VEGETATIONAL DEVELOPMENT ON YOUNG RAISED BEACHES IN NORTHWESTERN ONTARIO

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By

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ABSTRACT

The vegetational colonization and development preceding the establishment of lichen-heath was examined on a Hudson Bay coastal raised-beach system. A continuous and directional developmental sequence of approximately 200 years was quantified on both a coastal intraridge sample sequence and on an inland interridge sample sequence. Increasing gradients of elevation, soil peat thickness and soil organic matter coincide with the vegetational development, however no appreciable changes in soil pH or concentrations of available nutrients were detected and it is concluded that these parameters have little influence on the development of lichen-heath at this site. Community composition over the ridge profile forms a second major vegetational gradient which appears to be affected primarily by environmental factors related to ridge morphology and orientation. The interactions of environmental factors in the development of lichen-heath are discussed.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. Kenneth A. Kershaw for his initiation and supervision of this study. Thanks are also extended to Dr. Douglas W. Larson, Mr. John MacFarlane and Mr. Michel Grandmaison for their advice and help in the field. Additional assistance in various aspects of the study from my wife Marie, Mr. Andrew Karp, Ms. Margaret Webber and the other members of the lab is also appreciated.

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INTRODUCTION

In recent years large areas of northern Canada have experienced a rapid increase in human activity, particularly in natural resource exploration and development. The vast Hudson Bay region has been the site of extensive oil, gas and mineral exploration and shipping, all of which may bring appreciable economic development and human impact to the region (Buck and Dubnie 1968). In contrast to the rise in technological information and expertise, our ecological understanding of this region is still very poor, especially concerning the distribution and structure of the vegetation.

Although a number of vegetation surveys in this region have provided useful taxonomic and biogeographical information (cf. Polunin 1948, Hustich 1957) almost no quantitative analyses of species' distribution and abundance have been done. Such data are a prerequisite to studies of the factors controlling the distributions of plant species and their roles in the environment. Accordingly, this study was initiated to provide a quantitative description of the colonization sequence of upland vegetation on the southern shore of Hudson Bay as a basis for further research in this system.

(1.1) The Hudson Bay Coastal Tundra

The southern shore of Hudson Bay supports a narrow strip of arctic tundra which is considered a distinct physiographic and vegetational zone (Coombs 1954). The tundra is dominated by poorly-drained meadows and, to a lesser extent, by well-drained upland sites which support a rich flora composed primarily of lichens, mosses and dwarf heath.

The most conspicuous and common upland landforms of the coastal zone are complexes of raised-beach ridges. These ridges are the result of post-glacial isostatic uplift of the Hudson Bay region and the subsequent recession of the post-Wisconsinan Tyrrell Sea; processes which began approximately 8,000 years ago and continue today (Lee 1968). The ridges are composed of marine surficial deposits of sand and sandy gravel which overlie Palaeozoic, fossiliferous, limestone bedrock which is rich in carbonates (Pelletier _et al_ 1968). The coastal tundra lies within the zone of continuous permafrost and ridges have variable soil active layer thicknesses of up to 2 m depending on soil thermal properties and seasonal weather conditions (Brown 1970, McGregor 1975).

This coastal zone has a typically arctic climate which may be characterized as cold, dry and windy (Thompson 1968). This extreme southward penetration of arctic climate is due primarily to the proximity of the cold waters of Hudson Bay and the frequent presence of arctic cold air masses which may move southward, unimpeded by landform barriers, across the

Hudson Bay basin (Thompson 1968). In many respects then, the climate of this coastal area will bear strong similarity to that of Churchill, Manitoba (see below, Figure 3) which has a mean annual temperature of -6°C, 38 cm of annual precipitation and 63 frost-free days per year (Thomson 1962).

The general nature of beach ridge lichen-heath vegetation has been known for some time (cf. Polunin 1948, Moir 1954, Hustich 1957), however, detailed studies of its structure and ecological relationships have only recently appeared. Neal and Kershaw (1973 a,b) and Kershaw and Rouse (1973) have made quantitative studies of the general structure of lichen-heath at Cape Henrietta Maria and on the mainland opposite East Pen Island, respectively. In these areas the dominant vegetation type is a general lichen-heath composed predominately of *Alectoria ochroleuca* (Hoffm.) Massal., *Cetraria nivalis* (L.) Ach., *C. islandica* (L.) Ach., *C. cucullata* (Bell.) Ach., *Cladina mitis* (Sandst.), *C. rangiferina* (L.) Wigg, *Dryas integrifolia* Vahl. and *Rhododendron lapponicum* (L.) Vahl. in varying abundances.

(1.2) The Research Site

The existence of an oil company survey camp and airstrip on the mainland opposite East Pen Island in Hudson Bay (56°46'N, 88°47'W; Figure 1) offered access to a large coastal raised-beach ridge system. The ridge system consists of a fan-shaped series of parallel, physiographically-similar, raised beaches (Figure 2). The geomorphic origin of the ridge system has not

Figure 1.

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

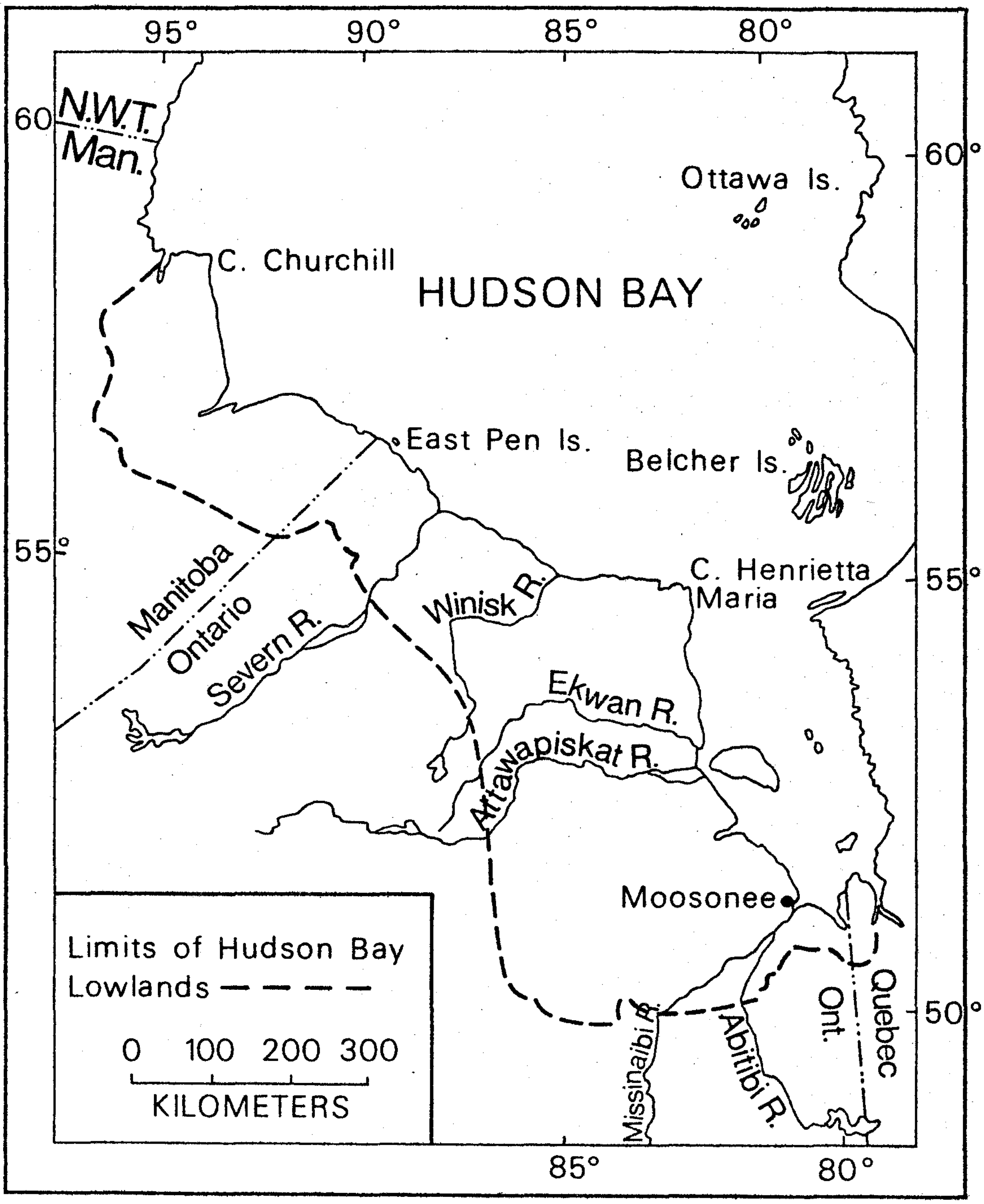
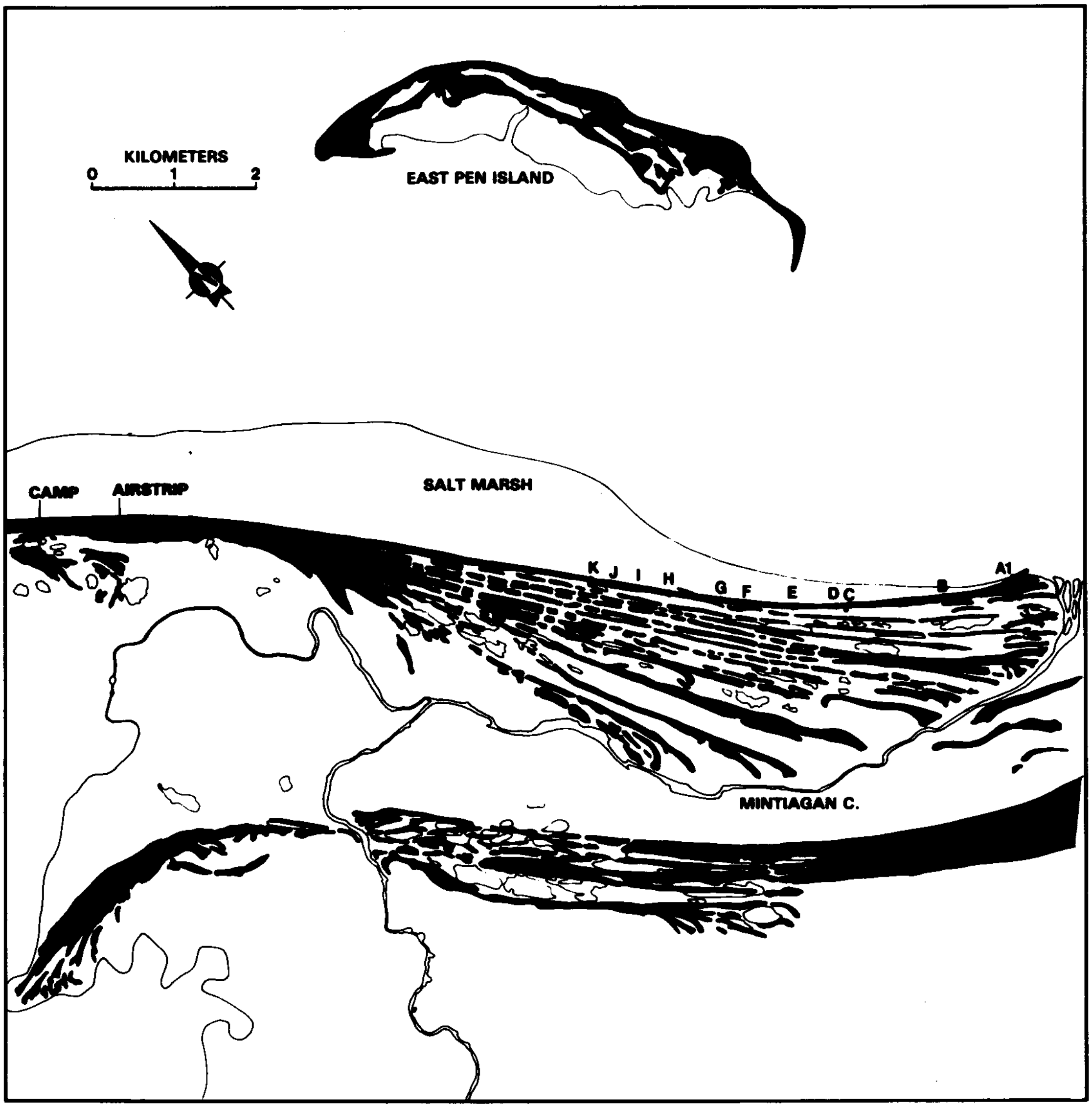

95°
90°
85°
80°
60
N.W.T.
Man.
60°
Ottawa Is.
C. Churchill
HUDSON BAY
East Pen Is.
Belcher Is.
55°
55°
C. Henrietta Maria
Manitoba
Ontario
Severn R.
Winisk R.
Ekwan R.
Attawapiskat R.
Moosonee
Limits of Hudson Bay Lowlands
0 100 200 300
KILOMETERS
Missinaibi R.
Abitibi R.
Ont.
Quebec
50°
85°
80°

Figure 2.

Diagrammatic representation of the raised-beach ridge systems (shaded) in the East Pen Island region showing the locations of the coastal, intraridge sample sequences (areas A1 to K) and the inland, interridge sample sequence (areas A1 to 5) on the coastal raised-beach ridge system.

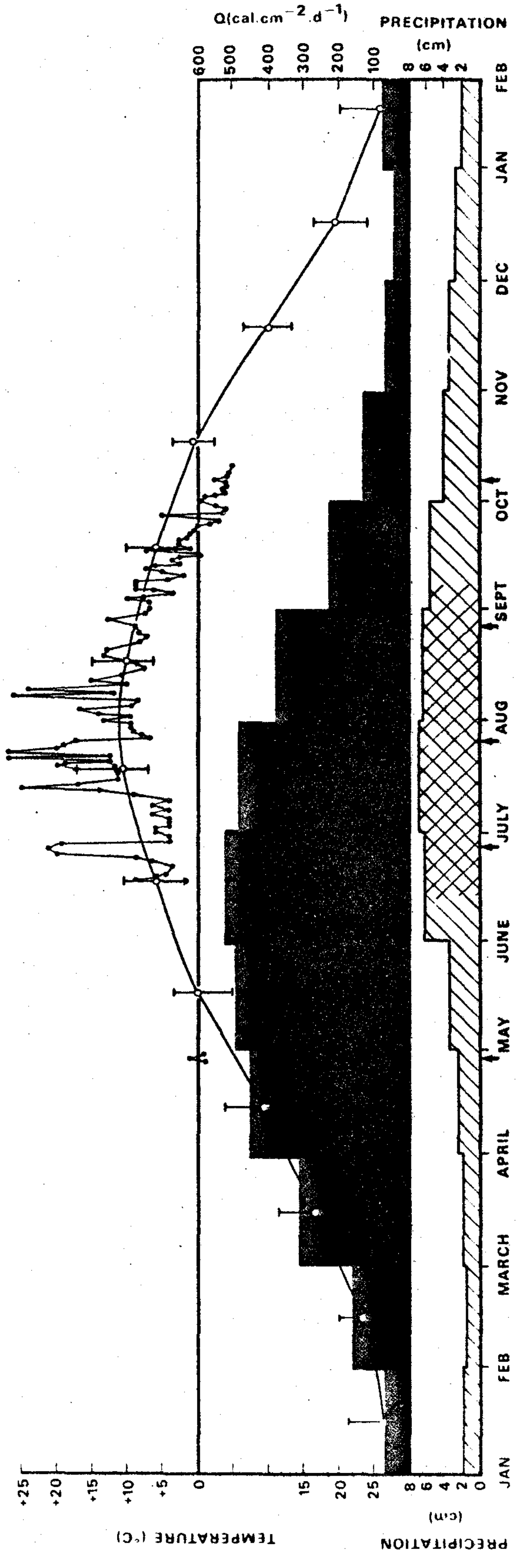

KILOMETERS
0
1
2
EAST PEN ISLAND
CAMP
AIRSTRIP
SALT MARSH
K
J
I
H
G
F
E
D
C
B
A1
MINTIAGAN C.

been established, however each ridge is the result of coastal depositional processes and post-glacial, isostatic uplift. In the general coastal situation, sand may drift outward from a point of accumulation to form a foundation on which dunes can develop, either fan-wise by apposition of new material on the seaward side or terminally along shore (Ranwell 1972). In the Hudson Bay region uplift of the land allows stabilization of the beach parallel to the receding shoreline. The subsequent formation of a new beach may result from an emergent bar or by excessive deposition by high energy waves during a storm (King 1972). These processes create a series of zones of increasing age from the distal to the proximal end of a beach and also a series of apposition raised-beach ridges of increasing age from the shore, landward.

The principal characteristics of the climate at the Pen Island site are presented in Figure 3. The growing season, roughly July and August, has relatively long days and generally cool temperatures. The low temperatures are almost always associated with onshore winds and are often accompanied by fog or mist. High temperatures are infrequent but have reached 32°C and are associated with southerly winds. Summer precipitation may be quite variable from year to year and usually occurs in the form of drizzle. In contrast to the high arctic, this site has a number of severe thunderstorms each summer which may be responsible for starting many of the localized forest fires seen south of the treeline. Windspeeds are

Figure 3.

General features of the yearly climatic patterns at the Pen Island site. Shown are monthly average values for (1) precipitation as snow (hatched) and rainfall (crosshatched); (2) incoming solar radiation, Q (stippled); (3) screen height monthly mean, maximum and minimum air temperatures (open circles plus vertical bars). Superimposed upon the monthly mean air temperature curve are the observed screen height daily average air temperatures for 1974 (solid circles). Data are abstracted from Thompson (1968) and from the Churchill weather office records. (from Larson 1975)


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

usually moderate and prevail from the north-northwest.

A primary vegetational survey of the ridge system (Kershaw and Rouse 1973) noted definite trends in the major plant species and their associations on a transect going inland from the coastal ridge. The trends were thought to be indicative of a general developmental sequence and as a result, two forms of the general lichen-heath association were identified. The general lichen-heath II, containing both _Cladina_ _mitis_ and _C._ _rangiferina_, is characteristic of older, inland ridges while the general lichen-heath I of younger coastal ridges lacks these two species. Rouse and Kershaw (1973) studied the interaction of vegetation, soil organic matter and soil moisture along the developmental sequence of lichen-heath. They found that differences in soil moisture and seasonal evapotranspiration along the sequence were closely related to the organic content of the soil.

The extensive nature and sampling methods of these surveys, although exposing major trends, obscured the detailed vegetational structure and environmental variation of any one ridge (Kershaw and Rouse 1973). Thus, a secondary survey of higher resolution was done (Larson and Kershaw 1974) to examine the patterns of the vegetation and more apparent edaphic factors within and between ridges of the general lichen-heath I. They quantified the marked, developmental sequence on ridges approximately 250 to 800 years old but also identified considerable intraridge variation in major species' abundance which appears to be the result of environmental parameters which are independent of the developmental sequence.

These studies provide detailed information concerning the beach ridge vegetation and environment which may form the basis for detailed autecological studies of lichen-heath species. However, no information is available on the vegetational structure and development leading to the lichen-heath community at this site. The present study was initiated to examine the colonization of young raised beaches and the vegetational development preceding the establishment of the general lichen-heath I. A vegetational survey was done to quantify the distribution and abundance of individual species both along the developmental sequence and over the ridge profile. In addition, the trends of ridge topography and some of the major soil parameters were measured to gain insight concerning the environmental factors affecting the development and structure of the vegetation.

Section 2.

METHODS

The first coastal ridge (Figure 2) exhibits a relatively uniform morphology with a long, northeast-facing foreslope and a shorter, shallow backslope. A continuous change in plant community structure is apparent along the 6 km section of ridge from the mouth of the Mintigan Creek to the first lichen-heath plot described by Larson and Kershaw (1974). Ten sample areas (B to K) were chosen within this section, each of which extended for 60 m along the ridge. An additional sample area (A1) was established near the creek mouth on a fore-dune which is still undergoing sand desposition and active plant colonization. A continuous change in vegetation towards lichen-heath is also apparent on a landward, interridge sequence. Accordingly, a comparative vegetational sequence was also studied by establishing sample areas (2 to 5) on four major ridges occurring inland from area A1.

Within each sample area five ridge zones were defined on the basis of ridge morphology. A sample transect was established along the ridge at the center of each zone and ten replicate 1 - m^2 quadrats were positioned randomly on the transect. The abundances of plant species were measured as percentage cover which is easily sampled in tundra lichen-heath since it essentially forms a single vegetation stratum. Cover is evaluated using a frame of ten vertical pins arranged in a row. Cover is defined as the total number of points of contact between different species and each pin (as viewed from above) divided by the total number of pins. In each 1 - m^2 quadrat cover was evaluated at 10 randomly chosen pin frame positions. In addition, independent measures of the performances of three of the more abundant species were obtained. Measurements of aerial plant parts over a large sample area have been found to be useful indications of performance (Phillips 1954; Kershaw 1960, 1962). Random samples of the aerial parts of Elymus arenarius L., Dryas integrifolia and Hedysarum mackenzii Rich. were collected near the end of the growing season and the following measurements were made: Elymus inflorescence height and number of rachillae per inflorescence; Hedysarum leaf length and length of the terminal leaflet; Dryas leaf length and width. Plant phenology can be a useful tool in helping to describe microenvironmental differences between various habitats (Bliss 1962). Accordingly, the general phenological developments of several widely distributed species along the sample sequences were observed once a week through the growing season.

The absolute elevation of each sample area was surveyed in relation to a high-tide datum point situated in the salt marsh (see Kershaw 1976a). Measurements over the ridge profile were taken every 0.6 m on line transects at each end and the center of each area. The three profiles were averaged to describe the ridge morphology and to estimate the elevation of each zone transect.

The thickness of the soil peat layer was measured regularly along each zone transect at a total of 60 points. Duplicate soil samples from three depths were collected from each zone transect of 10 sample areas. The three soil layers were defined as the peat layer, the top 10 cm and below 15 cm in the mineral soil. The two mineral soil samples were fractionated for particle-size analysis using Endicott sieves for the fraction of less than 2 mm diameter. Coarse-fine sand and fine sand-silt fractioning was done using 500μ and 74μ sieves, respectively, in an Allen-Bradley Sonic Sifter. The duplicate samples for each layer were combined for subsequent analyses. Percentage organic matter in each sample was determined by air dry weight loss on digestion in 30% hydrogen peroxide. Soil pH was measured using a Corning glass electrode pH meter by the paste method.[1] The nutrients phosphorus, potassium, calcium, magnesium and nitrate were analysed for their exchangeable concentrations. Phosphorus was extracted using sodium bicarbonate (pH 8.5) and measured with a Technicon Autoanalyser. Neutral normal ammonium acetate (pH 6.8) was used to extract potassium, magnesium and calcium for measurement on an atomic absorption spectrophotometer. Nitrate was determined by the paste method using an Orion Ionalyser with a nitrate-specific electrode.

Analysis of the relationships between ridge areas in the sample sequences was done using principal component analysis, an ordination technique which has been used extensively in ecological research (e.g. Orloci 1966; Austin and Greig-Smith 1968; Neal and Kershaw 1973a,b). Principal component analysis orders plots on the basis of a species' similarity matrix (in

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[1] The analyses of soil pH, phosphorus, potassium, calcium and magnesium were done by the Ontario Soil Testing Laboratory, University of Guelph.

this case, a covariance matrix) calculated from the raw quadrat cover values. The ordinated data is presented in graphical form (Kershaw and Shepard 1972) for the first three component axes, each of which represents a decreasing amount of uncorrelated variance in the data set. Graphical overlays of plot numbers, species cover values and environmental data are used to identify any correlated trends present. Principal component analysis was applied to the total quadrat cover data of the 66 most abundant species at both the area plot and zone transect levels of integration. Apparent relationships between species' abundance and environmental parameters were also examined using linear regression.

Section 3.

RESULTS

The existence of two distinct vegetational gradients is visually apparent on these young raised-beach ridges. The first gradient is the largescale change in vegetation from the site of present colonization to the general lichen-heath I. Superimposed upon this sequence is a smallscale, intraridge gradient involving marked changes in the distribution of species over the ridge profile. The plant community development towards lichen-heath and the accompanying changes in the topography and the edaphic environment will be considered first.

