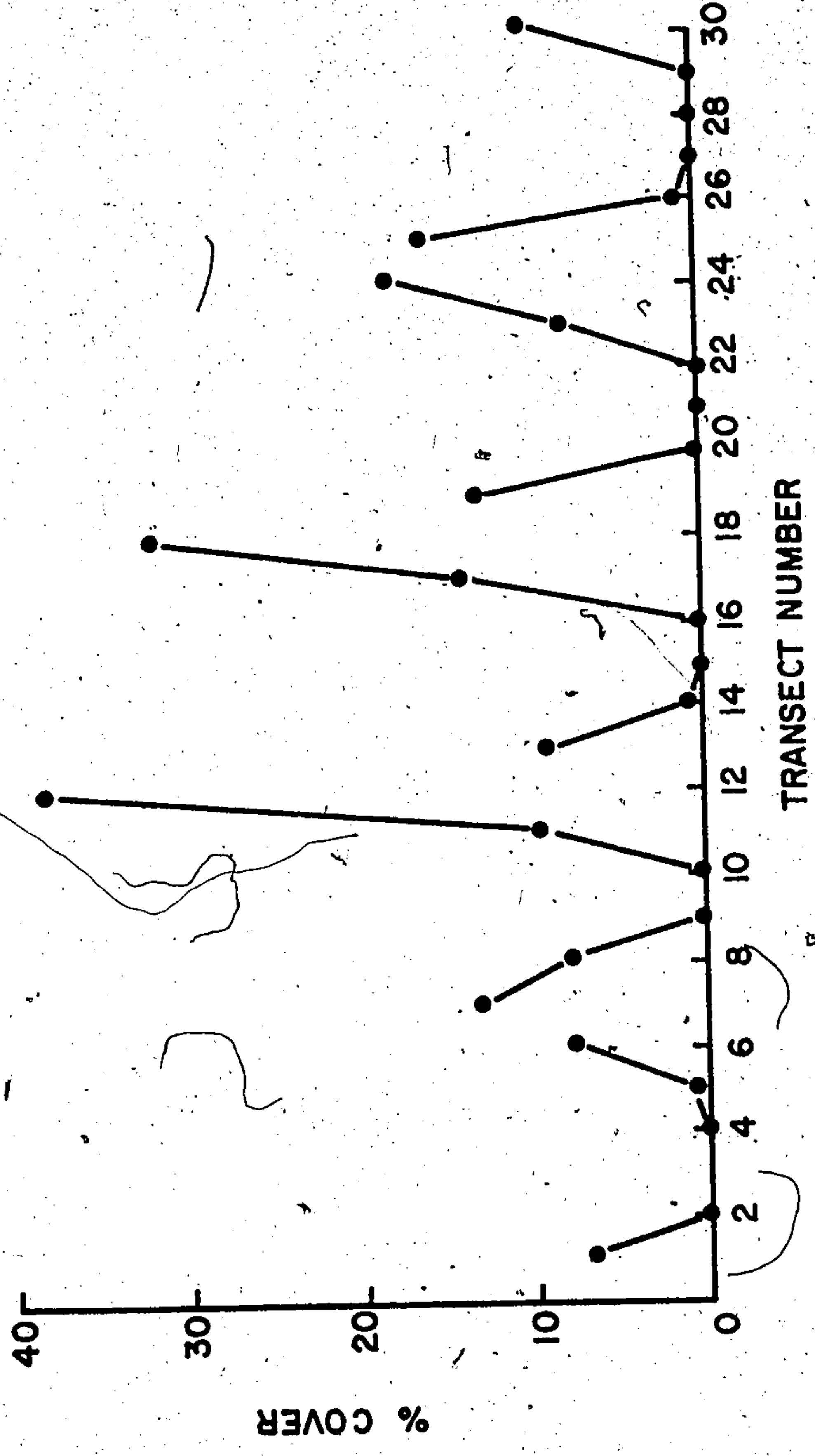
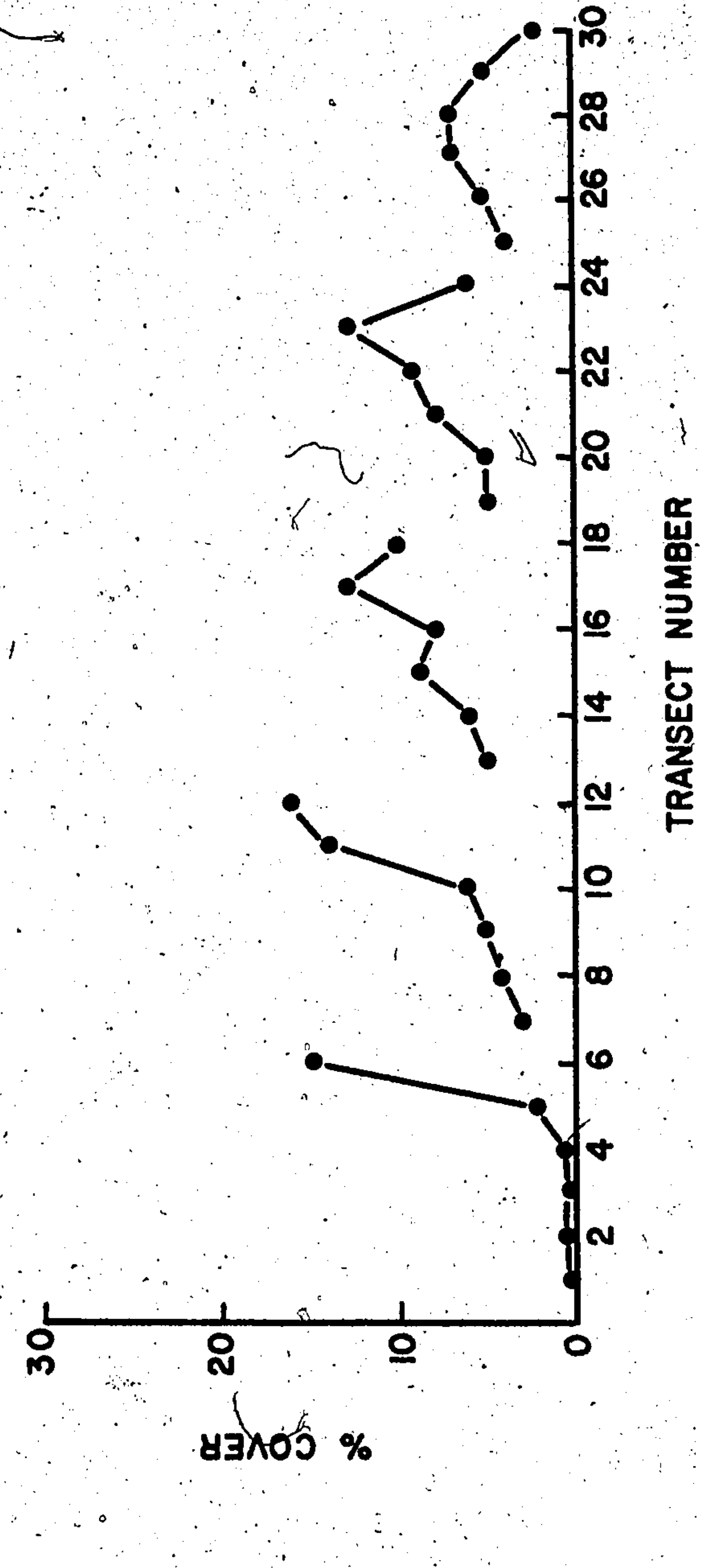