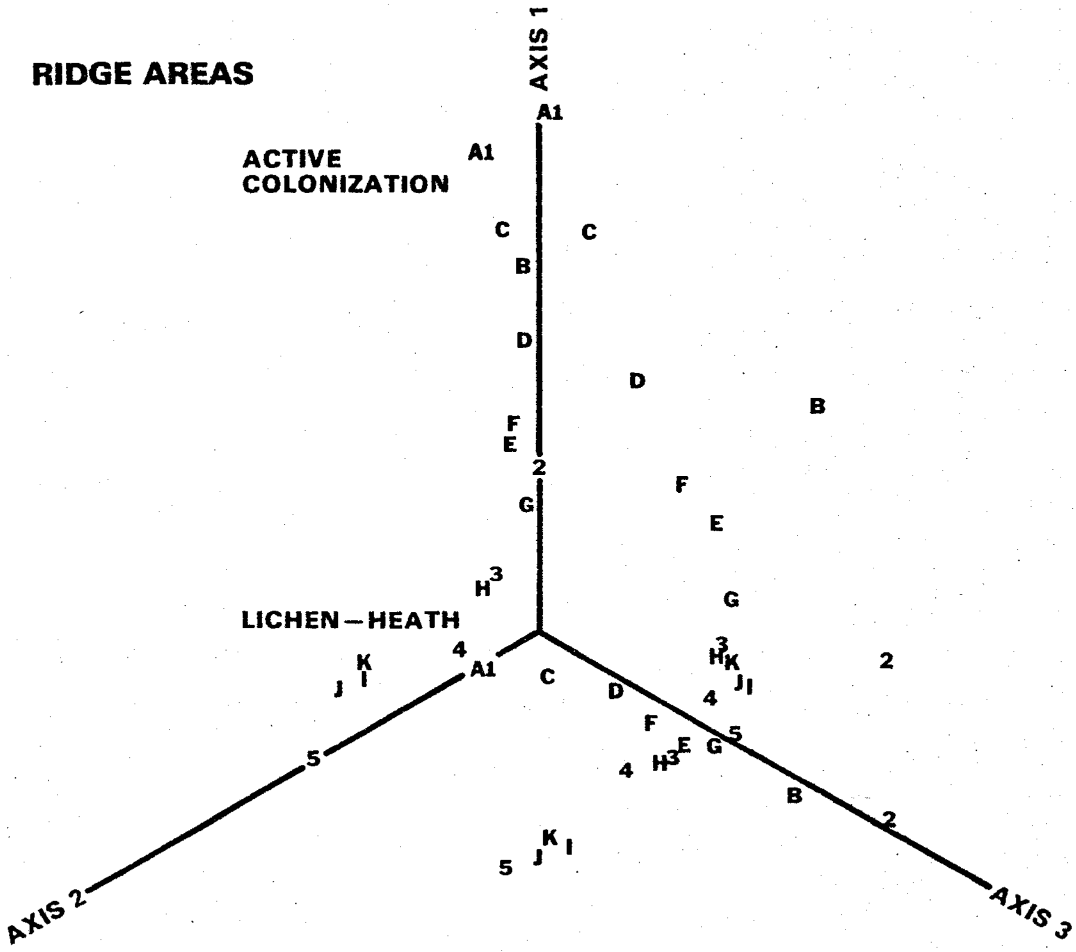
(3.1) The Development of Lichen-Heath

A. Vegetational Gradients

The nature of the change in vegetation along the area sample sequences was examined using ordination analysis. Principal components ordination objectively orders sample plots on the basis of the abundance of the species they contain. The graphical proximity of plots in the ordination diagram is based on their similarity in vegetation composition. The area plot ordination of the 15 sample areas (Figure 4) supports the subjective observation of a directional change in the vegetational composition from the site of active plant colonization (area A1) to the lichen-heath areas. The earlier areas of the sequence show a strong progression towards the origin of axis 1 while later lichen-heath areas show a divergent trend along axis 2. These

Figure 4.

Ridge sample areas ordination showing a marked directional change in vegetational composition along both the coastal sample sequence (areas A1 to K) and the inland sample sequence (areas A1 to 5) from the site of present active colonization to the lichen-heath areas.


RIDGE AREAS
AXIS 1
AXIS 2
AXIS 3
ACTIVE COLONIZATION
LICHEN—HEATH
A1
A1
A1
C
C
C
B
B
B
D
D
D
F
E
F
E
F
E
G
G
G
H
H
H
2
2
2
3
3
3
4
4
4
5
5
5
K
I
J
K
J
I
K
J
I

trends are indicative of both the continuous nature of the community change and the close correspondance of the coastal and inland vegetational sequences.

The area plot ordination is very efficient in extracting variance from the data set since 61% and 16% of the total variance are found along axes 1 and 2, respectively. Axis 3 extracts 9% of the total variance, however, no discernable trend in sample areas is correlated to this source of variance. Clearly the change in community composition along the sample sequences accounts for a large amount of the vegetational heterogeneity at the area plot level of integration.

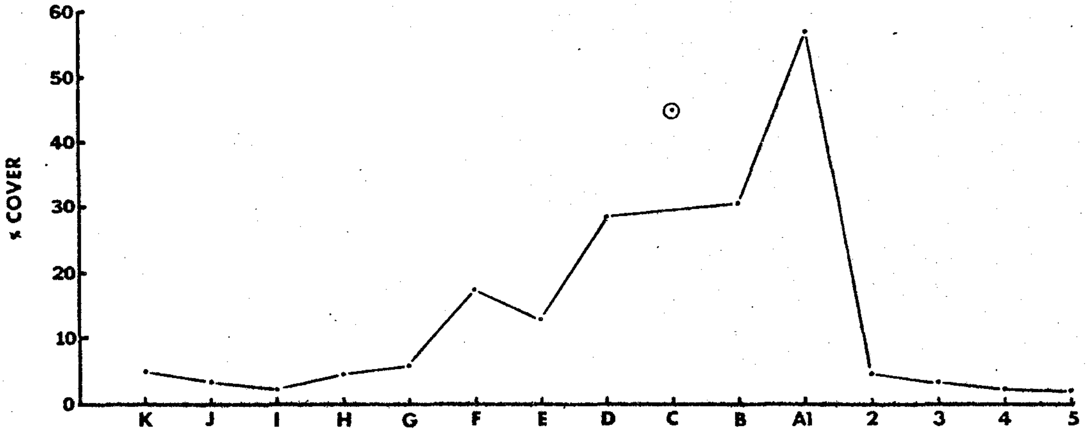
Graphical overlays of the abundance of eight dominant species and non-vegetated ground reveal trends (Table I, Appendix A) which follow either axis 1 or 2. These trends reflect the nature of each species' distribution along the sample sequences and give a general indication of species with similar distribution patterns. The ordination trends for non-vegetated ground, Elymus arenarius and Hedysarum mackenzii show decreasing abundances along axis 1. A marked decline in percentage cover of non-vegetated ground (Figure 5) is present on the coastal and inland sequences. Since major erosional features are largely absent from the sample areas, the decrease in non-vegetated cover (i.e. bare ground and litter) is indicative of the degree of colonization which has occurred since ridge deposition. The number of macrophytic plant species in each area (Figure 6) also demonstrates that active colonization is still occurring in the early areas of the coastal sequence where species number is low.

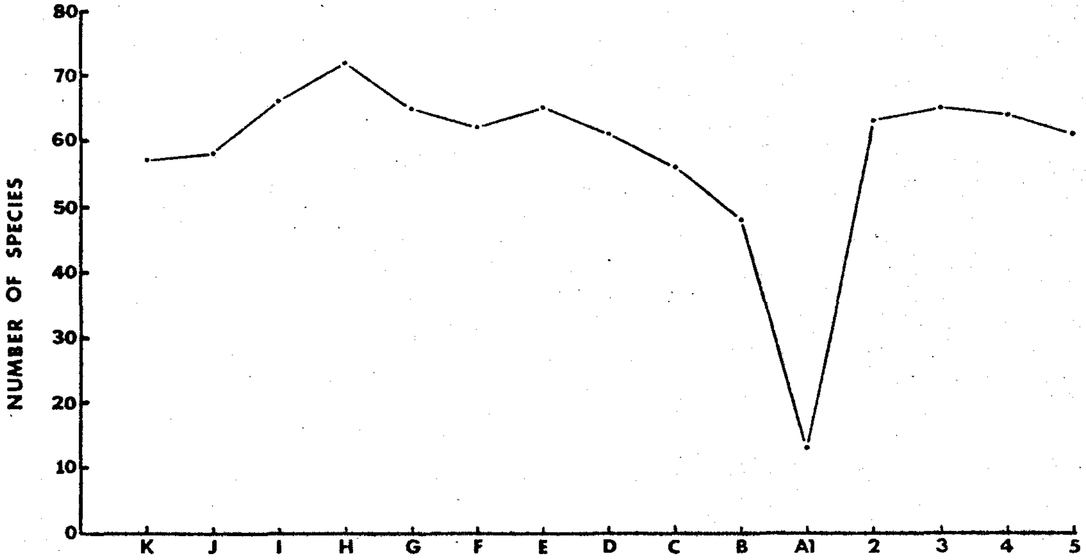
Figure 5.

Percentage cover of non-vegetated ground showing a marked decrease along the coastal and inland sample sequences. Area C has been omitted because of human disturbance.

Figure 6.

Number of macrophytic species in each sample area shows that active colonization is still occurring in the areas of the sample sequence nearest the creek mouth (area A1).


% COVER
60
50
40
30
20
10
0
⊙
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5


NUMBER OF SPECIES
80
70
60
50
40
30
20
10
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

The high percentage cover and performance of *Elymus* (Figure 7 a,b,c) show that it is an important early colonizer of newly-deposited beach ridges. However, the decline in cover and performance toward lichen-heath areas indicate that this species is intolerant of community development. Although also an early colonizer, *Hedysarum* demonstrates a much wider range of high percentage cover than *Elymus* but generally its abundance and performance also decrease along the developmental sequence (Figure 8 a,b). Two other abundant colonizing species, *Saxifraga tricuspidata* Rottb. and *Poa alpina* L. did not exhibit distinct abundance trends in the area ordination. However, the percentage cover of *Saxifraga* (Figure 9) and *Poa* (Figure 10) show their highest abundance in the areas of the vegetational sequence preceding the lichen-heath.

Cetraria islandica (agg.) (Figure 11) and *Cetraria nivalis* ✓ (Figure 12) are the earliest abundant lichens to appear in the vegetational sequence and both species show strong ordination trends along axis 1 (Table I, Appendix A). *C. islandica* is the single most abundant species in the vegetational sequence reaching optimal percentage cover in the youngest lichen-heath areas then declining in abundance in the older lichen-heath. *C. nivalis* also demonstrates a similar peak in abundance which occurs somewhat later in the lichen-heath development. Another important lichen, *Cetraria cucullata*, does not appear until the early lichen-heath (Figure 13) and maintains its highest percentage cover throughout the lichen-heath areas.

The abundance trend of *Salix reticulata* also lies along

Figure 7.

(a) Percentage cover of *Elymus arenarius* shows a marked decrease along the coastal and inland sample area sequences. Area C has been omitted because of human disturbance.

(b) Inflorescence height and (c) number of rachillae show declines in *Elymus* vigour which coincide with decreasing cover. Inflorescence sample sizes are approximately 100. Standard error of the mean given.

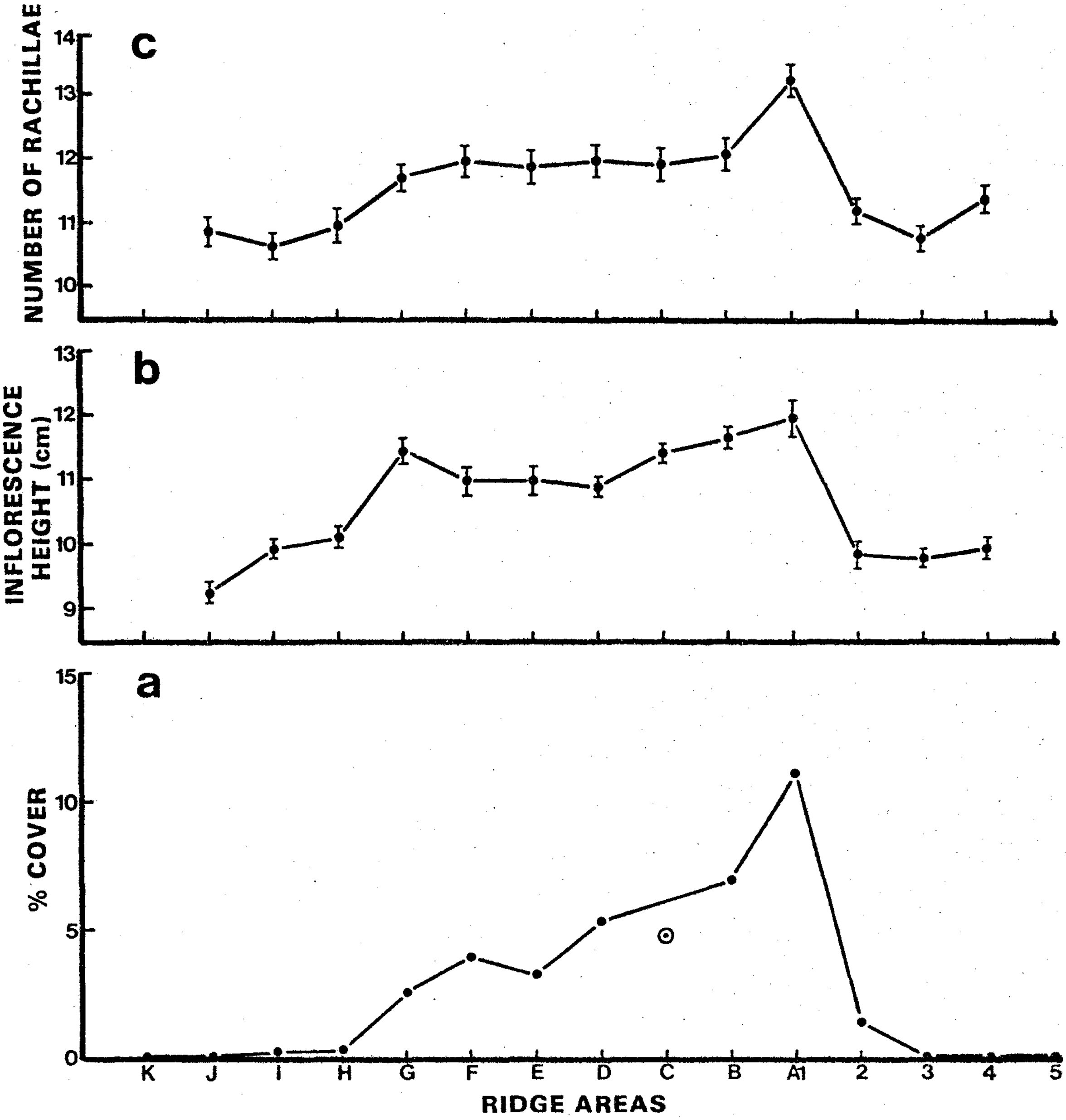

c
NUMBER OF RACHILLAE
14
13
12
11
10
b
INFLORESCENCE HEIGHT (cm)
13
12
11
10
9
a
% COVER
15
10
5
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5
RIDGE AREAS

Figure 8.

(a) Percentage cover of *Hedysarum mackenzii* shows the wide distribution of this species and a decline in its abundance in the lichen-heath along the coastal and inland sample sequences. (b) Leaf and terminal leaflet lengths show a change in *Hedysarum* performance which parallels the decrease in cover. Leaf sample sizes are greater than 50. Standard errors of the means are less than 1.66 and 0.63 for leaf and terminal leaflet lengths, respectively.

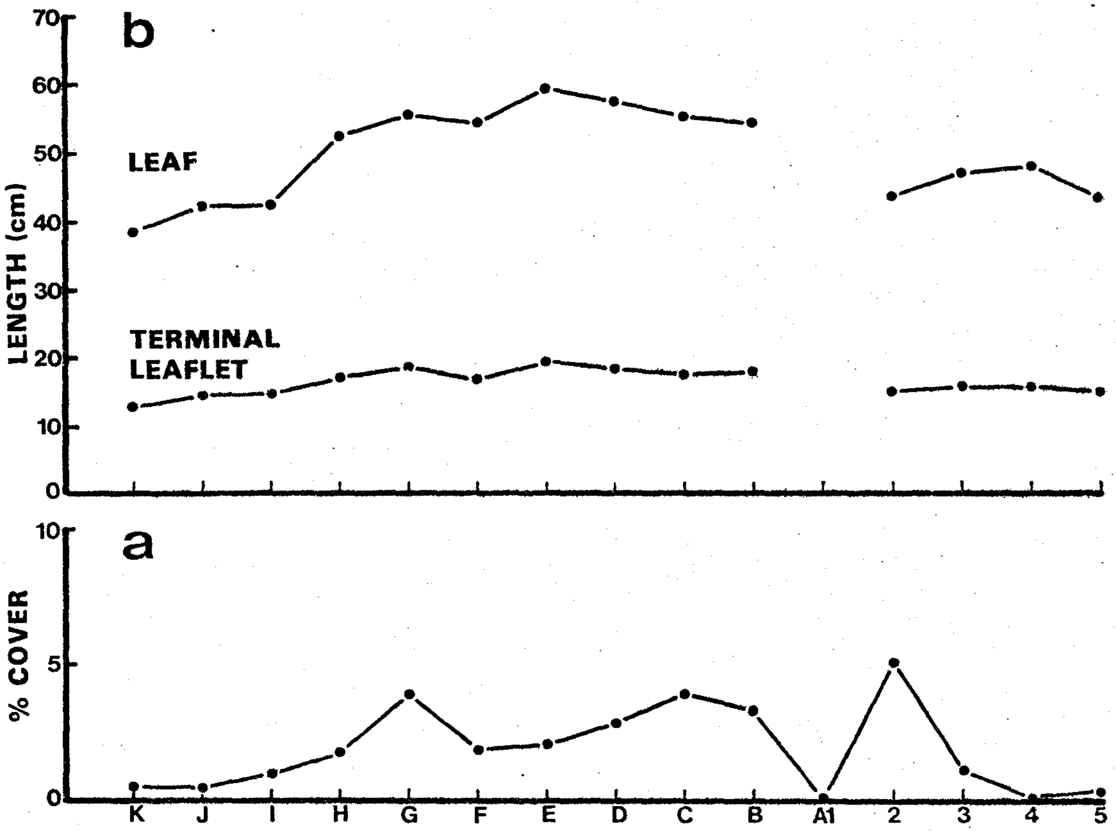
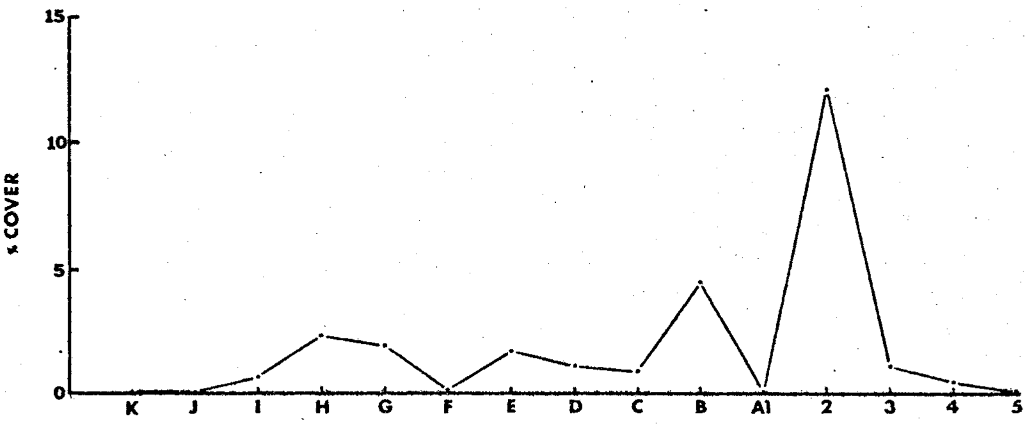

b
a
LENGTH (cm)
% COVER
LEAF
TERMINAL LEAFLET
0
10
20
30
40
50
60
70
0
5
10
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

Figure 9.

Percentage cover of Saxifraga tricuspidata shows highest abundance in early areas of colonization but is widely distributed along the coastal and inland sample sequences.

Figure 10.

Percentage cover of Poa alpina shows highest abundance in areas of the vegetational sequences preceding the lichen-heath.


% COVER
15
10
5
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

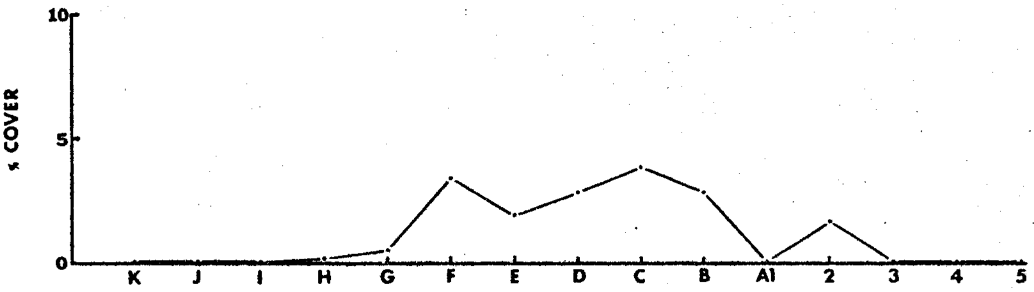
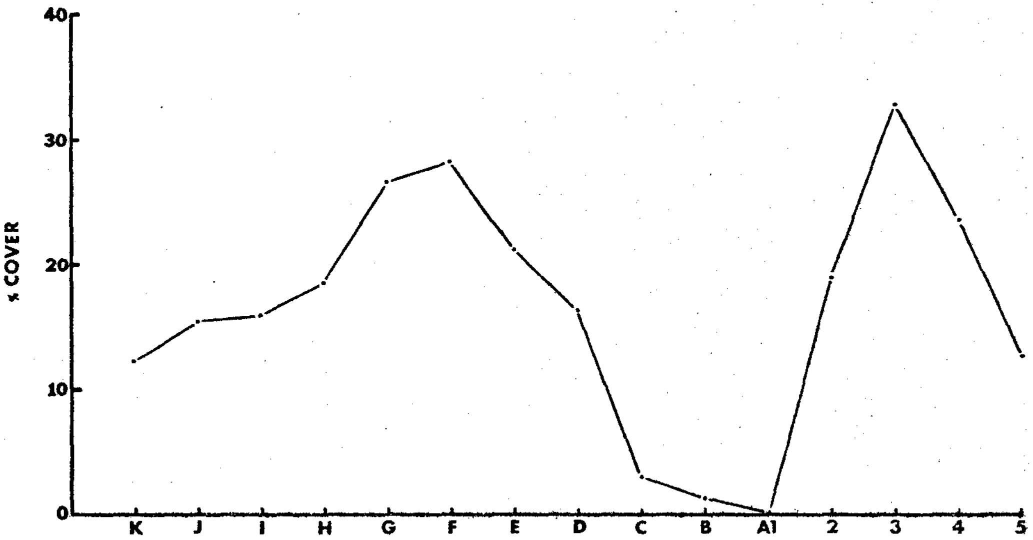

% COVER
10
5
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

Figure 11.

Percentage cover of _Cetraria islandica_ shows highest abundance in areas preceding the lichen-heath.

Figure 12.

Percentage cover of _Cetraria nivalis_ shows highest abundance in the early areas of the lichen-heath.