% COVER
40
30
20
10
0
TRANSECT NUMBER
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Figure 54.

The lack of interridge pattern in *Rhododendron lapponicum* contrasts with the considerable intraridge variation as seen on ridges 1,2,7 and 9.


% COVER
0
10
20
30
TRANSECT NUMBER
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Cetraria islandica (agg.)

The presence of at least two chemical forms (K- and K+ red) of C. islandica, morphologically identical in the field, necessitates an aggregate grouping. C. islandica is abundant on the most recently formed ridges where peat thickness is small and surface soil moisture is low, but maintains a relatively high biomass over the remainder of the ridge system (Figure 55). However the data in Table IX also shows that the cover values correlate with north facing position on ridges where peat is thick and soil moisture contents are high. There are several explanations for these inconsistencies. It is possible that there are two or more subspecies which are physiologically distinct. Alternatively, there is but one major species which is extremely variable physiologically. Thirdly, the influence of surface soil moisture and peat depths on the distribution of this species may be small.

C. cucullata

There is a general reduction in cover of this species on progressively older ridges (Figure 56) but with no marked pattern at the intraridge scale. The interridge pattern is correlated at the 5% level with a decrease in peat depth (Table IX).

C. nivalis

As shown in Figure 18, this species has a higher biomass on the older ridges although it maintains a relatively high biomass throughout the ridge system. The pattern of C. nivalis biomass is similar to that of soil moisture (c.f. Figure 21,22). This is substantiated by the correlation coefficient and the ordination results (Figure 57 and Table IX). Its relatively bright yellow colour and high cover values at ridge edges

Figure 55.

Variation in biomass of *Cetraria islandica* (agg.) across ridge profiles and throughout the ridge system. Highest levels of standing biomass were found on the youngest ridges of the ridge system.