40
30
20
10
0
% COVER
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

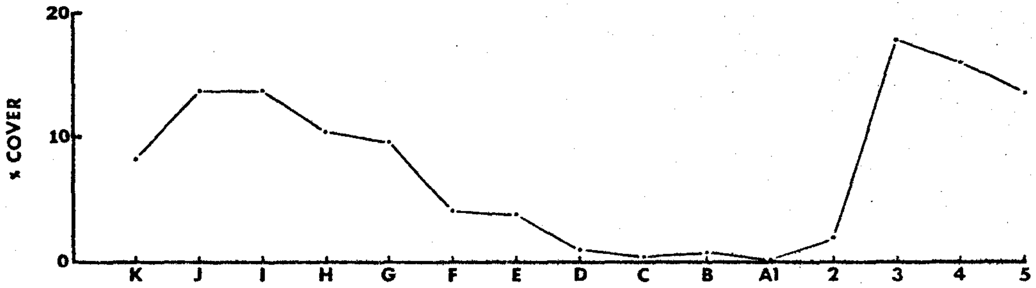
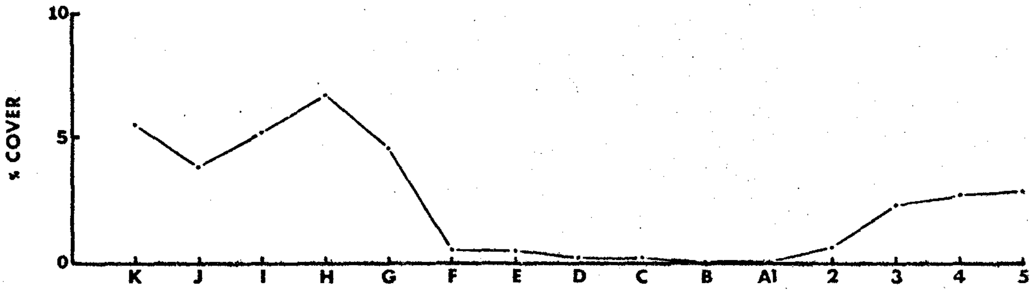

20
10
0
% COVER
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

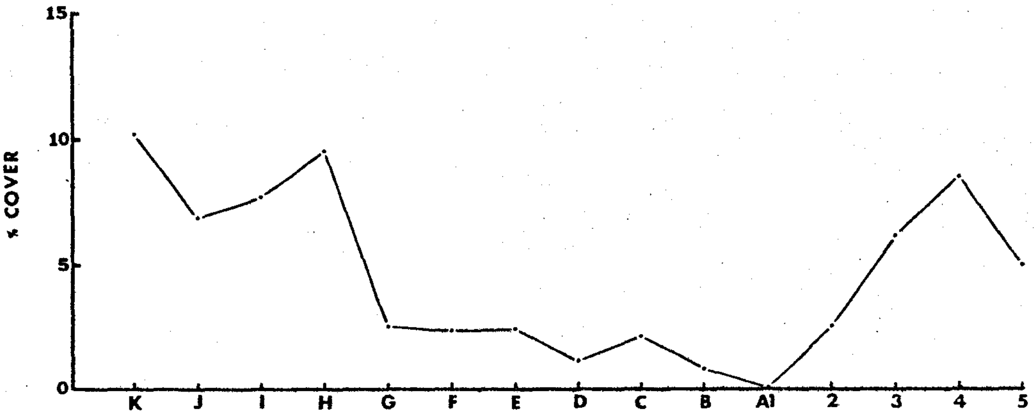
Figure 13.

Percentage cover of _Cetraria cucullata_ shows it does not become abundant in the coastal and inland sample sequences until the early lichen-heath.

Figure 14.

Percentage cover of _Salix reticulata_ shows its wide distribution along the coastal and inland sample sequences but highest abundance is present in the lichen-heath.


10
5
0
% COVER
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5


15
10
5
0
% COVER
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

axis 1 of the area ordination (Table I, Appendix A) and the percentage cover (Figure 14) demonstrates that the optimal abundance of this widely distributed species is in lichen-heath areas.

Three dominant lichen-heath species, *Cornicularia divergens* Ach. *Alectoria ochroleuca* and *Dryas integrifolia*, show strong ordination abundance trends along axis 2 (Table I, Appendix A). *Cornicularia* (Figure 15) and *Alectoria* (Figure 16) do not appear until the early lichen-heath and exhibit very similar patterns in percentage cover along the coastal and inland sequences. *Dryas* appears much earlier in the sequence but also increases to optimal percentage cover in the oldest lichen-heath (Figure 17a). Leaf performance (Figure 17b) shows that the vigour of this species is not necessarily correlated with cover.

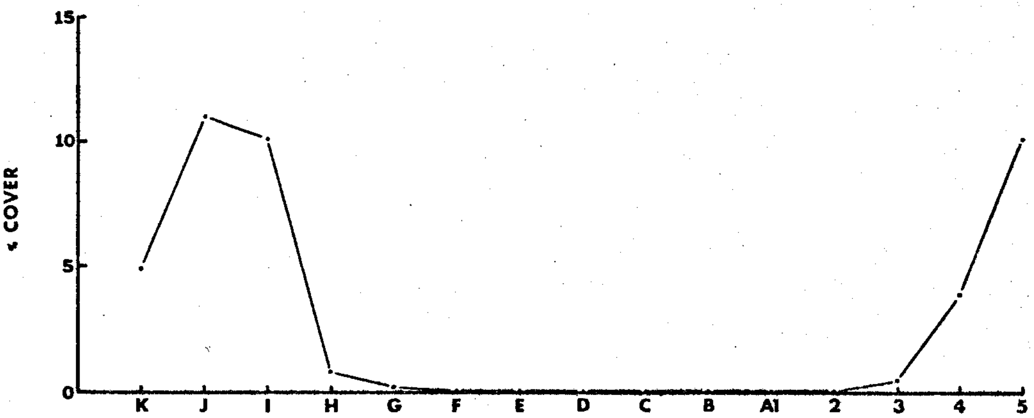
The phenological development of several widely distributed species was followed along the coastal and inland sequences for one summer. The dates and relative degrees of flowering for *Elymus arenarius* (Table I) and *Dryas integrifolia* (Table II) are presented. The start of flowering in *Elymus* was first evident in area A1, the site of highest abundance and performance. As the season progressed the degree of flowering, and later the degree of seed set, was greatest in areas of high cover and vigour, but decreased towards areas of low cover and vigour. The flowering and seed set of *Dryas*, however, did not follow a seasonal progression related to the area percentage cover, but rather, were most advanced in the areas of highest performance (cf. Figure 17b).

Figure 15.

Percentage cover of *Cornicularia divergens* shows highest abundance in the lichen-heath on the coastal and inland sample sequences.

Figure 16.

Percentage cover of *Alectoria ochroleuca* shows highest abundance in the lichen-heath on the coastal and inland sample sequences.


15
10
5
0
% COVER
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

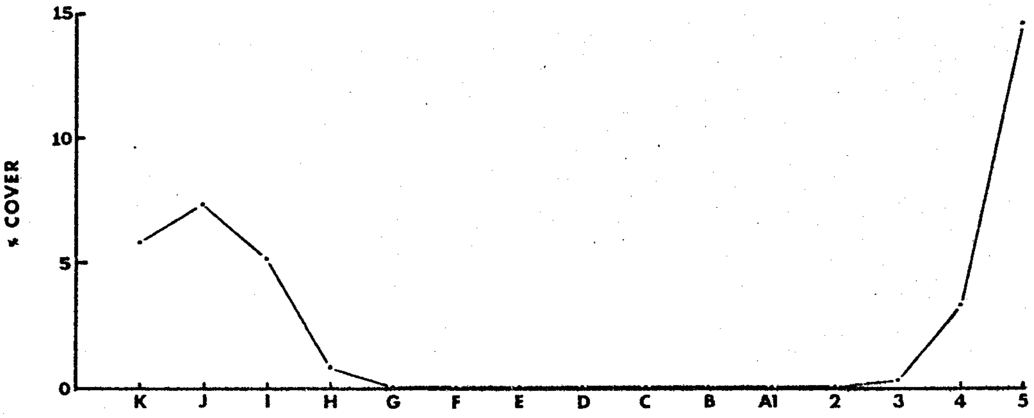

15
10
5
0
% COVER
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

Figure 17.

(a) Percentage cover of Dryas integrifolia shows an increase along the coastal and inland sample sequences to maximum abundance in the lichen-heath. (b) Leaf performance index of Dryas indicates that cover and vigour are not strongly correlated along the sample sequences. Leaf sample sizes are greater than 500. Standard errors of the means are less than 2.12.

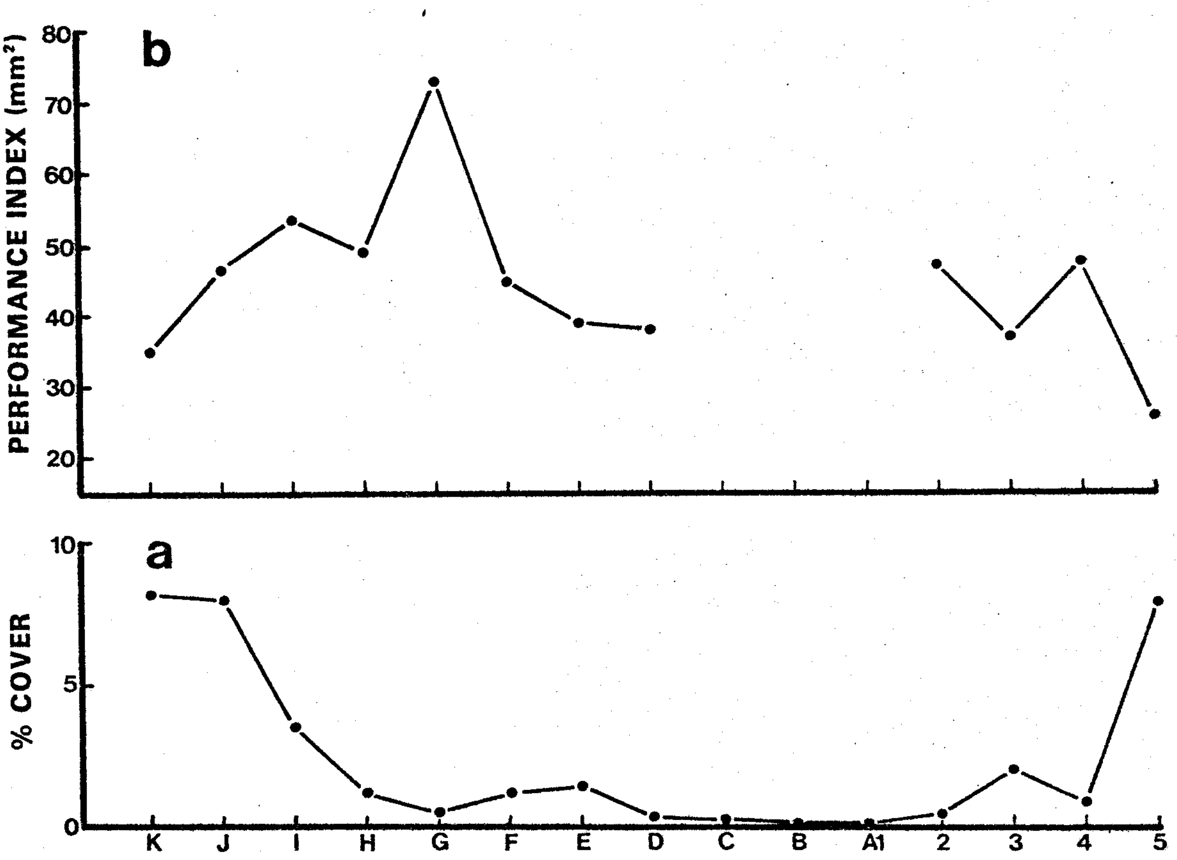

b
PERFORMANCE INDEX (mm²)
80
70
60
50
40
30
20
a
% COVER
10
5
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

Table I

Aspects of the phenological development of *Elymus arenarius* during the 1974 growing season. Subjective phenological stages: *, early flowering; **, mid-flowering; ***, late flowering; s, early seed set; ss, mid-seed set.

Sample Areas

Date	K	J	I	H	G	F	E	D	C	B	A1	2	3	4	5
July 1															
7											*				
15					*	*	*	*	*	*	**	*		*	
22			*	*	**	**	**	**	**	***	***	**	*	*	
30			**	***	***	***	***	***	***	***	s	s	***	***	
Aug 5			***	***	***	***	***	***	***	***	ss	s	***	***	
12			s	s	s	s	s	s	s	s	ss	s	s	s	

Table II

Aspects of the phenological development of *Dryas integrifolia* during the 1974 growing season. Subjective phenological stages: *, early flowering; **, mid-flowering; ***, late flowering; t, seed tassel appearance; s, early seed set.

Sample Areas

Date	K	J	I	H	G	F	E	D	C	B	A1	2	3	4	5
July 1	**	**	*	*	**	**	**	*				**	**	**	**
7	***	***	***	***	***	***	***	***				***	***	***	***
15	***	***	***	***	***	***	***	***				***	***	***	***
22	***	t	ts	t	t	ts	t	t				s	ts	s	ts
30	ts	ts	ts	ts	s	ts	ts	ts				s	ts	s	ts
Aug 5	ts	ts	ts	ts	s	s	ts	s				s	s	s	s
12	s	s	s	s	s	s	s	s				s	s	s	s

B. Environmental Gradients

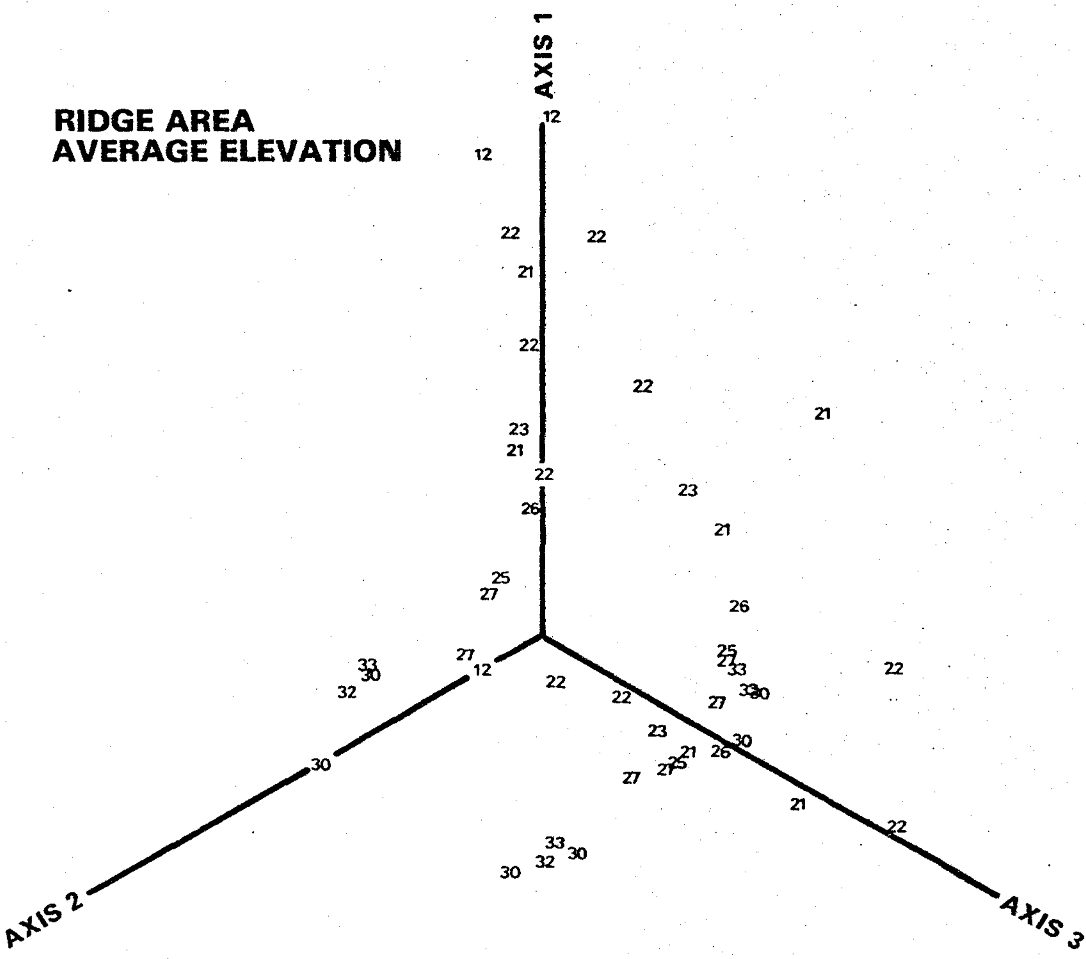
The ordination overlay of area average elevation (Figure 18) shows that there is a continuous increase in ridge elevation along the coastal and inland area sequences which coincides with the directional vegetational change. Since ridge morphology is relatively uniform, zone transect elevations also increase continuously along the area sequence (Figure 19). The presence of isostatic uplift in this region allows the ridges to be aged from the crest elevations. Using the formula of Webber *et al* (1970) the recent uplift rate was calculated to be 0.9 meters per 100 years which gives area A1 the age of 115 years while the lichen-heath areas K and 5 are approximately 350 years old. These age estimates are considered to be somewhat high since ridge growth due to isostatic uplift has been supplemented by depositional processes. However, the relative change in area age along both the coastal and inland sequences is about 235 years. This estimate agrees well with the age of the first lichen-heath plot determined by Larson and Kershaw (1974).

The ordination trend of area average peat thickness in the soil (Table I, Appendix A) exhibits a definite trend along axes 1 and 2 which parallels the trend for elevation. The area average peat thickness (Figure 20) shows an almost linear increase along the area sequences, however, the variability also increases substantially as a result of intraridge heterogeneity in peat development (see below, section 3.3).

The results of soil analyses in ten ridge areas show that major changes in some of the soil parameters occur along the

Figure 18.

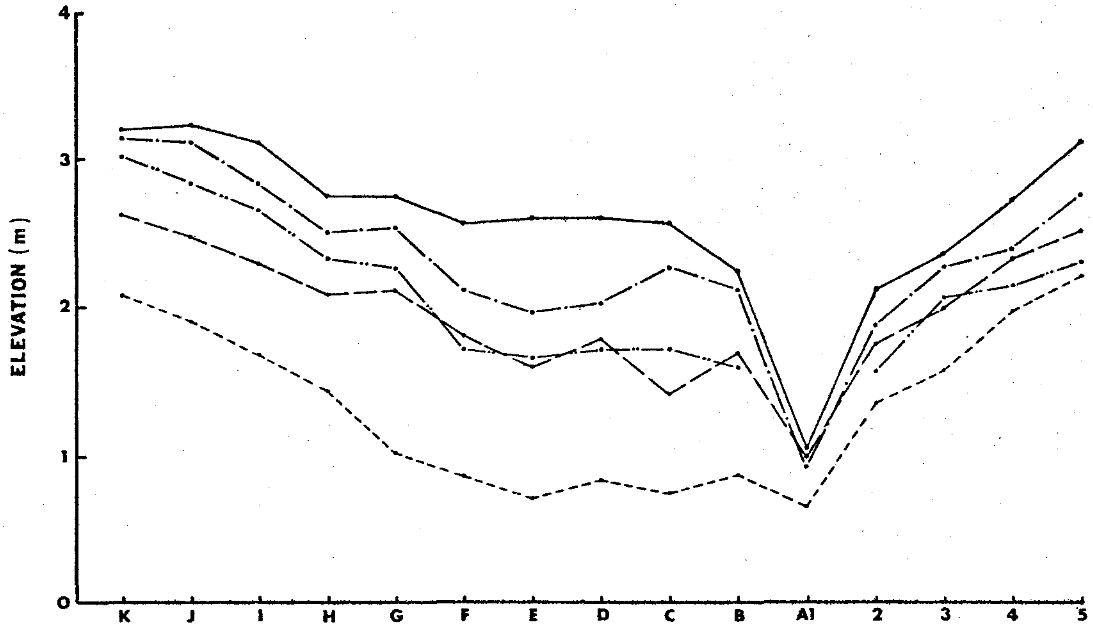
Ordination overlay of ridge area average elevations (dm) demonstrates continuous and similar increases in elevation along the coastal and inland sample sequences which coincide with axes 1 and 2.



RIDGE AREA
AVERAGE ELEVATION

Figure 19.

Zone transect elevations show general increases along the coastal and inland sample sequences from the site of active colonization and beach desposition to the lichen-heath. Zone transect elevation curves: •---• lower front; •— —• upper front; •——• crest; •—·—• upper back; •—··—• lower back.


ELEVATION (m)
0
1
2
3
4
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

area sequences and with depth in the soil while other parameters exhibit no trends. The area average results of particle-size analyses (Figure 21 a,b) reveal that the ridge soils are almost entirely sands and gravels of somewhat variable composition. The gravel fraction declines along the area sequences, however, no other trends in composition are apparent either along the sequences or in the soil profile. The silt-clay fraction is less than 5.0% of any soil sample and often was negligible.

The percentage of oxidizable organic matter in the soil (Figure 22) shows a distinct increase along the area sequence which generally coincides with the increasing peat thickness (cf. Figure 20). In the soil profile organic matter comprises a relatively large part of the peat layer but falls to very low values in the mineral layer. No trends in soil pH (Table III) are evident along the area sequences but in almost every sample the soil is less acidic with depth. The exchangeable concentrations of phosphorus (Figure 23), potassium (Figure 24) and magnesium (Figure 25) show a general decline along the area sequences and a marked decrease in the soil profile from the peat layer to the mineral soil layers. Exchangeable calcium concentrations (Figure 26) exhibit much more variability along the sequences but are generally highest in the peat layer. The variability in calcium is probably the result of the locally abundant deposits of shells apparent on the ridges. Nitrate concentrations (Figure 27) also show a great deal of variability in the peat layer but maintain very low, relatively uniform values in the mineral soil layers. The large amount

Figure 20.

Area average peat layer thickness shows an almost linear increase along the coastal and inland sample sequences. Sample sizes are 300. Standard error of the mean given. Area C has been omitted because of human disturbance.

Figure 22.

Area average percentage organic matter in the peat layer shows increases along the coastal and inland sample sequences which parallel increasing peat thickness. Area average percentage organic matter in the mineral soil layers remains uniformly low along the sample sequences. Sample sizes 5. Standard error of the mean given for the peat layer values. Soil layers: •——• peat layer; •— —• top 10 cm of mineral soil; •- - -• below 15 cm of mineral soil.

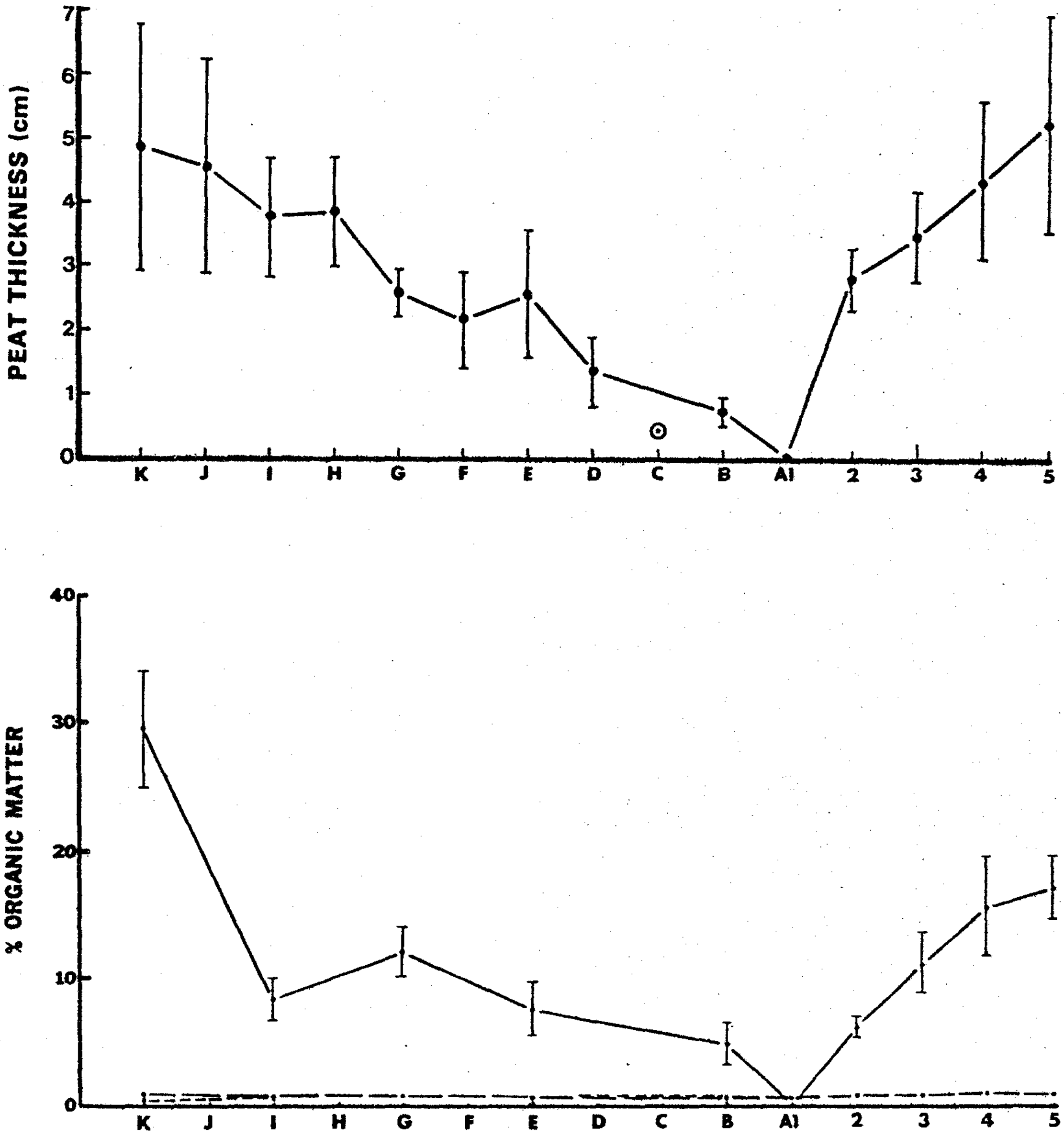

PEAT THICKNESS (cm)
7
6
5
4
3
2
1
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5
% ORGANIC MATTER
40
30
20
10
0
K
J
I
H
G
F
E
D
C
B
A1
2
3
4
5

Figure 21.

Area average percentage particle size composition (by weight) of (a) the top 10 cm in the mineral soil (b) below 15 cm in the mineral soil, along the coastal and inland sample sequences. Particle size classes: ■ silt-clay; □ fine sand; ▨ coarse sand; ▧ gravel.

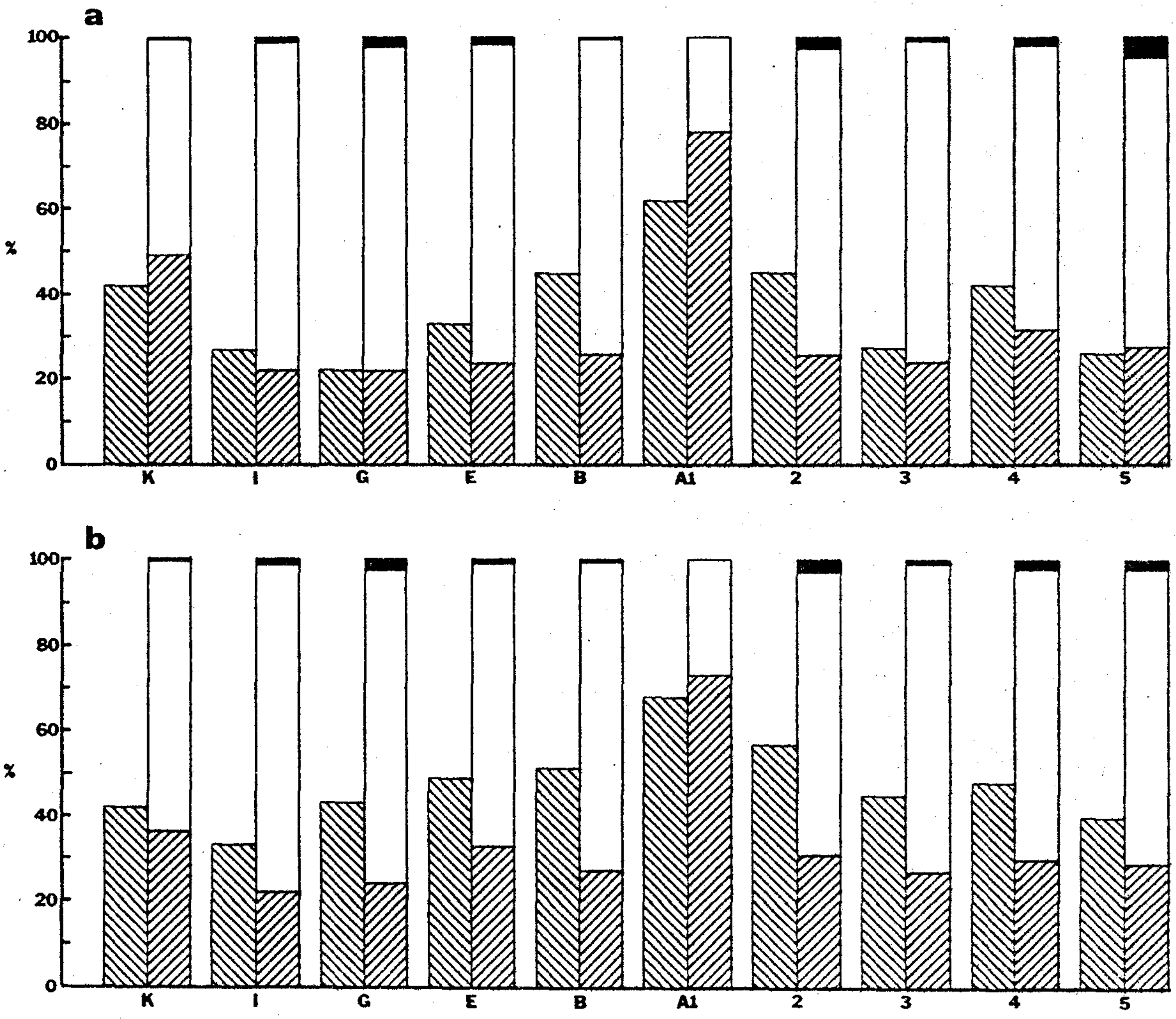

a
100
80
60
40
20
0
%
K
I
G
E
B
A1
2
3
4
5
b
100
80
60
40
20
0
%
K
I
G
E
B
A1
2
3
4
5

Table III

Area average soil pH in 10 sample areas of the coastal sequence (areas A1 to K) and inland sequence (areas A1 to 5). Soil layer abbreviations: O, peat layer; M_1, upper 10 cm of mineral soil; M_2, below 15 cm in mineral soil.

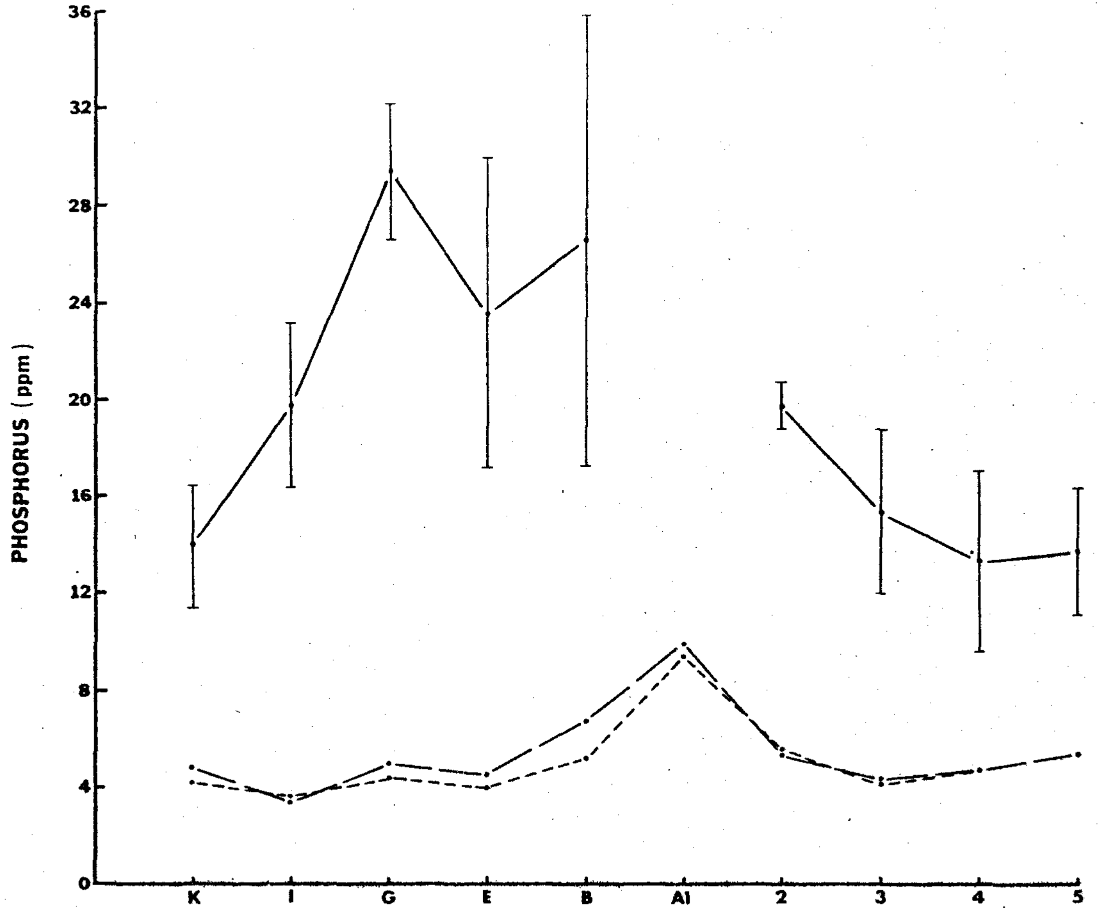
	Sample Area									
Soil Layer	K	I	G	E	B	A1	2	3	4	5
O	7.0	6.9	6.6	6.9	6.8	-	6.6	6.8	6.7	6.9
M_1	7.3	7.6	7.5	7.6	7.5	7.7	7.5	7.6	7.5	7.7
M_2	7.6	7.7	7.7	7.7	7.5	7.7	7.6	7.8	7.6	7.6

Figure 23.

Available soil phosphorus concentrations along the coastal and inland sample sequences are much higher in the peat layer than in the mineral soil layers. Sample sizes are 5. Standard error of the mean given for the peat layer. Soil layers: •——• peat layer, •— —• upper mineral layer, •- - -• lower mineral layer.

Figure 24.

Available soil potassium concentrations along the coastal and inland sample sequences are much higher in the peat layer than in the mineral soil layers. Sample sizes are 5. Standard error of the mean given for the peat layer. Soil layers: •——• peat layer, •— —• upper mineral layer, •- - -• lower mineral layer.


PHOSPHORUS (ppm)
0
4
8
12
16
20
24
28
32
36
K
I
G
E
B
A1
2
3
4
5

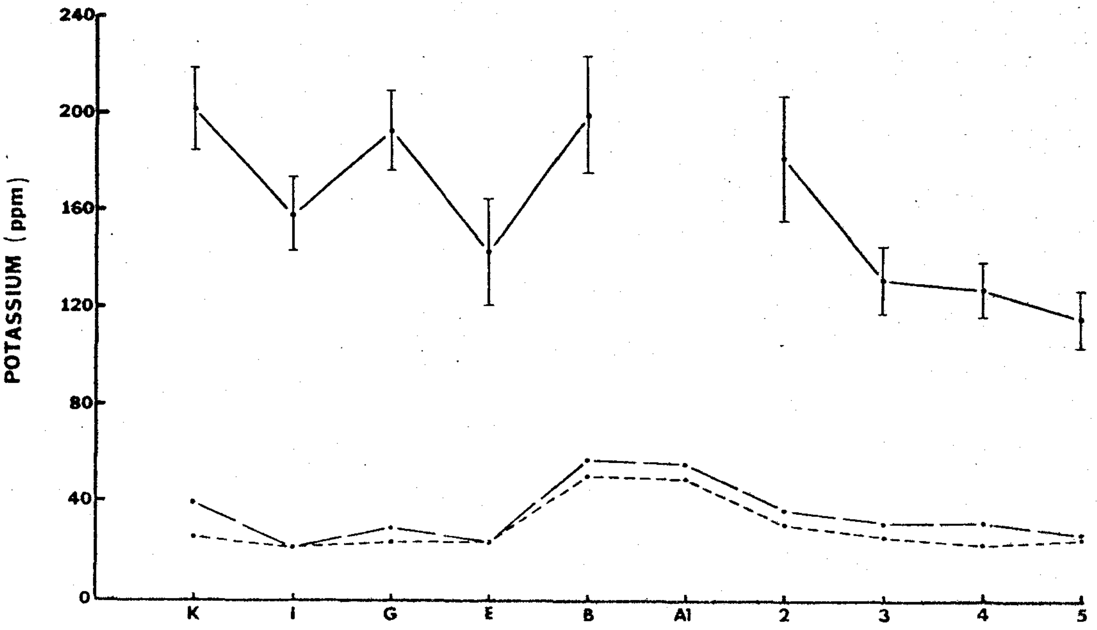

POTASSIUM (ppm)
0
40
80
120
160
200
240
K
I
G
E
B
A1
2
3
4
5

Figure 25.

Available soil magnesium concentrations along the coastal and inland sample sequences are much higher in the peat layer than in the mineral soil layers. Sample sizes are 5. Standard error of the mean given for the peat layer. Soil layers: •——• peat layer, •— —• upper mineral layer, •- - -• lower mineral layer.

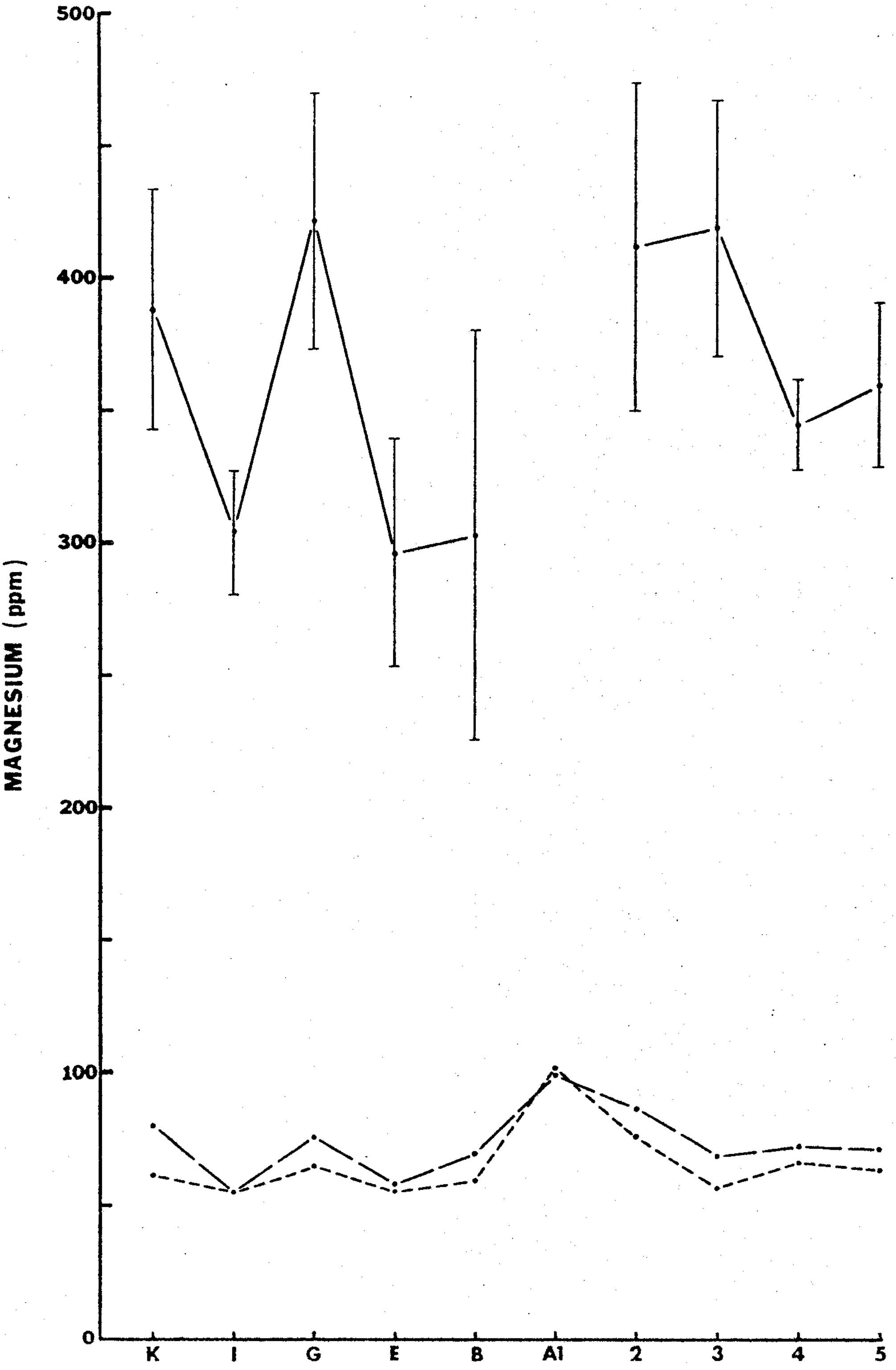
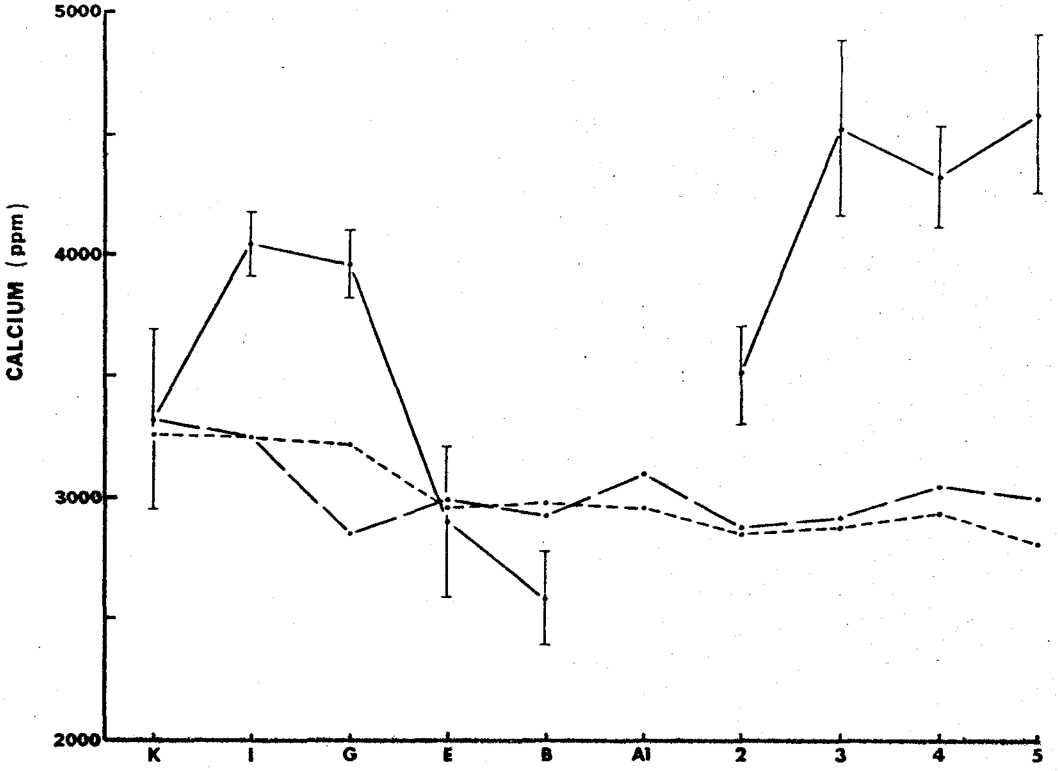

MAGNESIUM (ppm)
500
400
300
200
100
0
K
I
G
E
B
A1
2
3
4
5

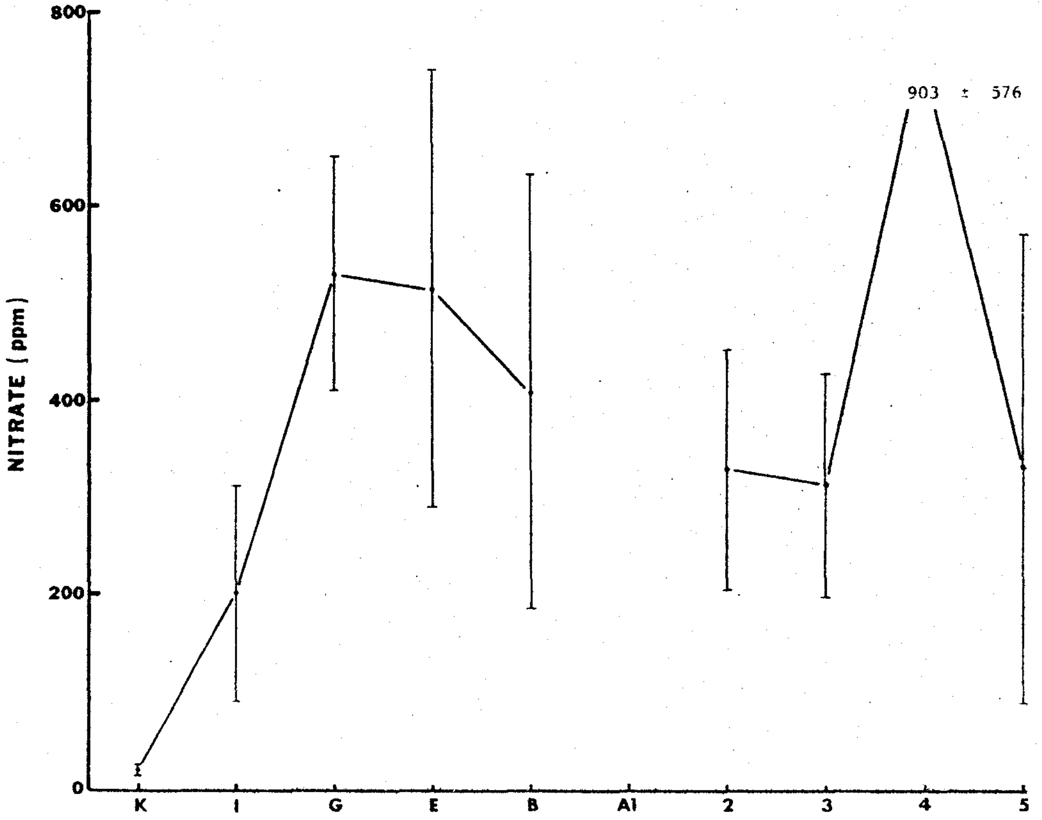
Figure 26.

Available soil calcium concentrations along the coastal and inland sample sequences are quite variable but generally are highest in the peat layer. Sample sizes are 5. Standard error of the mean given. Soil layers: •——• peat layer, •— —• upper mineral layer, •---• lower mineral layer.

Figure 27.

Peat layer available soil nitrate concentrations along the coastal and inland sample sequences are much higher and more variable than concentrations in the mineral soil layers which are all less than 10 ppm. Sample sizes are 5. Standard error of the mean given.


CALCIUM (ppm)
5000
4000
3000
2000
K
I
G
E
B
A1
2
3
4
5


NITRATE (ppm)
800
600
400
200
0
903 ± 576
K
I
G
E
B
A1
2
3
4
5

of variability and the small sample size for nitrate (i.e. only 5 per area) may be obscuring the identification of trends along the area sequences.

The area ordination results and species' distributions along the coastal and inland area sequences confirm the visual impression of a vegetational development toward the general lichen-heath community. This developmental sequence lacks major discontinuities and is repeated on areas of similar elevation and age. A corresponding soil developmental sequence is present which demonstrates marked increases in soil peat thickness and organic matter.

(3.2) Community Composition over the Ridge Profile

A. Vegetational Gradients

A considerable degree of vegetational heterogeneity is visually evident over the ridge profile within any sample area. The nature of the intraridge community composition and its relationship to the largescale developmental sequence was examined by ordination of ridge zone transects. A directional change in plot vegetational composition towards lichen-heath is shown in the ordination of zone transects (Figure 1a, Appendix A). The ordination diagram demonstrates the same progression of younger sites along axis 1 as the area ordination (Figure 4), however the lichen-heath zone transects diverge along axis 3 rather than axis 2. The zone transect ordination is less efficient than the area ordination, extracting only 37% of the total variance on axis 1 while 15% and 11% are extracted by axes

2 and 3, respectively.

When the zone transect ordination is dissected into individual zone patterns, the upper front, crest and upper back zones (Figure 1c,d,e, Appendix A) reveal trends along axes 1 and 3 which are consistent with the pattern of the whole vegetational sequence. However, the lower front zone pattern (Figure 1b, Appendix A) exhibits only a weak trend on axis 1 and no trends are apparent in the ordination pattern of the lower back zones (Figure 1f, Appendix A). Abundance trends in the zone transect ordination of non-vegetated ground and eight dominant species (Table I, Appendix A) are very similar to those of the area ordination, although in this case *Hedysarum mackenzii* and *Salix reticulata* exhibit no definite patterns.