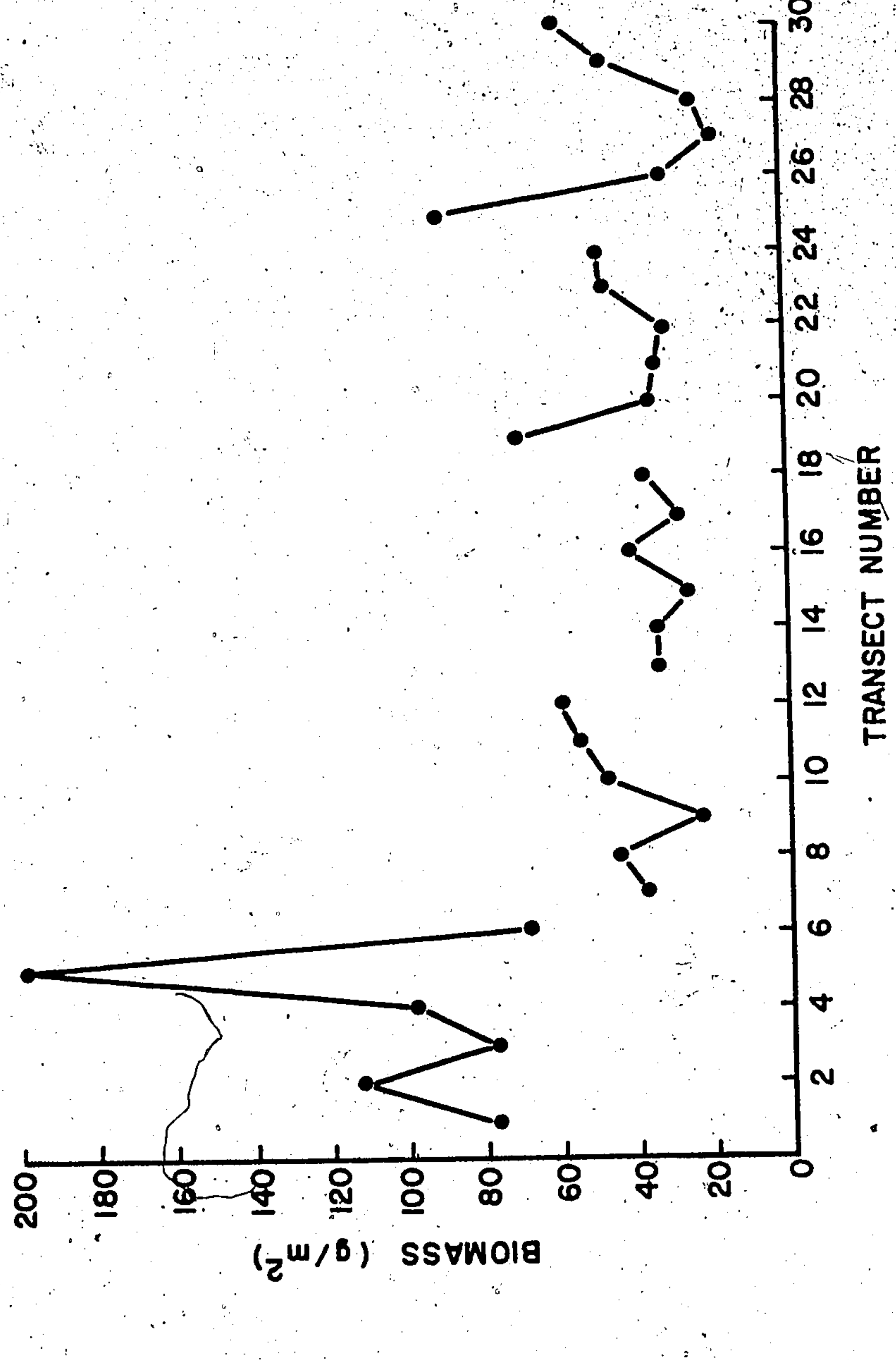

BIOMASS (g/m^2)
200
180
160
140
120
100
80
60
40
20
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
TRANSECT NUMBER

Figure 56.

The percentage cover of Cetraria cucullata decreases with progressively older ridges in the ridge system.