The zone transect percentage cover for non-vegetated ground and eighteen abundant species is presented to show the influence of ridge profile distribution on community composition. In addition to those species presented in the lichen-heath developmental sequence (section 3.1, above), the distributions of a number of locally important species are described. Cover (i.e. the area) of non-vegetated ground (Figure 28) shows a good deal of variability over the ridge profile in the younger areas. However, in lichen-heath areas the greatest non-vegetated cover is found on the upper slope and crest zones. *Elymus arenarius* and *Tortula ruralis* are the earliest abundant species in the developmental sequence (Figure 29). The highest *Elymus* cover is found on the lower front zone and crest in many areas of the coastal sequence but is almost entirely absent

Figure 28.

Percentage cover of non-vegetated ground over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Although quite variable in the younger sample areas, non-vegetated ground has highest cover on the lower front and crest zones in many areas. Area C upper front zone has been disturbed. Zone transect abbreviations: LF, lower front; UF, upper front; CR, crest; UB, upper back; LB, lower back. No lower back ridge zone was defined in area A1.

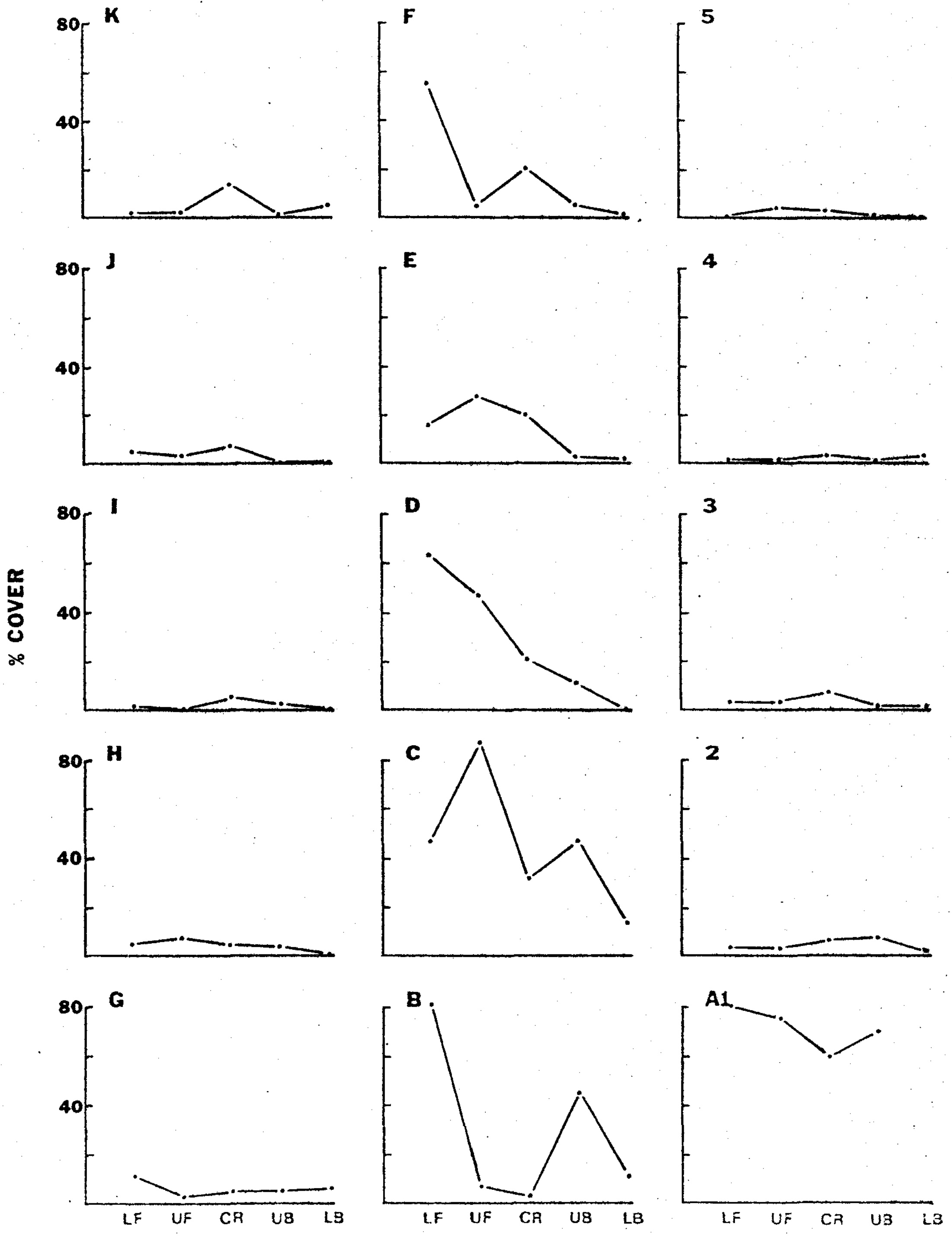
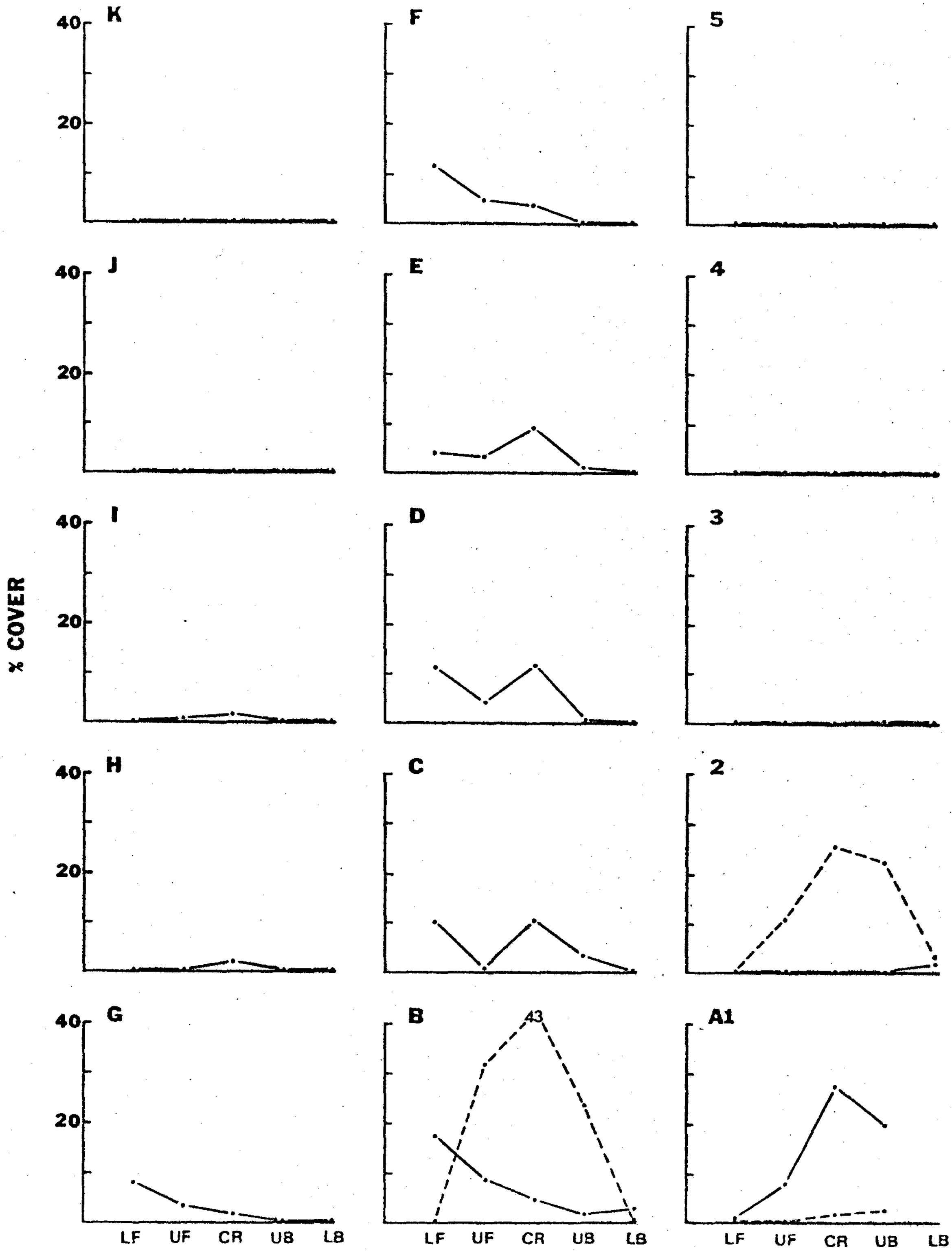

% COVER
80
40
K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
LF
UF
CR
UB
LB

Figure 29.

Percentage cover of *Elymus arenarius* (solid line) and *Tortula ruralis* (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). *Elymus* is widely distributed and exhibits a front slope preference in most areas while *Tortula* is locally abundant near the creek mouth on upper slope ridge zones. Area C upper front zone has been disturbed. Abbreviations as in Figure 28.


K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
43
% COVER
40
20
LF
UF
CR
UB
LB

from the ridge profile on the inland sequence. *Tortula* first appears on the backslope of area A1 where it is often hidden beneath *Elymus* litter. This moss reaches very high percentage cover in the upper slope zones of nearby areas B and 2 but is absent from any other ridge sample areas.

Although *Hedysarum mackenzii* and *Saxifraga tricuspidata* have similar abundance trends along the developmental sequence their ridge profile distributions (Figure 30) show different ridge zone preferences. The percentage cover of *Hedysarum* is somewhat variable but a shift of highest zone cover from backslope to crest and foreslope is apparent along the developmental sequence. *Saxifraga*, however, shows a consistent, optimal cover on the upper front and crest zones in all areas.

Two graminoid species, *Poa alpina* and *Festuca brachyphylla* Schult. also become established early in the developmental sequence (Figure 31) *Festuca* reaches its highest cover on the crest of later areas of the developmental sequence. *Poa* is more variable in ridge profile distribution than *Festuca* but prefers the ridge foreslope. This species is one of the first colonizers of the disturbed upper front zone of area C.

Salix callicarpea and *Salix cordifolia* Pursh. both appear early and exhibit wide distributions along the developmental sequence (Figure 32). *S*. callicarpea demonstrates a shift in ridge profile distribution from the lower back zone in early areas to the upper front zone in lichen-heath, although it is virtually absent from the inland sequence. In contrast, *S. cordifolia* is quite variable in ridge profile distribtuion but is present

Figure 30.

Percentage cover of *Hedysarum mackenzii* (solid line) and *Saxifraga tricuspidata* (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). These species are quite abundant in the early developmental sequence and exhibit upper slope distributions over the ridge profile. Area C upper front zone has been disturbed. Abbreviations as in Figure 28.

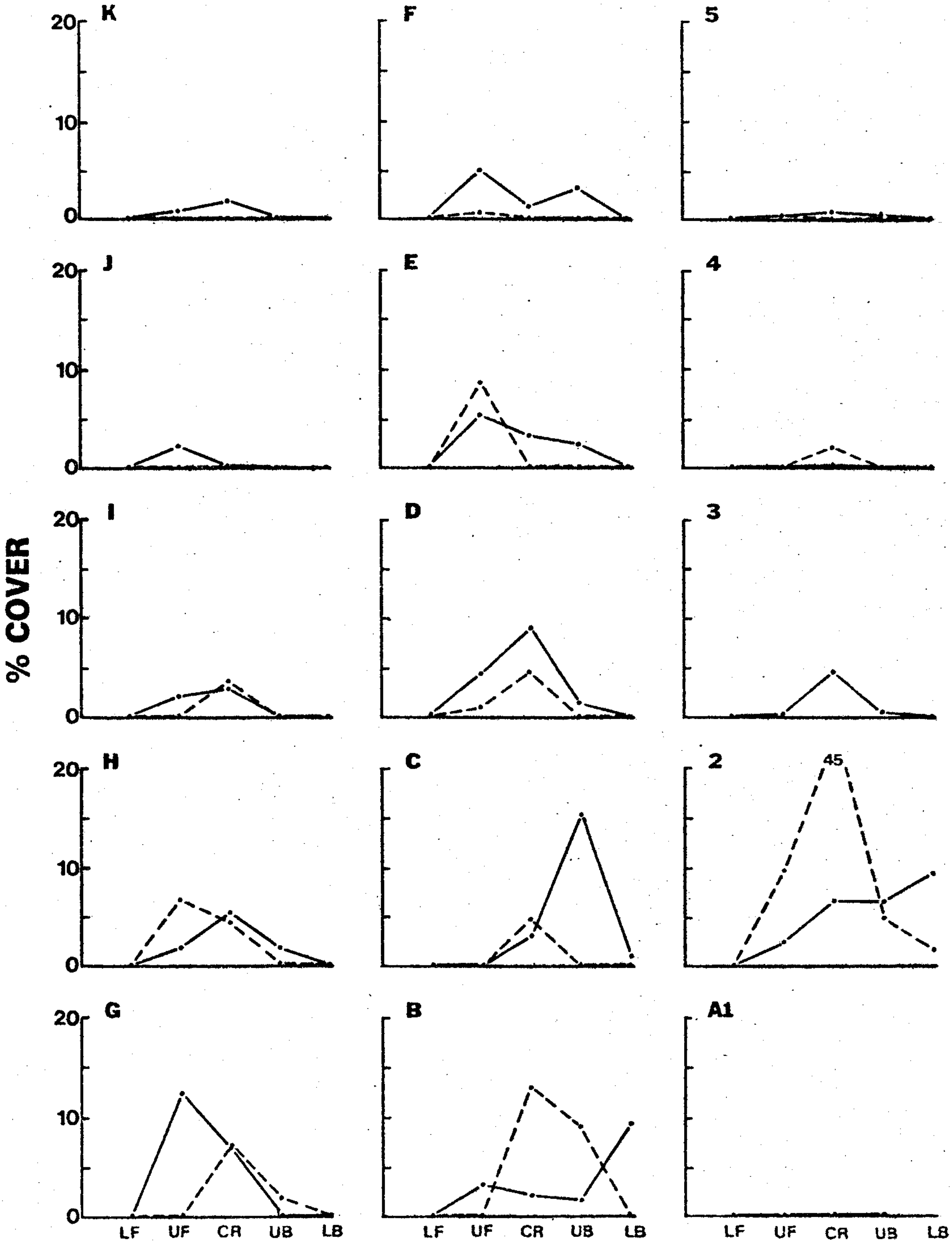

% COVER
K
F
5
J
E
4
I
D
3
H
C
2
45
G
B
A1
20
10
0
LF
UF
CR
UB
LB

Figure 31.

Percentage cover of _Poa alpina_ (solid line) and _Festuca brachyphylla_ (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). _Festuca_ shows a consistent upper slope preference over the ridge profile while _Poa_ is more variable and is most abundant on the front slope. Area C upper front zone has been disturbed. Abbreviations as in Figure 28.

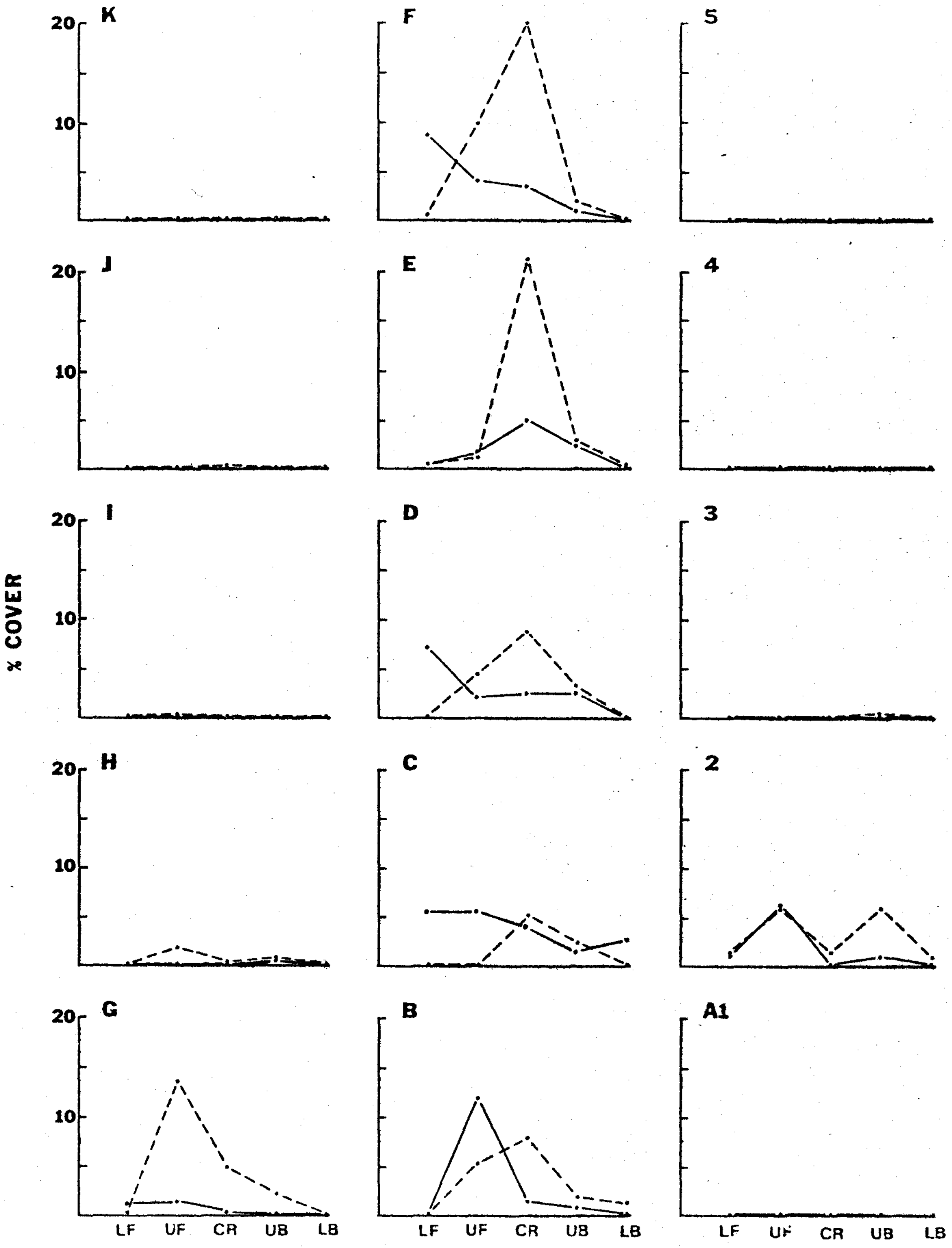
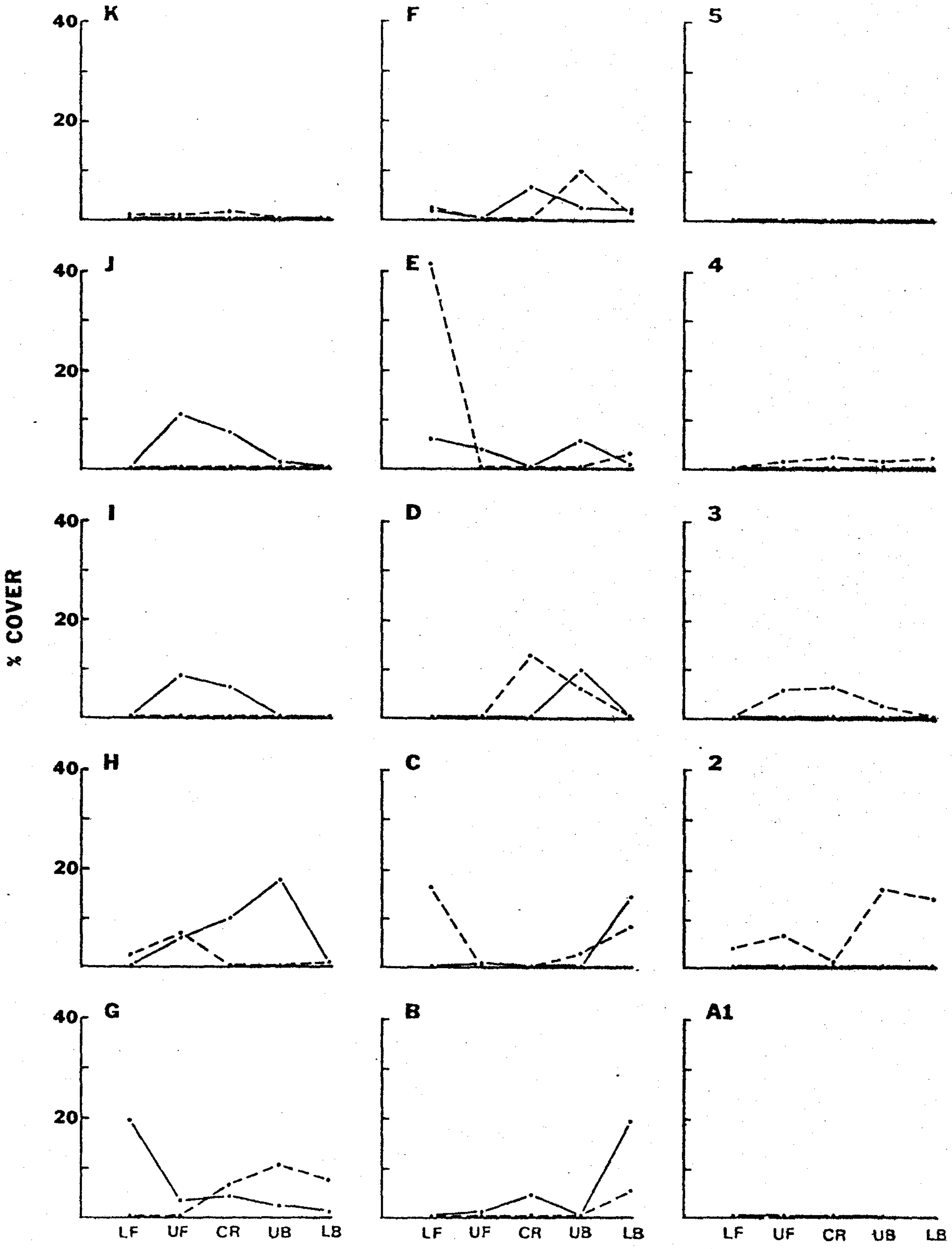

% COVER
K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
20
10
LF
UF
CR
UB
LB

Figure 32.

Percentage cover of *Salix callicarpea* (solid line) and *Salix cordifolia* (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Area C upper front zone has been disturbed. Abbreviations as in Figure 28.


K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
% COVER
40
20
LF
UF
CR
UB
LB

on both the coastal and inland sequences.

The abundances of *Cetraria islandica* and *Cetraria nivalis* over the ridge profile both demonstrate a shift of highest cover from backslope to foreslope along the developmental sequence (Figure 33). In many ridge areas, also, both species show a distinct bimodal peak in abundance. The appearances of *Cornicularia divergens* and *Alectoria ochroleuca* in the early lichen-heath coincide exactly (Figure 34). However, the percentage cover of *A. ochroleuca* is generally greatest on the crest while *C. divergens* is consistently most abundant on the upper back ridge zone.

Cetraria cucullata and *Dryas integrifolia* are abundant species on the crest zone of the lichen-heath (Figure 35). *Dryas* appears early in the developmental sequence on the lower back zone of areas C and 2 but shows a shift in highest cover to the crest. *C. cucullata* appears somewhat later and maintains a consistent crest and upper slope preference.

The species discussed thusfar have demonstrated their highest cover predominantly on upper slope sites, however a number of other species have their optimal abundance on lower ridge zones. *Salix reticulata* and *Aulacomnium palustre* Schwaegr. are very wide ranging species which reach high percentage cover on the lower front zones in the lichen-heath (Figure 36). *S. reticulata* is generally more abundant than *Aulacomnium* especially on upper front and lower back zones. *Equisetum variegatum* and *Vaccinium uliginosum* also have ridge profile distributions similar to the two previous species (Figure 37) but usually show highest

Figure 33.

Percentage cover of *Cetraria islandica* (solid line) and *Cetraria nivalis* (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Both species exhibit a bimodal peak in abundance in many areas and a shift from backslope to foreslope along the developmental sequence. Area C upper front zone has been disturbed. Abbreviations as in Figure 28.

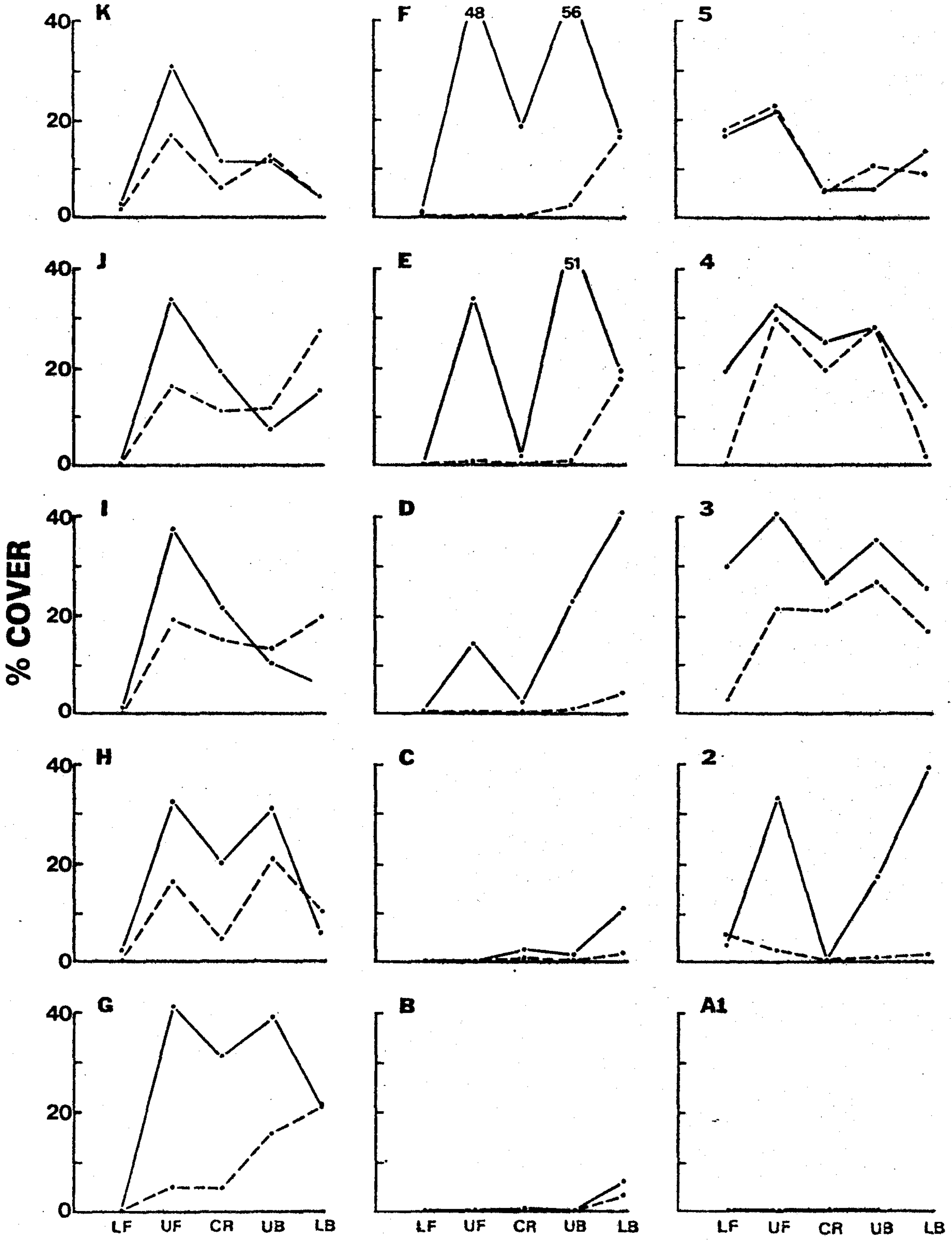

K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
48
56
51
% COVER
40
20
0
LF
UF
CR
UB
LB

Figure 34.

Percentage cover of *Cornicularia divergens* (solid line) and *Alectoria ochroleuca* (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). These species are most abundant on the backslope of lichen-heath areas. Abbreviations as in Figure 28.

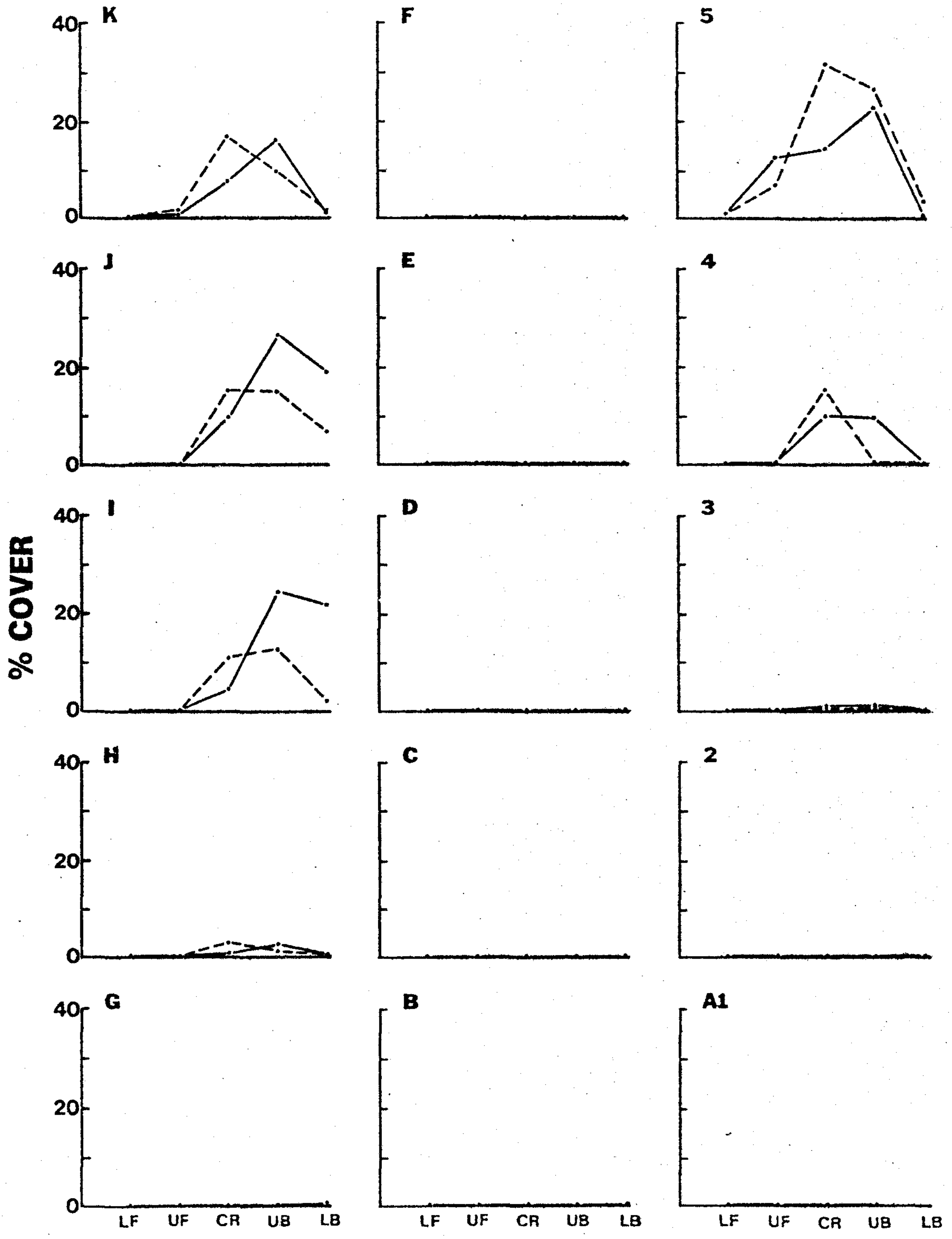
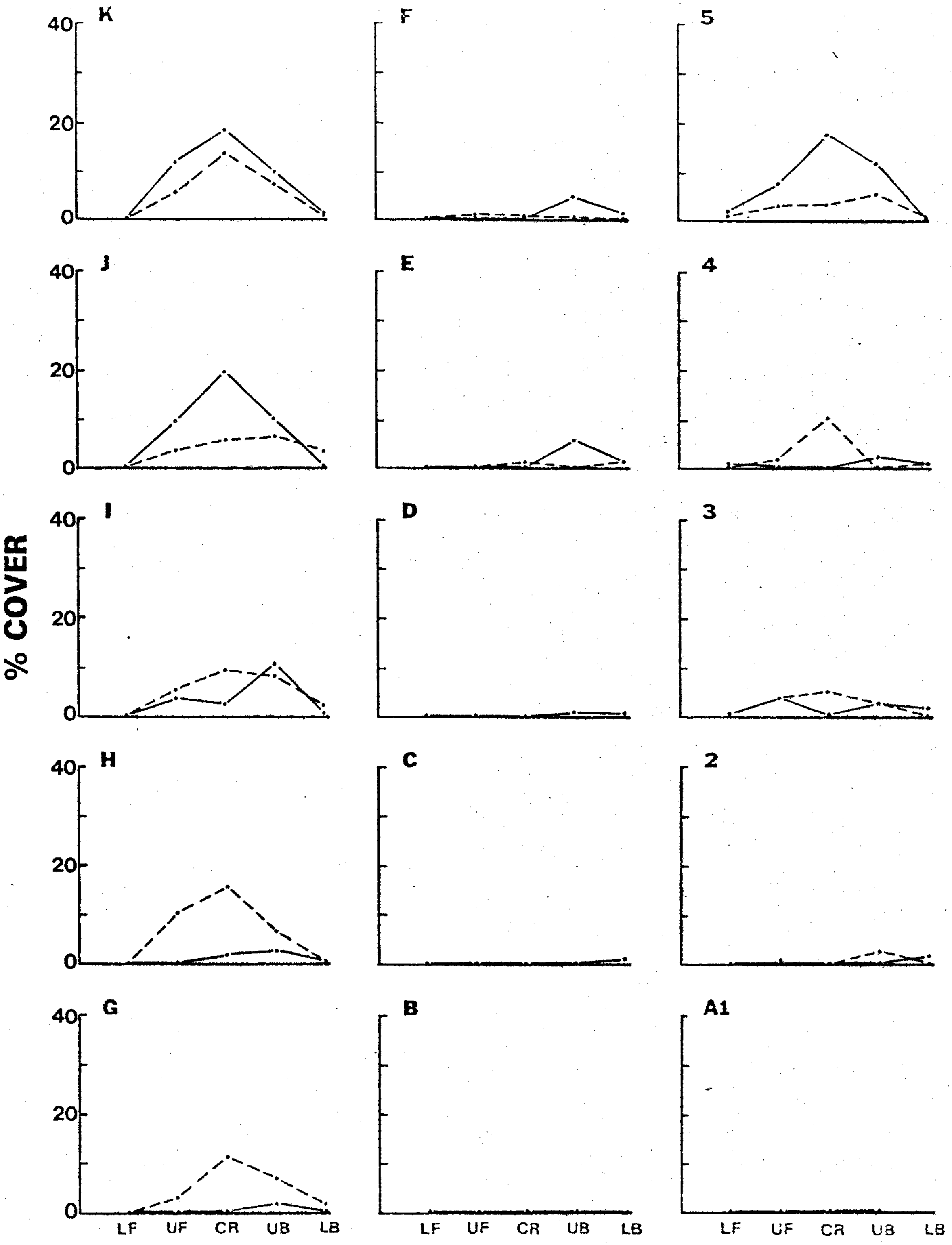

% COVER
K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
40
20
0
LF
UF
CR
UB
LB

Figure 35.

Percentage cover of <u>Dryas</u> <u>integrifolia</u> (solid line) and <u>Cetraria</u> <u>cucullata</u> (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Both species are most abundant on the upper slope of lichen-heath areas. Abbreviations as in Figure 28.


K
F
5
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E
4
I
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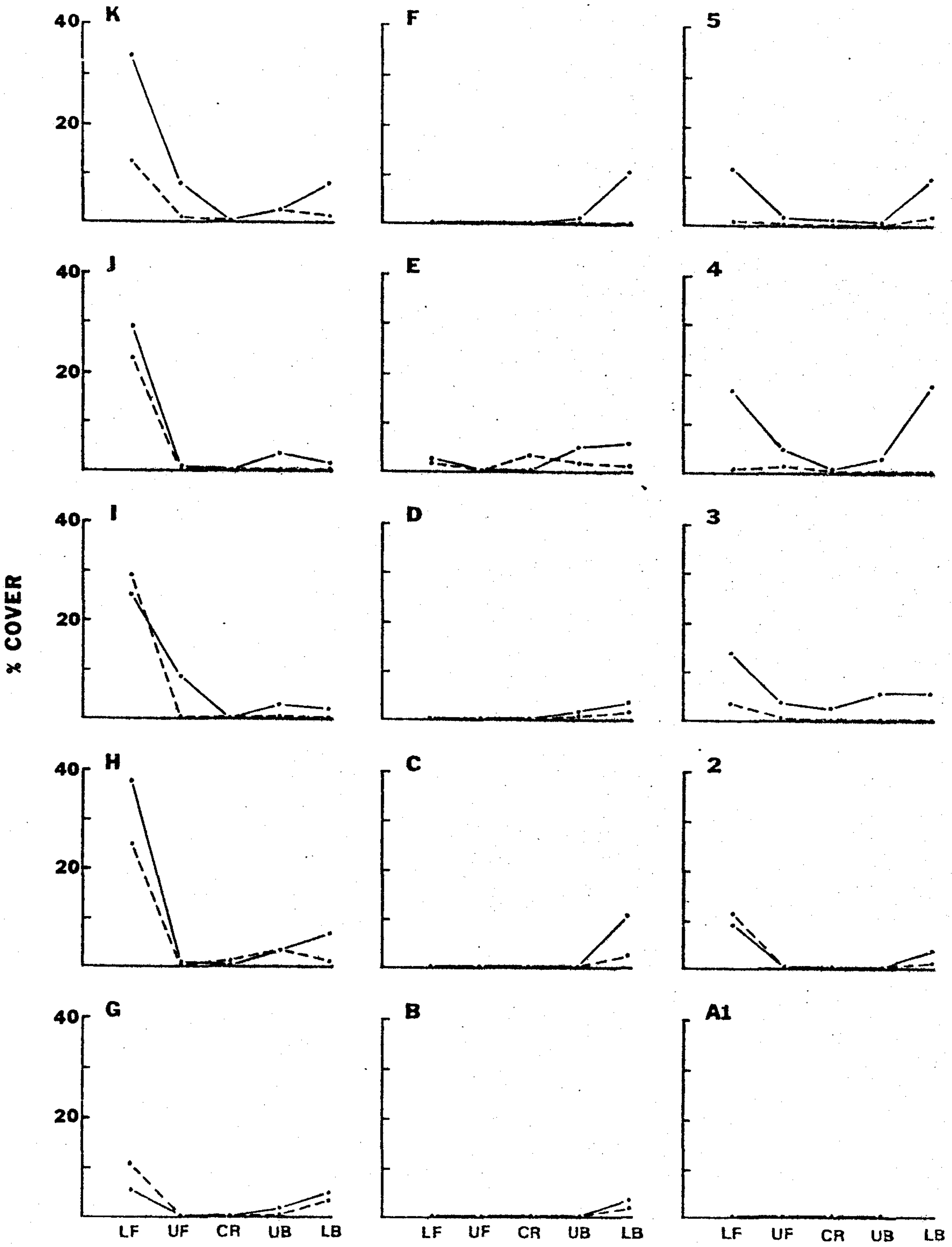
3
H
C
2
G
B
A1
% COVER
40
20
0
LF
UF
CR
UB
LB

Figure 36.

Percentage cover of *Salix reticulata* (solid line) and *Aulacomnium palustre* (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Both species have highest abundance on the lower front zone in later areas of the developmental sequence. Abbreviations as in Figure 28.


K
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G
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A1
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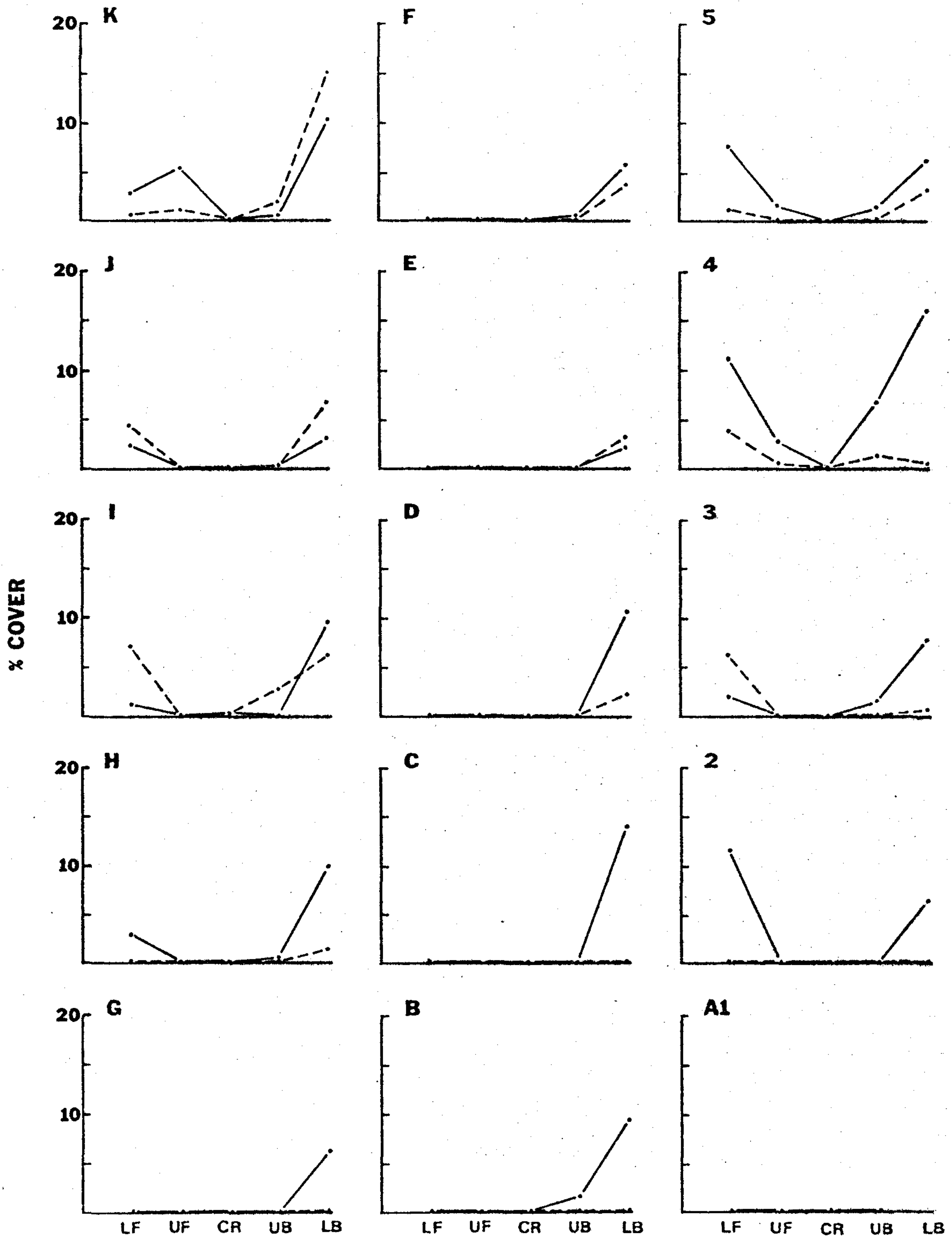
% COVER
LF
UF
CR
UB
LB

Figure 37.

Percentage cover of Equisetum variegatum (solid line) and Vaccinium uliginosum (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Although restricted to the lower back zones of the early coastal sequence, both species are abundant on lower front and lower back zones in the lichen-heath. Abbreviations as in Figure 28.


% COVER
20
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K
F
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E
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A1
LF
UF
CR
UB
LB

abundance on lower back zones in the lichen-heath. *Empetrum nigrum* L. and *Rhododendron lapponicum* show very similar lower back ridge profile distributions in almost every sample area (Figure 38) but neither species has a very high percentage cover at any site.

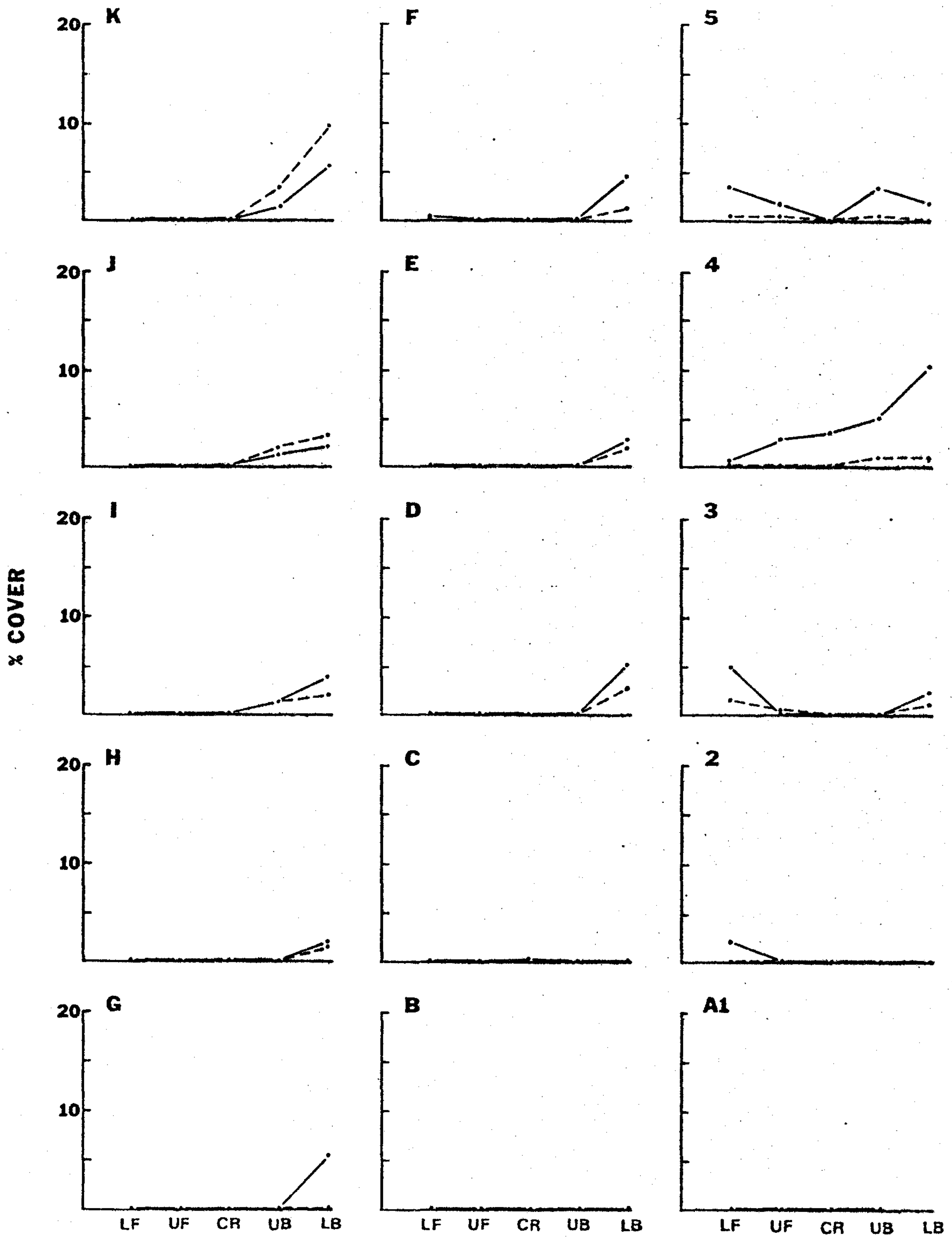
B. Environmental Gradients

The marked changes in the distribution of species over the ridge profile are accompanied by equally distinct environmental gradients. The relatively uniform ridge morphology and orientation are the bases of similar ridge profile gradients in surface slope and aspect along the coastal and inland sequences. However, since ridge width is up to 50% greater in the middle areas of the coastal sequence there is a greater difference in elevation between the lower ridge zones and the crest in these areas (see above, Figure 19).