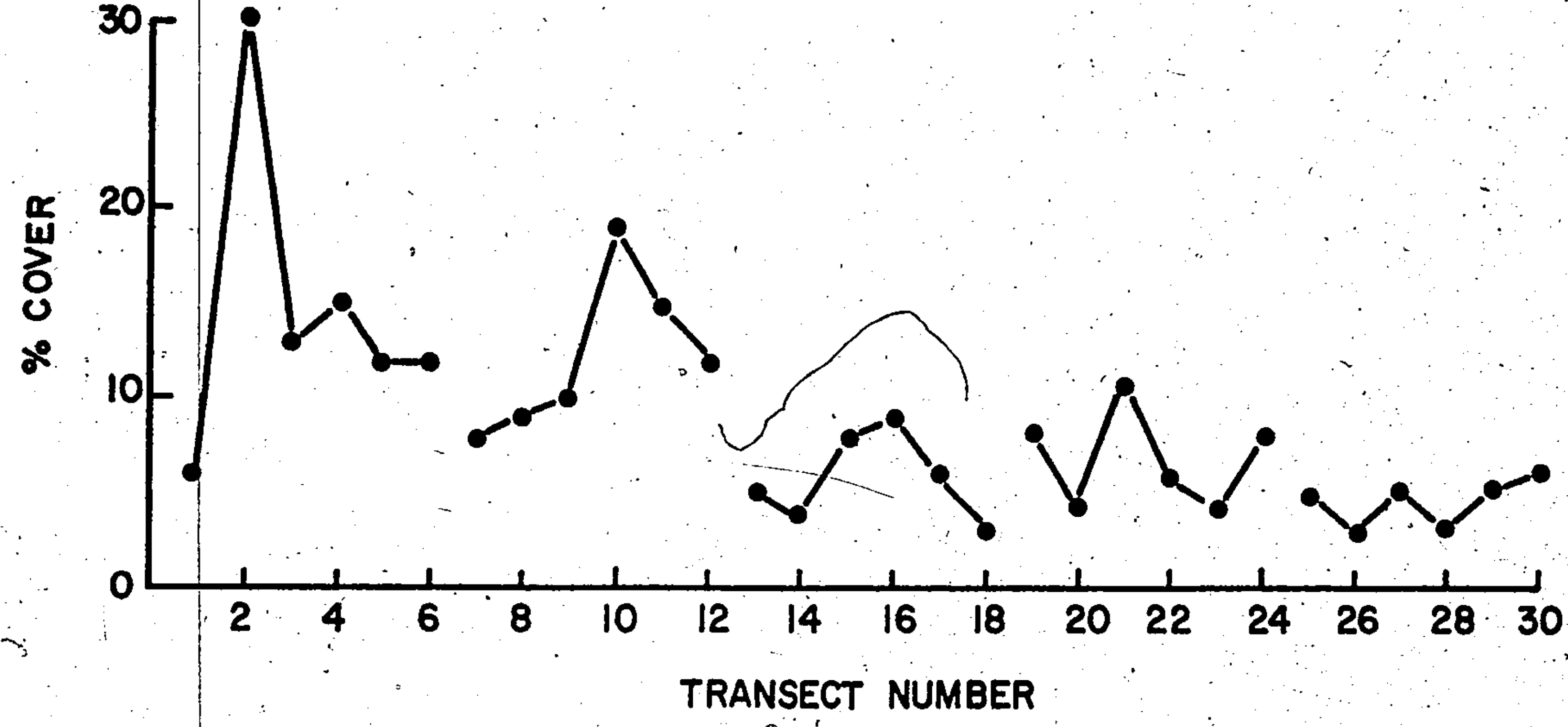
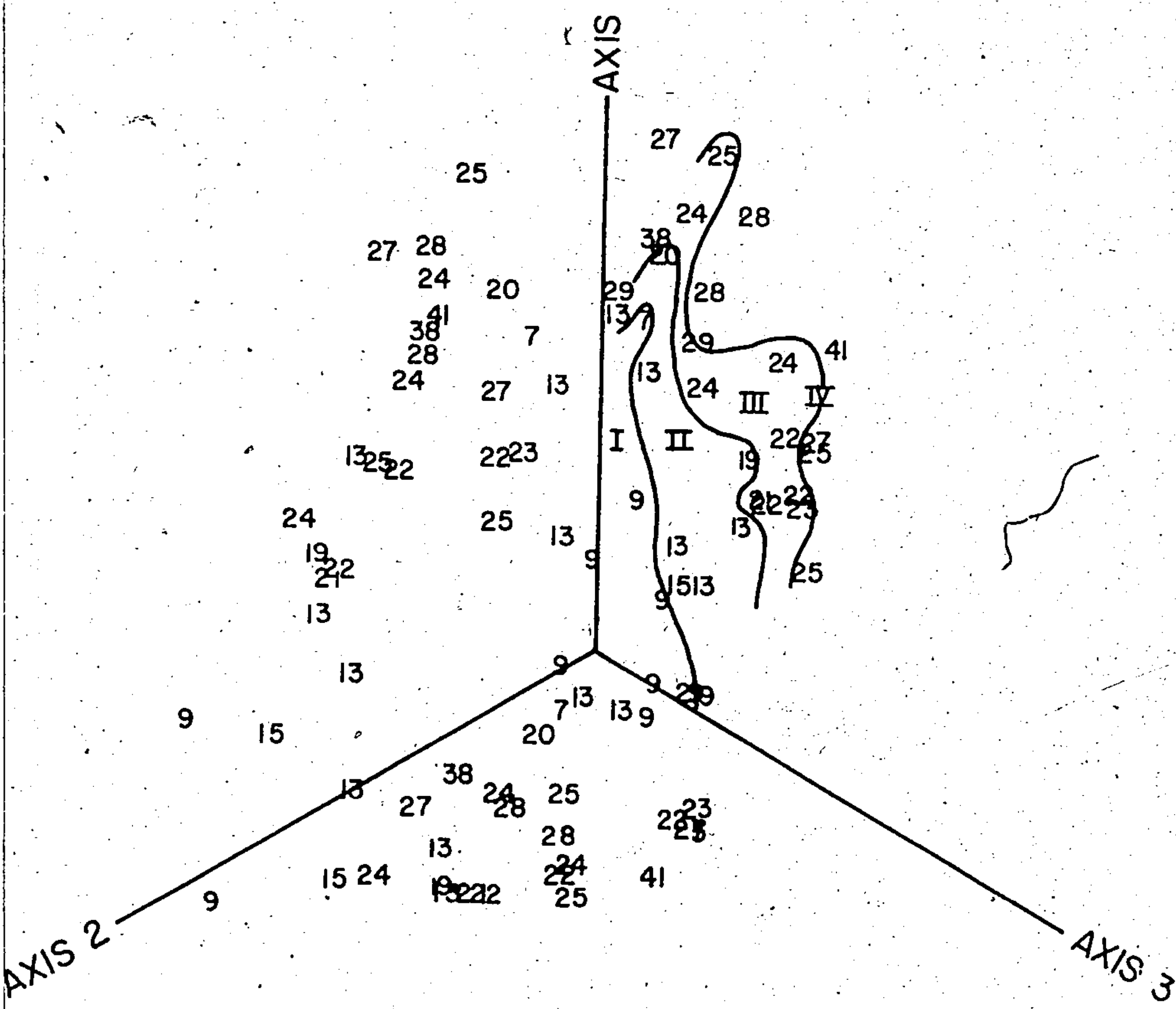