Peat thickness (Figure 39) shows little difference over the ridge profile in the early areas of the developmental sequence. Peat development appears to increase more rapidly on the lower ridge zones and results in a decreasing gradient of peat thickness from lower zones to the ridge crest. Peat thickness is generally least on the upper front zones of the coastal sequence and the crest zone of the inland sequence. Soil percentage organic matter also demonstrates a ridge profile gradient which parallels the peat thickness (see below, Table IV). The ridge profile results of soil particle composition, pH and available nutrient analyses (not presented) are variable

Figure 38.

Percentage cover of _Empetrum nigrum_ (solid line) and _Rhododendron lapponicum_ (dashed line) over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Both species are restricted to backslope zones on the coastal sequence but are present on front and back slopes of the inland sequence. Abbreviations as in Figure 28.


% COVER
K
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C
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A1
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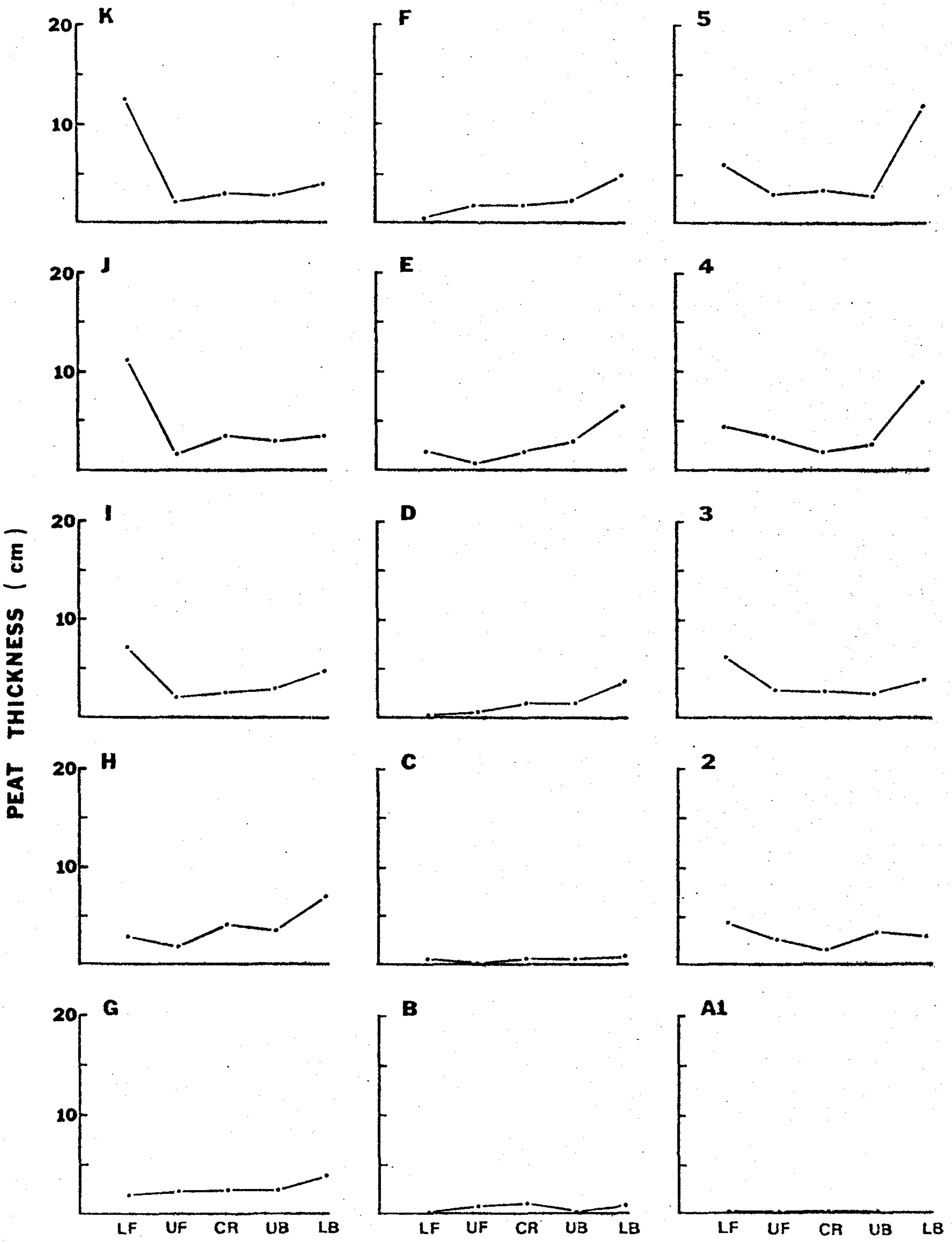
10
LF
UF
CR
UB
LB

Figure 39.

Peat thickness over the ridge profile along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5). Peat exhibits a gradual increase along the developmental sequence to greatest thickness on the lower front zone of the coastal sequence and lower back zone of the inland sequence. In lichen-heath areas peat thickness is least on the front slope. Abbreviations as in Figure 28.


PEAT THICKNESS (cm)
K
F
5
J
E
4
I
D
3
H
C
2
G
B
A1
20
10
LF
UF
CR
UB
LB

within many areas but show no trends.

Other potentially important environmental gradients over the ridge profile were not measured, in particular the winter factors of snow depth and duration which are affected by elevation and aspect. A number of factors are also related to elevation including wind speed which in some sites may have erosional and dessication effects. Soil moisture may be an important ridge profile gradient which is closely related to peat thickness (see below, section 4.1).

(3.3) Regression Analysis

Linear regressions were done between dominant species and environmental variables for all zone transect samples (Table IV). *Elymus arenarius* has highly significant negative correlations with elevation and peat thickness and a positive correlation with non-vegetated ground. *Hedysarum mackenzii* also shows a significant negative correlation with peat thickness. The dominant upper slope species of the lichen-heath community, *Cetraria islandica*, *C. nivalis*, *C. cucullata*, *Cornicularia divergens*, *Alectoria ochroleuca* and *Dryas integrifolia* show a significant positive correlation to elevation while no significant correlations were found for peat thickness. Conversely, lower slope species of the lichen-heath, *Salix reticulata* and *Equisetum variegatum* have a significant positive correlation with peat but not elevation. Linear regression analysis thus confirms the relationships between many of the ordination abundance trends

(Table I, Appendix A) and indicates groupings of species which distinguish the colonizers from the lichen-heath as well as the community change over ridge profile within the lichen-heath.

A highly significant positive correlation is also present between organic matter and peat thickness. This relationship is evident from the distributions of these variables along the developmental sequence and over the ridge profile.

Table IV

Significant correlations and linear regressions of species' cover and environmental variables for zone transect samples. Significance levels: *, $p<.05$; **, $p<.001$. All sample sizes are 74 except that of percentage organic matter and peat which is 49. Abbreviations: r, correlation coefficient; $S.E._b$, standard error of the slope; T_b, t-value for slope of regression line.

Species	variable	r	regression equation	$S.E._b$	T_b
Elymus arenarius	elevation	.49**	10.46-3.75X	0.79	-4.77**
	peat	.45**	5.27-0.87X	0.21	-4.22**
	non-vegetated	.65**	0.56+0.14X	0.02	7.24**
Hedysarum mackenzii	peat	.25*	2.81-0.31X	0.14	-2.26*
Cetraria islandica	elevation	.25*	4.87+5.74X	2.63	2.19*
Cetraria nivalis	elevation	.47**	-5.25+6.32X	1.40	4.50**
Cetraria cucullata	elevation	.62**	-4.44+3.34X	0.50	6.65**
Cornicularia divergens	elevation	.53**	-7.69+5.12X	0.97	5.27**
Alectoria ochroleuca	elevation	.54**	-7.89+5.07X	0.93	5.43**
Dryas integrifolia	elevation	.56**	-5.37+3.77X	0.67	5.67**
Salix reticulata	peat	.68**	-1.28+2.02X	0.25	7.97**
Equisetum variegatum	peat	.43**	0.52+0.72X	0.18	4.08**
percentage organic matter	peat	.64**	4.57+2.20X	0.39	5.60**

Section 4.

DISCUSSION

A study was done in the summer of 1974 to examine the colonization and vegetational development preceding the establishment of lichen-heath on young raised-beach ridges. The existence of two vegetational gradients is shown by the results. The first gradient consists of a largescale, directional change in vegetational composition towards lichen-heath which is accompanied by changes in elevation and soil development. This gradient represents a continuous temporal development of the vegetation which is repeated on the coastal and inland sample sequences. A second vegetational gradient over the ridge profile is superimposed upon the developmental sequence. The characteristic ridge profile distributions of dominant species indicate their responses to environmental factors related to the ridge topography.

The results of the survey concerning both types of vegetational and environmental gradients will be discussed separately below before consideration of the nature of vegetation-environmnet interaction in lichen-heath development.

(4.1) The Developmental Gradient

The continuous and repeated development of the ridge community towards lichen-heath is evident in both the area ordination results and the distribution of dominant species. Colonization begins primarily with the establishment of *Elymus* *arenarius*. The decline in *Elymus* abundance and performance away from the creek mouth is significantly correlated with the decrease in non-vegetated ground as other species also become established. Statistically significant negative correlations are also present between the abundance of *Elymus*, elevation and peat thickness. These relationships indicate that this species is intolerant of the vegetational development which involves the colonization of bare ground and the development of soil peat. Other vascular species, *Hedysarum mackenzii*, *Saxifraga tricuspidata* and *Poa alpina*, appear early in the developmental sequence and decline substantially in abundance in the lichen-heath. Two dominant lichens, *Cetraria islandica* and *C. nivalis* attain their highest abundance in the early lichen-heath but appear to decline as development continues. In contrast, *Cetraria cucullata*, *Cornicularia divergens* and *Alectoria ochroleuca* first appear later in the developmental sequence and are most abundant in the older lichen-heath areas. *Dryas integrifolia* and *Salix reticulata* exhibit much wider distributions since both become established quite early in the developmental sequence and reach their highest cover in the older lichen-heath areas.

The presence of isostatic uplift in this region allows the spatial vegetational sequence along the elevational gradient to be quantified as a developmental sequence of approximately 200 years. The directional and consistent change of community composition and degree of soil development correspond well with the presumed geomorphic development of these beach ridges. Thus, the vegetational development has a basis in the increasing ridge elevation and factors related to area age.

Peat thickness demonstrates an almost linear increase proceeding along both the coastal and inland sequences. Peat thickness is a function of many factors including time, soil moisture and temperature, vegetation cover and type. The vegetational factors will themselves be complex functions of climatic and edaphic parameters which influence species' establishment and productivity. Peat depth, therefore, is indicative of the past community productivity and the soil development which underlie the development of lichen-heath.

The percentage of oxidizable organic matter in the soil is closely correlated with the peat development. The decomposition of plant and animal material is important in the release of mineral nutrients and other compounds thus contributing to soil development and fertility. The high cation exchange capacity of the remaining humified organic matter makes it the major reservoir of exchangeable nutrients (Black 1968). However, a comparable increase in the available concentrations of soil nutrients was not found with the increase of organic matter along the developmental sequence. Although the mean area concentrations of phosphorus, potassium and magnesium show decreases while calcium and nitrate show general increases along the developmental sequence, the large degree of variability in each area obscures the actual trends which may be present. In addition, changing nutrient concentrations along the developmental sequence may be further enhanced or offset by the increase in the peat layer which is the major nutrient reservoir.

Although the nutrient concentrations are not easily compared to the results of this study, chemical analyses of several dune soils (Gorham 1958; Willis et al 1959; Etherington 1967; Chandapillai 1970) have shown a gradual decrease in nutrient concentrations as the vegetation developed. In a stabilized dune soil the decreasing nutrient concentrations are primarily the result of leaching and plant uptake. Etherington (1967) shows the importance of potassium income in sea spray in compensating for potassium loss by leaching and suggests the same situation may be true for other nutrients. However, observation of storm waves on the very shallow Hudson Bay indicates that the sea spray effect will probably be of importance to only the foredune sample site (area A1). A more intensive analysis of these Pen Island soils is required to establish the existence or absence of such trends.

The soil pH is remarkably uniform along the developmental sequence. The absence of a pH gradient contrasts with the results of many dune studies where pH decreased as much as several units during soil development (Salisbury 1925; Willis et al 1959; Ranwell 1959; Wilson 1960). The acidification of calcareous dune soils is largely due to the leaching out of calcium carbonate and the increase of organic acids from the decomposition of organic matter (Olson 1958a; Wilson 1960). However, Olson notes that no exchangeable acids were detectable in the 10-40 cm horizon of Lake Michigan dune soils up to several hundred years old, presumably because of neutralization by soil carbonates. This may also be the case in these relatively young Pen Island soils since this site lies within the region of sediments containing 30-50% calcium carbonate (Pelletier _et al_ 1968).

Soil particle composition, although variable, exhibits no trends along the developmental sequence. The absence of appreciable amounts of silt-clay and organic matter in the mineral layers causes these soils to be low in ionic exchange sites and to have low water-retaining capacities. Rouse and Kershaw (1973) found the soil moisture characteristics under all lichen-heath sites to be virtually the same at depths below 30 cm. Soil moisture differences between sites were found to be closely related to the organic content of the soils and Larson and Kershaw (1974) found a highly significant correlation between peat thickness and surface soil moisture in the lichen-heath. Soil moisture is generally regarded as one of the most important factors affecting the distribution of arctic and alpine plants (Billings and Mooney 1968). This is probably true also of the Pen Island situation because of the low amount of precipitation during the growing season (Figure 3) and the poor moisture retaining characteristics of the sandy soils which are improved by peat development and the incorporation of organic matter.

The peat layer appears also to be important to the soil temperature regime during the growing season. McGregor (1975) modelled the soil temperature profile under different lichen-heath associations and found that the peat layer had essentially no effect on the soil energy transfer during the summer months.

However, he postulated that different peat thicknesses between sites cause a differential rate of spring thaw which would account for the observed differences in both the temperature of the rooting zone and the depth of the permafrost table.

The absence of appreciable trends in particle size composition, pH or available nutrients along the developmental sequence suggests that these factors have little influence on the development of lichen-heath at this site. On the other hand, definite increases in peat thickness and organic matter are present which parallel the increasing elevation and community development towards lichen-heath. Previous studies (Rouse and Kershaw 1973; Larson and Kershaw 1974) have also found the continued increase of peat thickness and surface soil moisture in the later development of the lichen-heath.

Thus it is evident that peat development and soil moisture are among the controlling factors in the development of vegetation towards lichen-heath at this site. However, since lichens do not have root or vascular systems it is questionable whether the consideration of peat thickness and soil moisture has any direct bearing on the distribution of these plants in the lichen-heath. The significant correlations between lichen species and zone transect elevation (Table IV) may indicate a response either to the degree of ridge exposure, slope or aspect or to the time period of vegetation development as evidenced by isostatic uplift. Examination of the ridge profile vegetational and environmental gradients may help to resolve this question.

(4.2) Ridge Profile Gradients

In a study of the interaction of general lichen-heath I and edaphic factors, Larson and Kershaw (1974) note that variation in vegetational structure over the ridge profile indicates the considerable importance of environmental parameters independent of the age sequence. The ordination of their zone transect cover data reveals that 40% of the variation in the vegetation is related to the contrasting topographic positions of beach ridges. The same observation may be true of the development preceding the lichen-heath since a much lower amount of variance was extracted along the developmental sequence by the zone transect ordination than by the area ordination (Table I, Appendix A).

The ordination of the 74 zone transects in this study reveals trends in the upper front, crest and upper back sites which demonstrate the continuous vegetational development towards lichen-heath. The lower front and lower back transects, however, have no definite ordination patterns. These lower slope trends are more consistent with the ordination trends for the vegetation of the wet sedge meadows at this site (Kershaw 1975). Kershaw identified an _Equisetum-Drepanocladus_ association, on the dry extreme of a "water table" gradient, which bears strong similarity to the lower slope community. Common species include _Equisetum variegatum_, _Drepanocladus uncinatus_, _Bartsia alpina_, _Tofieldia pusilla_ and _Vaccinium uliginosum_.

Many species which exhibit marked changes in abundance along the developmental sequence, for example, _Hedysarum mackenzii_, *Saxifraga tricuspidata*, *Alectoria ochroleuca*, *Dryas integrifolia* also have characteristic ridge profile distributions. This is especially true of species with crest or upper slope preferences. Species which have their greatest abundance on the lower slope, for example *Salix reticulata*, *Equisetum variegatum* and *Aulacomnium palustre*, are also widely distributed along the developmental sequence but generally do not exhibit as great a change in abundance as upper slope species. Similarly, variation in cover over the ridge profile is often much greater in dominant lower slope species than the change in their area average cover over much of the developmental sequence. This presumably is due to the presence of more pronounced environmental gradients over the ridge profile to which these species are sensitive.

As a result of isostatic uplift, elevation is indicative of the ridge age, but in addition, elevation and ridge morphology affect factors of the physical environment such as temperature, wind speed, evaporative demand, snow depth and duration. Kershaw and Larson (1974) found that ridge top sites are characteristically more windy, cooler and have higher evaporative rates than corresponding ridge bottom positions. They conclude that although the level of topographically-related microclimatic differences are small they are consistent and when integrated over long time periods will have appreciable effects.

The spatial variations of snow depth and duration across raised beaches are closely related to ridge morphology. Larson and Kershaw (1975) report that in December, 1974 only a very thin snow cover was present on raised-beach crests while ridge meadows, only 1-2 meters lower in elevation, had a relatively thick snow cover of up to 2 meters. The amount of snow on ridge bottoms and slopes will depend on the degree of protection from wind afforded by the ridge orientation and morphology. Snow cover may be extremely important in the winter survival of many species. A snow depth greater than 20 cm effectively damps cold temperature fluctuations experienced at the snow surface (Bergen 1968). A snow cover also protects plants from the dessication effects of wind and damage by ice particle abrasion (Warren-Wilson 1959).

Snow duration also shows an important gradient over the ridge profile since the date of ridge site exposure in the spring is inversely related to the depth of snow cover (Larson and Kershaw 1975). Late-lying snow will give protection from late frosts to lower slope species and, in contrast, early melt on the crest will allow hardy species a much longer growing season. The amount and duration of snow will also have an extended effect on the soil moisture regime into the summer season. In the early summer the large peat layer under ridge bottom sites insulates the frozen soil to a great extent from soil heat flux thus reducing the rate of thaw of the active layer (Nakano and Brown 1972). The shallow active layer maintains a relatively high water table and, along with the high organic content of the ridge bottom soil, produces a very high soil moisture content. Conversely, the ridge tops, which have a thin snow cover and a rapidly increasing active layer, are extremely dry through most of the year (Rouse and Kershaw 1973). Larson and Kershaw (1974) measured a great increase in surface moisture content from lower front to lower back on the first coastal ridge while other inland ridges showed high soil moisture on both the lower front and lower back.

The distinct but puzzling shift in the distribution of *Hedysarum mackenzii*, *Salix callicarpea*, *Cetraria islandica*, *C. nivalis* and *Dryas integrifolia* from backslope to foreslope along the developmental sequence may have a basis in microtopographic factors. The prevailing NNW wind in this area results in the ridge backslope being generally the leeward side of the ridge and thus may constitute a better-protected site in severe weather. Similarly the SW aspect and inclination of the backslope constitute the ridge surface most perpendicular to the sun's rays and therefore with the warmest temperatures (Hansen 1973). The temperature regime, coupled with the wind shelter and snow cover effects and the generally high soil moisture conditions, give the ridge backslope the most hospitable conditions for the establishment and survival of many species.

Gradients of soil pH and available nutrient concentrations are very weak or absent over the ridge profile. The presence of greatest peat thickness at the ridge edges, however, may increase the supply of nutrients at these sites. Similarly, since drainage is reduced and soil moisture is high at ridge edges, leaching of nutrients may not be an important factor decreasing nutrient availability here.

The most important environmental gradients over the ridge profile appear to be those of elevation, aspect, peat thickness, organic matter, soil moisture, snow depth and duration. Of these factors only elevation, peat thickness and organic matter also exhibit significant changes along the developmental sequence. This survey has thusfar dealt only with general correlations between vegetation and the environment and has not considered the interaction of vegetational and environmental factors or the possible changes in the autecological requirements of different species in the development of lichen-heath.

(4.3) The Interaction of Environmental Factors in the Lichen-Heath Development

The development of raised-beach ridges from active beach or foredune to lichen-heath represent considerable changes in both the ridge environment and the vegetation. The newly-deposited beach ridge shares with maritime sand dune systems the dominant influences of sand and wind (Ranwell 1972). Sand dune particle sizes are generally comparable to those of these beach ridges with a very high proportion of medium-coarse sand and little silt-clay. Young dune and beach ridge sands have very low water-holding capacities and much of it is far above the permanent water table (Ranwell 1972; Rouse and Kershaw 1973).

The complex interrelationships of dune morphology wind profiles and vegetation have been studied by Olson (1958b) on large, mobile dunes. In this situation, wind creates maximum erosion on the upper, windward slope while the lower leeward sites have the greatest shelter and sand accretion. Wind profile measurements on a large raised-beach ridge (Kershaw and Larson 1975) confirm this pattern, however, young ridges appear to lack the mobility characteristic of many sand dune systems (Ranwell 1972). This may be explained, in part, by the small ridge size and the protective snow cover present approximately three-quarters of the year.

The colonization of sand dunes by perennial grasses is also extremely important in sand dune stabilization since their extensive horizontal and vertical rhizome systems develop quickly to bind the sand. In addition, the tall upright shoots greatly increase surface roughness thus resulting in the accretion of blowing sand in the vicinity of the plants (Ranwell 1972). On these beach ridges Elymus arenarius performs these roles exclusively. The presence of isostatic uplift of the low-lying beach aids the colonization of plants by removing the beach surface from the inundation of high tides and the destructive effects of storm waves.

Soil development on stabilized ridges proceeds with the build up and decomposition of plant material and the subsequent incorporation of organic matter into the mineral layer. Salisbury (1925) first reported the marked change in soil properties as dunes developed with increasing organic matter and decreasing pH and calcium carbonate. The interaction of factors favouring nutrient accumulation and nutrient depletion interact with the changing soil properties in rather complicated ways and nutrient cycles in sand dune systems are still poorly understood (Ranwell 1972). It is apparent that the nutrient status and pH of the Pen

Island soils (discussed above) do not agree with the general sand dune patterns, although this may be partially due to either the relatively short developmental period or the methods used. The rate of organic matter accumulation on the young beach ridge is comparable to that of many temperate dune systems (cf. Wilson 1960). However, since plant material accumulates much more slowly in the arctic, this may be the result of slower decomposition rates caused by the lower temperature and precipitation regimes, as is the case in many lichen-heath soils (cf. Rosswall *et al* 1975).

The decrease of *Elymus arenarius* cover and performance with soil and vegetational development is a striking feature of *Elymus* and *Ammophila* sand dune situations (Ranwell 1972). *Elymus* is known to flower erratically and only in habitats where it is uncrowded and has vigorous growth. Elsewhere it appears to be adversely affected by the competition from *Ammophila* and other plants (Bond 1952). Although the potential for seed reproduction is high, *Elymus* propagates largely by rhizomes and the conditions affecting the relative abundance of flowering shoots and horizontal rhizomes are not known (Bond 1952). The decline in vigour of *Ammophila arenaria* on fixed dunes is closely associated with the decreased rate of sand accretion so that horizontal rhizomes are prevented from producing adventitious roots by the dry surface sand (Olson 1958c). *Elymus* may also be intolerant of immobilized sand; however, no information on this is available. Ranwell (1972) emphasizes the importance of this and other inherent morphological, growth and senescence characteristics of dune dominants in relation to successional changes.

The high local abundance of *Tortula ruralis* in the unstabilized ridge areas reflects its importance as a sand-binding species. *Tortula* is common on dry, calcareous habitats throughout North America (Crum 1973). Ridge stabilization is accompanied by the establishment of several perennial herbs; most important are *Hedysarum mackenzii*, *Saxifraga tricuspidata*, *Poa alpina* and *Festuca brachyphylla*. These calcicolous species are widely known in dry open sandy or gravelly areas in boreal and arctic regions (Polunin 1959) and are commonly associated with *Elymus mollis* in western Greenland (Gelting 1955). Although direct comparisons are not possible, the early beach ridge community shares many features of the fixed dune pasture situation of temperate regions, in particular the predominance of tufted graminoid species, a dry, open surface and the poor degree of soil development (cf. Bond 1952; Willis et al 1959; Ranwell 1960; Etherington 1967).