30
20
10
0
% COVER
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
TRANSECT NUMBER

Figure 57.

Percent cover of <u>Cetraria nivalis</u> is correlated to axis 3 of the ordination in the same way that depth of peat is. Classes : I- 0-10%; II- 10-20 % ; III- 20-25 % ; IV - >25% .

CETRARIA
NIVALIS



contrast markedly with the abundance of A. ochroleuca on ridge crests, thus providing the visual impressions of patterns that initiated this study.

Cladina mitis

This species is abundant on ridges 7 and 9, but infrequent on the other ridges in the system (Figure 58). Its appearance in the developmental ridge sequence correlates with increases in peat thickness found on progressively older ridges (c.f. Figure 21,58,59). Again low soil moisture on ridge 12 correlates with the reduced biomass of C. mitis suggesting some interaction between these two variables.

Cornicularia divergens

The percentage cover of C. divergens is directly related to axis 2 of the ordination with highest values on ridge 2 and lowest on ridges 1 and 12 (Figure 60 and 61). Despite the abundance of this species, no significant correlations were obtained. It is therefore concluded that the distribution of C. divergens may not be controlled by the parameters measured in this study.

Alectoria ochroleuca

There is an inverse relationship between A. ochroleuca biomass and both peat thickness and surface soil moisture (Table IX) which is also evident in the ordination results (Figure 62). This is consistent with its high abundance on the most recently formed ridges (Figure 19); conversely, its relatively low biomass on ridge 12 (with its reduced surface soil moisture) suggests interaction of other factors.

The most interesting aspect of the distribution of this species is its optimum performance on ridge.top positions contrasting markedly with C. nivalis which is most abundant at the ridge edges. The two species appear to be mutually exclusive throughout the system on either the intraridge or interridge scales.

Figure 58.

The biomass of Cladina mitis is seen to increase on ridges 7 and 9 although very much reduced levels on ridge 12 are found. These patterns appear to be related to both peat layer accumulations and the soil moisture status of the ridges.

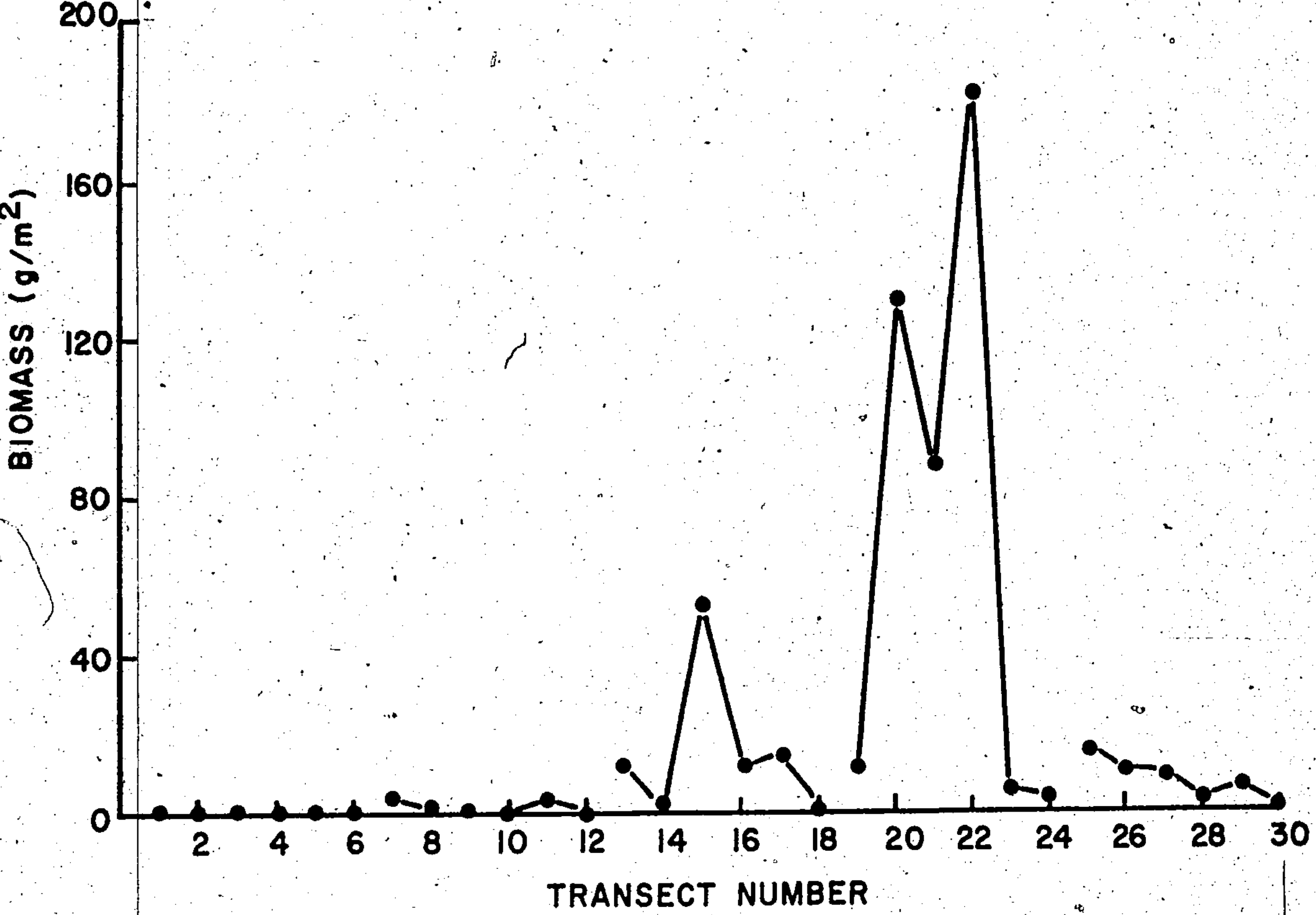

BIOMASS (g/m²)
200
160
120
80
40
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
TRANSECT NUMBER

Figure 59.

Ordination overlay of % cover for Cladina mitis . Values are correlated with peat layer thicknesses along axis 3. Classes: I- 0 ; II- >0 .