Ranwell (1972) observes that one of the most noticeable features of dune vegetation in the later stages of succession is the abundance of bryophytes and lichens. This pattern is due, presumably, to the inability of most lichen and bryophyte species to survive on the unstable, extremely dry dune surface in the early stages of succession. With the closing of the herb layer of vegetation and the build up of peat in the dune pasture soil these extreme factors are reduced thus allowing bryophyte and lichen establishment. The presence of *Cetraria* *islandica*, *C. nivalis* (Figure 33) and *Aulacomnium palustre* (Figure 36) on the leeward, lower back zones of the early areas, where non-vegetated cover is low and peat thickness is greatest, would appear to support this hypothesis in the ridge situation.

The early lichen-heath areas are distinguished by the general disappearance of the early colonizing species (discussed above) and the marked rise in abundance of the dominant lichen-heath species. The association of *Dryas integrifolia* and lichens is a widespread vegetation type which is described for arctic areas in Alaska (Hanson 1951), Baffin Island (Polunin 1948), Greenland (Gelting 1955) and in calcareous alpine areas of the Rocky Mountains (Bamberg and Major 1968). In addition, the strong ecological similarity and overlapping distribution of *Dryas octopetala* and *D. integrifolia* (Elkington 1965) give these combined *Dryas*-lichen associations a circumpolar arctic and alpine range (Gelting 1955). Although the florae of these diverse regions are somewhat different, many Pen Island species are commonly present in the arctic lichen-heath including *Dryas integrifolia*, *Vaccinium uliginosum*, *Empetrum nigrum*, *Saxifraga tricuspidata*, *Salix reticulata* (except Greenland), *Cetraria islandica*, *C. nivalis*, *C. cucullata*, *Alectoria ochroleuca*, *Cornicularia divergens* (cf. Hanson 1951; Gelting 1955; Elkington 1965).

Throughout this range *Dryas*-lichen heath is characteristically found on dry, calcareous, wind-swept, snow-free sites particularly on raw soil or fine rock debris (Bamberg and Major 1968). Although these habitat preferences are now well documented there is little detailed information or understanding of the factors which determine the structure of lichen-heath. Extensive distributional studies of *Dryas integrifolia* (Polunin 1948, Nordhagen 1955, Elkington 1965, Bamberg and Major 1968) indicate that, although a calciphile, this species is tolerant of a wide range of substrates from slightly acidic to quite alkaline parent materials with stable or unstable soil. The apparent physiological plasticity of *Dryas* proves puzzling in the Pen Island colonizing situation since it does not appear on unstable surfaces and reaches appreciable abundance only in the lichen-heath. The rapid establishment, vigour and abundance of *Dryas* in disturbed, peaty soil adjacent to the road near the ridge crest indicate that an edaphic requirement may be limiting its earlier appearance in the developmental sequence.

The dominant lichen species in this study area have not shown significant correlations with edaphic factors and Gelting (1955) observed that many of these species in west Greenland lichen-heath are indifferent indicators of nutrient-rich, calcareous soils. In contrast, the ridge profile distributions of these lichens are significantly correlated with elevation (Table IV) and characteristic topographic positions of many lichens on beach ridge systems have been found (Neal and Kershaw 1973, Larson and Kershaw 1974).

Kershaw and Larson (1975) suggest that these lichen associations are a function of the microclimate as affected by ridge topography. Recent comparative studies of *Alectoria ochroleuca* and *Cetraria nivalis* (Larson 1975, Larson and Kershaw

1976) have shown that the species' morphological and physiological adaptations to temperature, light and moisture factors of the environment are consistently related to their topographic distribution and to seasonal changes in the environment. Similar adaptive relationships will no doubt apply, to some degree, to the other lichen species in the lichen-heath.

The processes controlling the establishment and changes in abundance of lichen species along the developmental sequence are still unresolved. Since two dominant species have been shown to be sensitive to very small scale microclimatic factors, changes in the structure of the vegetation itself along the developmental sequence may be responsible for significant changes in the lichen microenvironment. For example, microclimatological studies (Rouse and Stewart 1972, Rouse and Kershaw 1971) have demonstrated the effectiveness of the lichen canopy as a mulch. In a more detailed study Field (1974) found that rapid changes in temperature and relative humidity occur near the top of a Cladina alpestris mat. These changes closely reflect the moisture status of the thalli and the temperature of the air. In contrast, temperature and humidity values lower in the mat remain relatively uniform. Other species in the lichen-heath may also be having a significant effect on the microclimate. For example, cushion plants such as Dryas are well known for their high resistance to evapotranspiration (Addison 1973).

In addition to the greater peat thickness (and hence, soil moisture), these aspects of the lichen-heath microenvironment provide a strong contrast with the open canopy and low peat thickness of the earlier "dune pasture" areas. Thus, as the community changes, the ridge microenvironment in any one topographic position may be undergoing continuous changes which are helping to alter the competitive relationships between species. However, the testing of this hypothesis would require especially sensitive environmental measurement and perhaps the use of methods not presently available. Certainly, though, the vegetation and the microenvironment are very interdependent and consideration of the effects of vegetation surrounding the individual plant is essential to understanding its autecology (Bamberg and Major 1968).

Section 5.

SUMMARY

1) A vegetational and soil survey was conducted during the summer of 1974 on young, physiographically-similar, raised beaches beside Hudson Bay in northwestern Ontario in order to study the developmental sequence preceding lichen-heath establishment.

2) Principal components ordination revealed a continuous, directional change in vegetational composition both along an intraridge sample sequence on the first coastal ridge and on an inland, interridge sample sequence running perpendicular to the coast. Continuous changes in the percentage cover of dominant species were found to correspond with the directional changes in vegetational composition along both sequences.

3) A continuous increase in ridge elevation was found to coincide with the vegetation change. The presence of post-Wisconsinan Age isostatic rebound in this region and the presumed geomorphic origin of the raised-beach ridge system allowed the spatial vegetational sequence to be quantified as a temporal developmental sequence of approximately 200 years.

4) Marked increases in the soil peat thickness and percentage oxidizable organic matter were found along the developmental sequence. However no appreciable changes were detected in soil pH or the available concentrations of soil phosphorus, potassium, magnesium, calcium and nitrate and it is concluded that these parameters have little influence on the development

of lichen-heath at this site.

5) Community structure over the ridge profile forms a second major vegetational gradient superimposed upon the developmental sequence. A number of dominant species exhibit characteristic distributions over the ridge profile as well as along the developmental sequence. Species' distributions over the ridge profile appear to be the result of environmental factors related to ridge morphology and orientation including wind exposure, aspect, peat thickness, organic matter, soil moisture, snow depth and duration.

6) The interactions of environmental factors in the development of lichen-heath are discussed with respect to other studies of lichen-heath vegetation.

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Appendix A

Table I

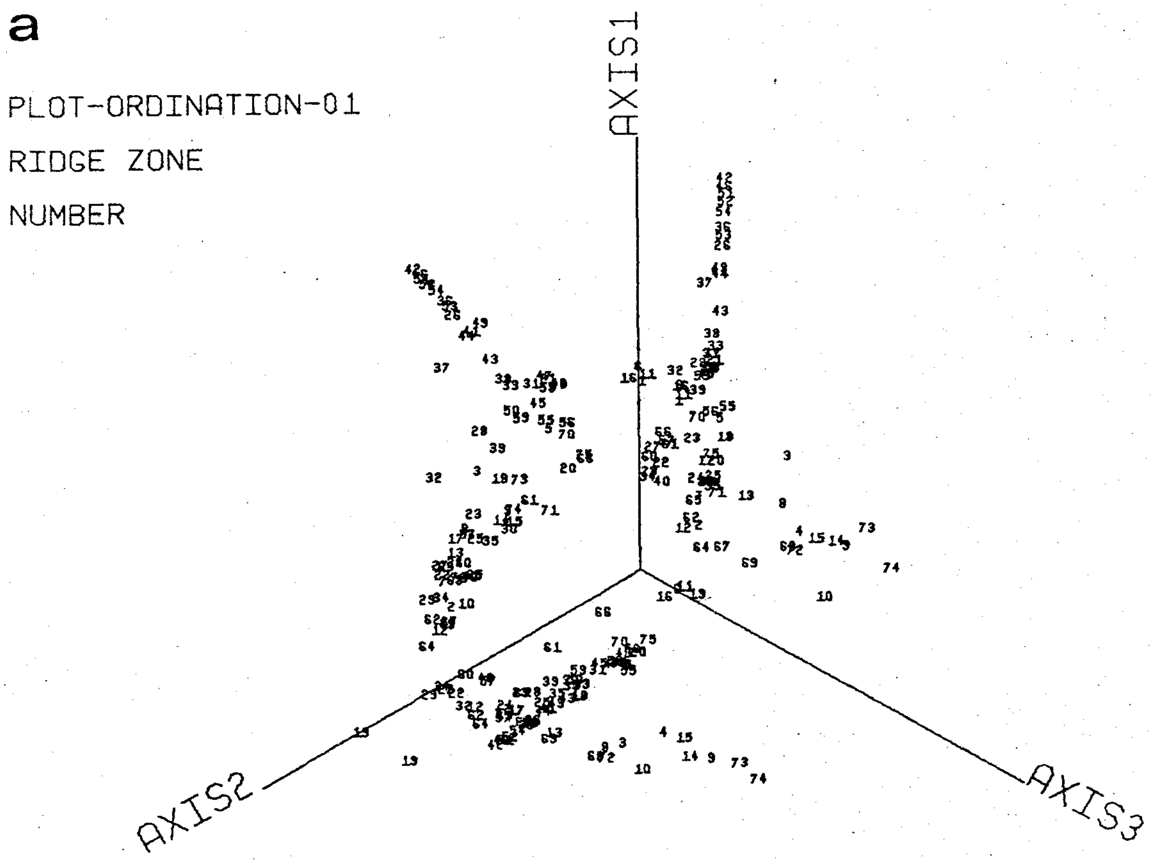
Major trends in abundance pf plant species and environmental factors for the area ordination (15 plots) and the zone transect ordination (74 plots). Abbreviations: -, increasing trend away from axis origin; +, increasing trend towards axis origin; c, central trend; w, weak trend.

	Area Ordination			Zone Transect Ordinatio		
Axis	I	II	III	I	II	III
Percentage of Total Variance	61	16	9	37	15	11
non-vegetated	-			-		
Elymus arenarius	-			-		
Hedysarum mackenzii	-(c)					
Cetraria islandica	+	+		+	+(w)	
Cetraria nivalis	+			+		
Salix reticulata	+					
Cornicularia divergens		-				-
Alectoria ochroleuca		-				-(w)
Dryas integrifolia		-				-(w)
elevation	+	-(w)		+(w)	-(w)	
peat thickness	+	-(w)		+(w)		

Appendix A.

Figure 1.

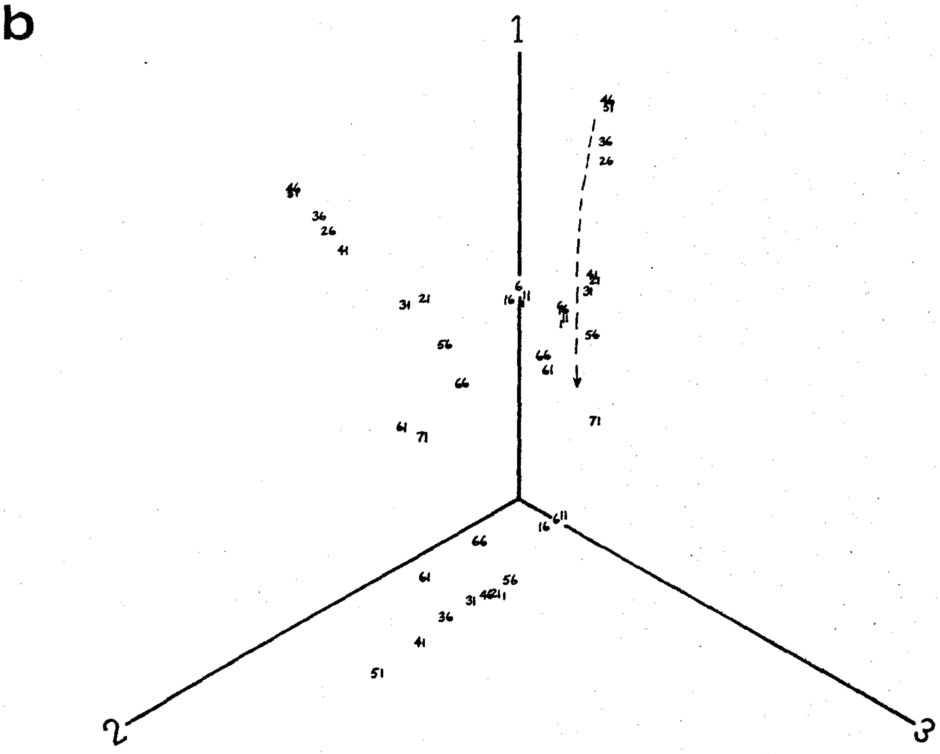
(a) Ridge zone transects ordination showing the directional change in vegetational composition of the transects along the coastal sequence (areas A1 to K) and the inland sequence (areas A1 to 5) which corresponds to axes 1 and 3. (b) Pattern of the lower front transects in the ordination reveals only a weak correspondance to axis 1 along the developmental sequence. (c) - (e) Ordination patterns of the upper front, crest and upper back transects exhibit very similar trends along the developmental sequence corresponding to axis 1 in the early areas and diverging along axis 3 in the lichen-heath. (f) No trends were apparent in the lower back transects indicating that the vegetational composition is not affected significantly by the developmental processes.



Key to Zone Transect Numbers

Sample Areas

Zone Transects	K	J	I	H	G	F	E	D	C	B	A1	2	3	4	5
LF	1	6	11	16	21	26	31	36	41	46	51	56	61	66	71
UF	2	7	12	17	22	27	32	37	42	47	52	57	62	67	72
CR	3	8	13	18	23	28	33	38	43	48	53	58	63	68	73
UB	4	9	14	19	24	29	34	39	44	49	54	59	64	69	74
LB	5	10	15	20	25	30	35	40	45	50	-	60	65	70	75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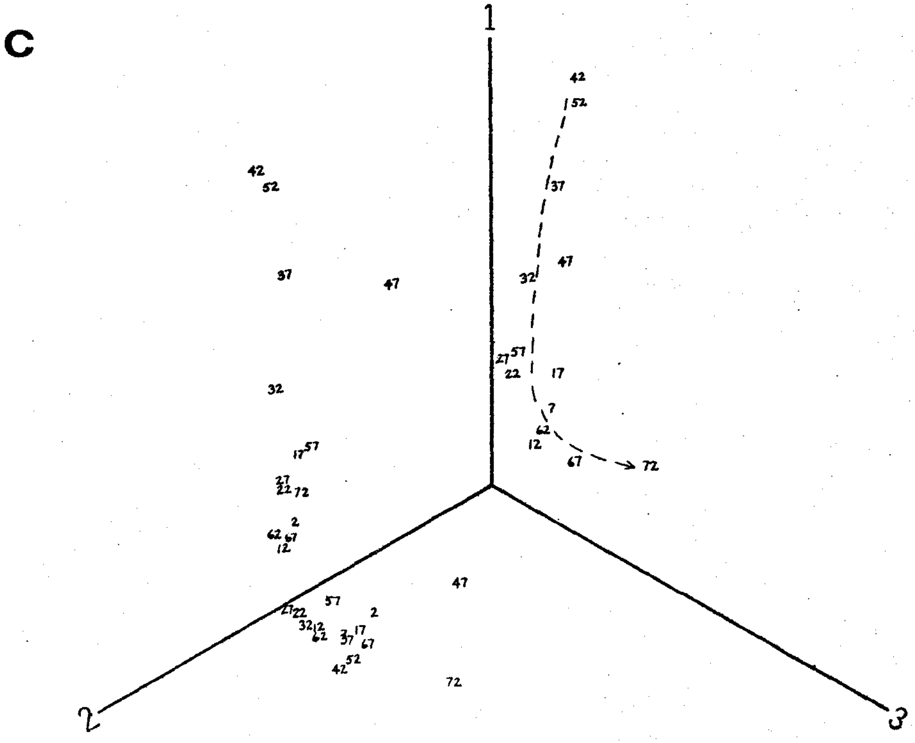
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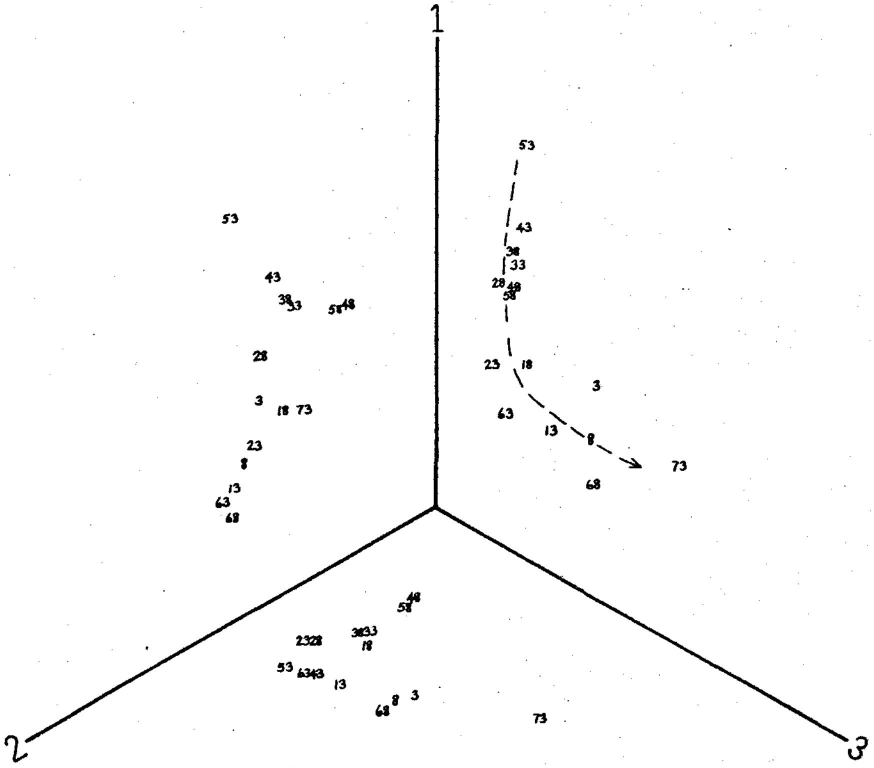
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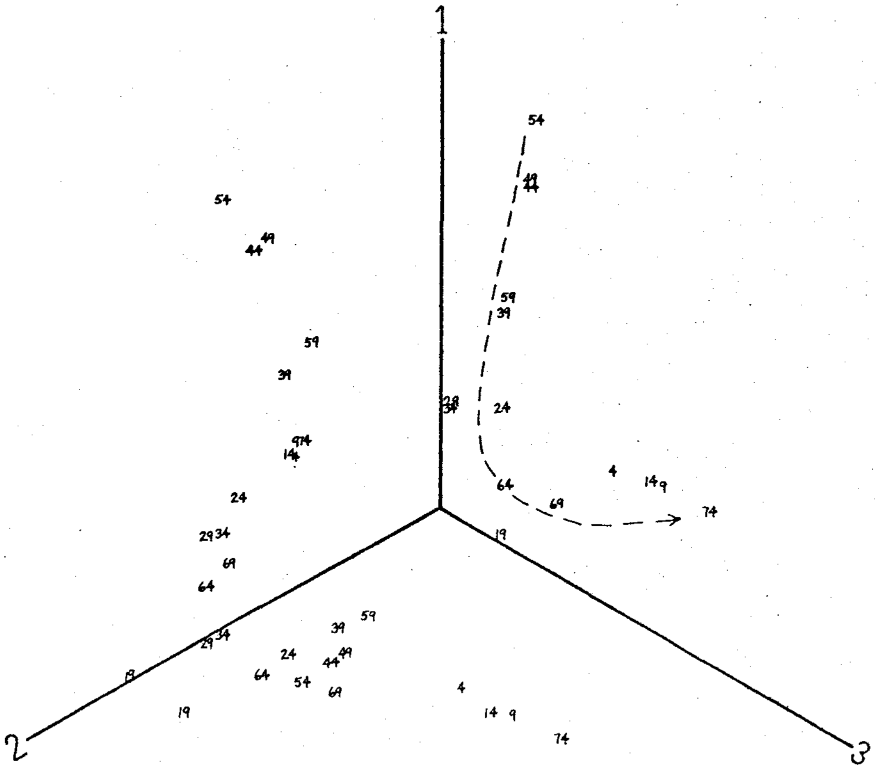
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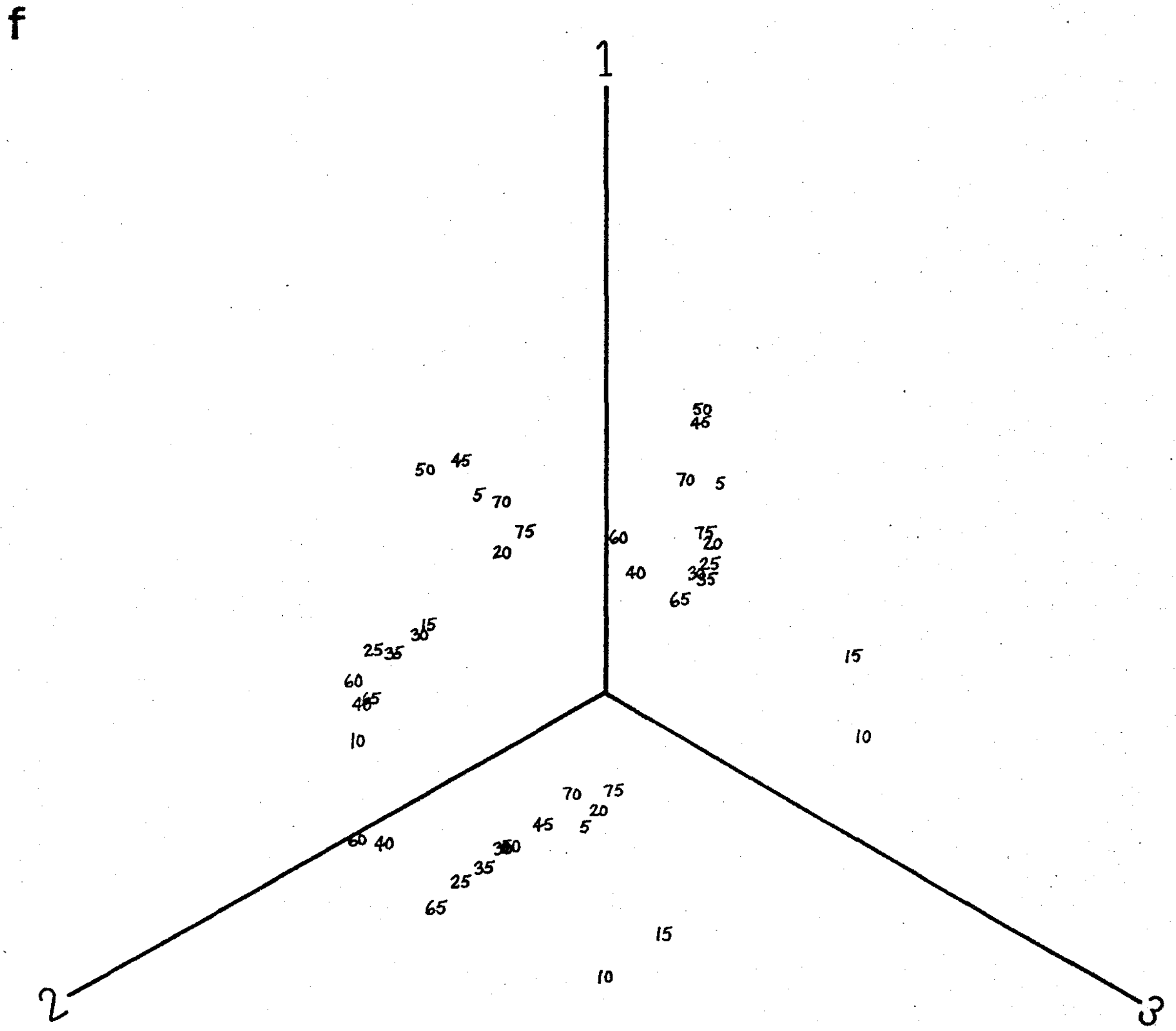
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