CLADINA
MITIS

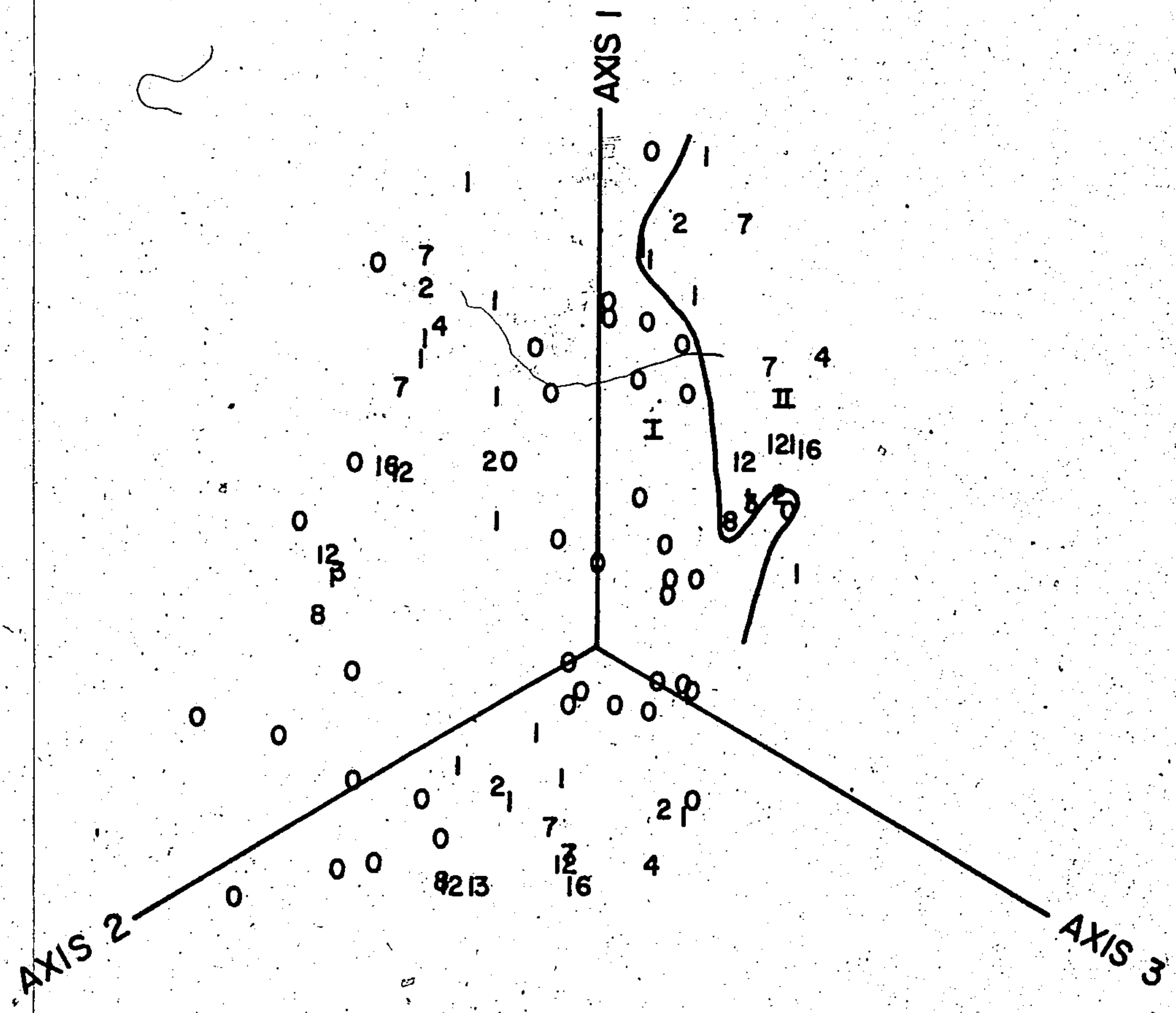


Figure 60.

The pattern of *Cornicularia divergens* biomass appears to be independant of patterns in the apparent environmental parameters observed here.

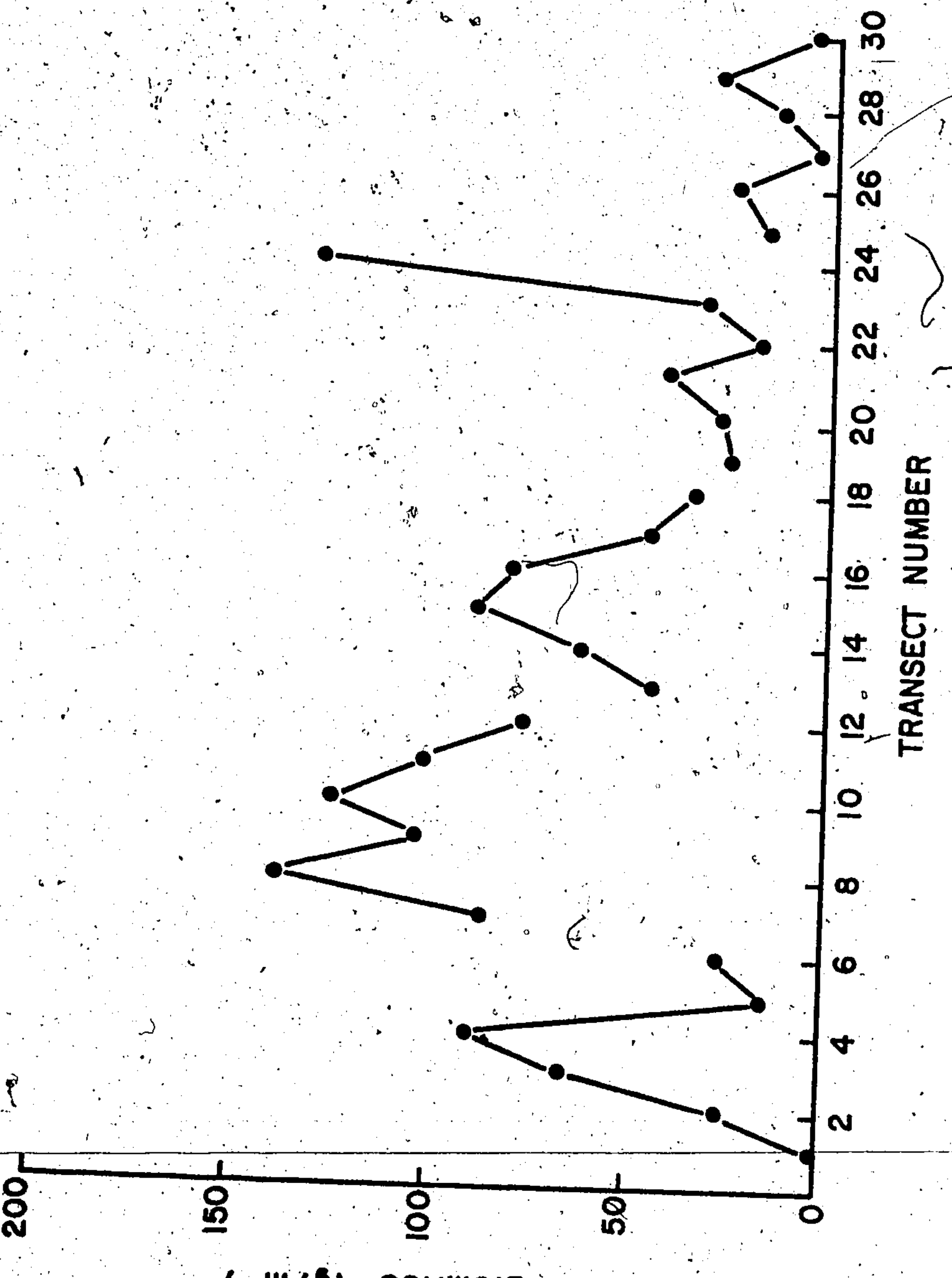

BIOMASS (g/m^2)
0
50
100
150
200
TRANSECT NUMBER
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

Figure 61.

The percent cover of Cornicularia divergens is related to the second ordination axis . A marked sequence of ridges also appeared related to axis 2 , but with no correlated environmental variables (c.f. Figure 23) . Classes : I- 0-10 % ; II - 10-30 % ; III- >30 % .

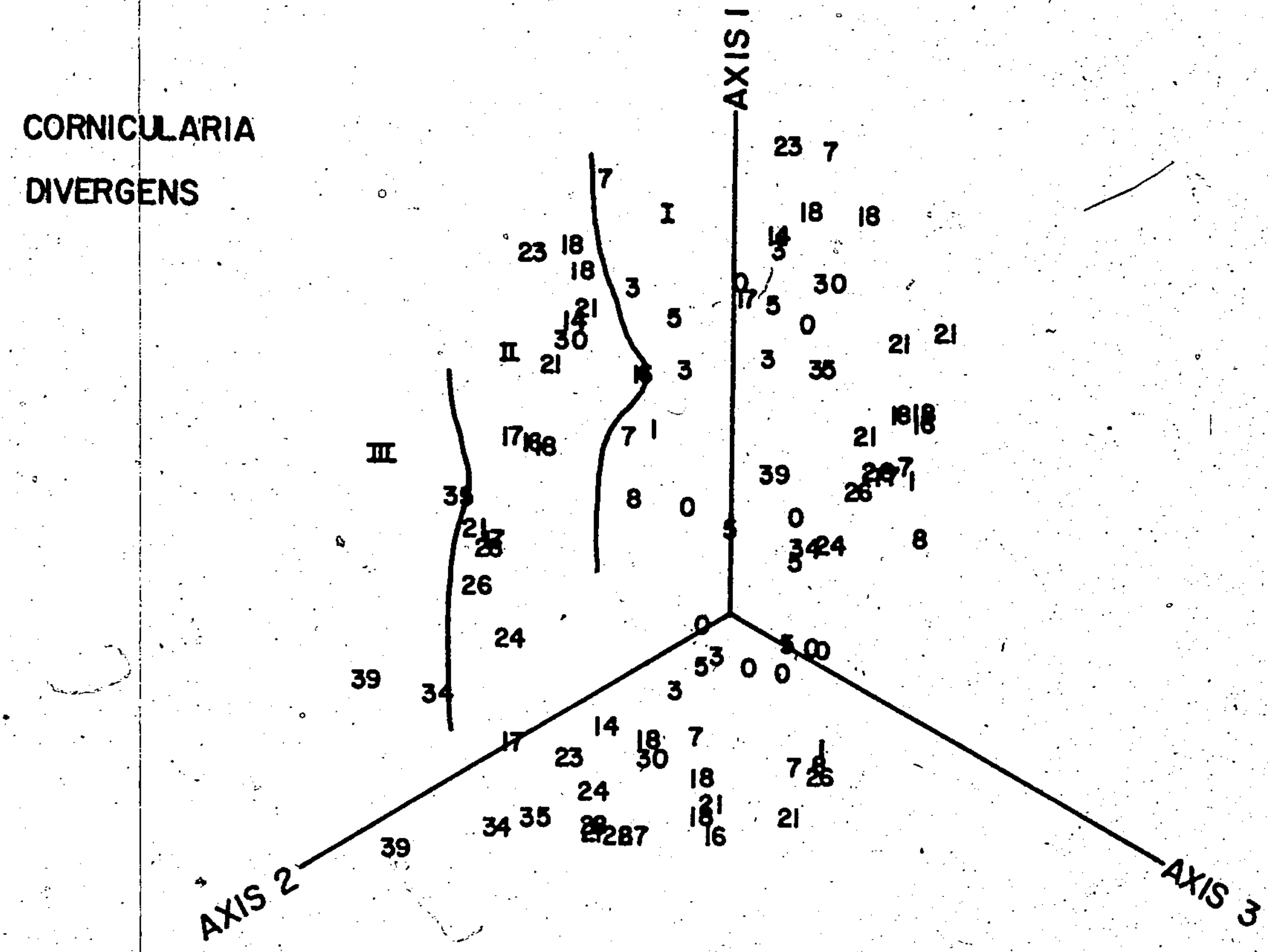

CORNICULARIA
DIVERGENS
AXIS I
AXIS 2
AXIS 3
I
II
III

Figure 62.

Ordination overlay for Alectoria ochroleuca as % cover. The relationship with the first axis is clear. Classes : I - 0-10 % ; II- 10-30 % ; III - >30%.

ALECTORIA
OCHROLEUCA