ASSOCIATION ANALYSIS OF SUBARCTIC RAISED BEACHES

THE ASSOCIATION ANALYSIS OF A LICHEN DOMINATED RAISED BEACH SYSTEM IN SUBARCTIC ONTARIO

By

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ABSTRACT

A modified version of the Braun-Blanquet technique for the analysis of plant associations was applied to an area of lichen dominated raised beach system at Cape Henrietta Maria in subarctic Ontario. Eleven such associations were extracted on this basis. Subsequently the data was subjected to principal components ordination methods from which it was concluded that the number of associations be reduced to nine. With the aid of multiple regression trend surface analysis a number of hypotheses concerning the ecological factors underlying the distribution of vegetation in the area were suggested, namely, that the associations are controlled by gradients of pH, the thickness of the underlying peaty substratum, and the distribution of late snow lie zones.

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Section I

INTRODUCTION

Lichen dominated vegetation accounts for some 92,870 square miles of the total land area of Ontario, or about 27 percent (Ahti & Hepburn, 1967). Despite its importance in terms of area covered or to the animals and people that live in these regions, few attempts have been made to find out more about this important natural resource.

What information is available treats the vegetation in a most superficial way. (Polunin 1948, Moir 1954, Hustich 1957, Ahti 1961, Ahti and Hepburn 1967, Webber et al 1970). Any sampling of the areas examined has been haphazard if done at all, the bulk of the work consisting of species lists taken by visual examination of the areas visited. While some of this work is useful for the taxonomic information it contains, it yields very little information concerning the ecology of the area, especially in a quantitative sense. Thus Moir (1954) characterizes stages of raised beach succession as follows: Close to the coast the most recently formed beach ridges are "sparsely vegetated by scattered colonies of *Mertensia maritima, Elymus arenarius* var *villosus* and *Arenaria peploides*. Between these coastal beaches and the forested beaches of the interior there is a zone characterized by a surface stabilized by low growing woody shrubs such as *Salix spp.*, *Shepherdia canadensis*, *Ledum groenlandicum*, *Empetrum nigrum*, *Rhododendron lapponicum* *Vaccinium uliginosum*, along with *Dryas integrifolia*, *Saxifrage tricuspidata* and lichens such as *Cladonia spp*. On the slopes of the ridges about two miles inland, a stunted and sparse growth of *Picea glauca* and *Larix laricina* is present." Several miles inland the beaches support open stands of mature Spruce-lichen woodland.

In detail, however, little is known about the ecology of these raised beaches, although recent work by Kershaw and Rouse (1971) indicates that the lichen mat of *Cladonia alpestris*, in Spruce-lichen woodland, is extremely important in the water budget of these systems.

In attempting an analysis of the plant associations in an area such as this, that is one in which even good preliminary studies are lacking, it is necessary to break up the vegetation into its component parts, since the whole system is too complex to study at once. This classification process provides a framework upon which to hang subsequent ecological studies, but we also know that the existing vegetation is the most sensitive indicator of ecological conditions. It would seem reasonable then that the associations that were derived, might themselves give some clue as to the factors that control this distribution of plants. In other words, the second aim is to generate hypotheses concerning the ecology underlying their distribution.

With this end in mind, two approaches were carried out, one subjective, the other objective, with the further aim of developing a system for the preliminary survey of unexplored areas of vegetation. The prime directives behind this development were that a maximum of information be extracted from a rapidly conducted sampling process, utilizing a minimum of equipment, and a low degree of sophistication in the field.

(1.2) The Choice of Sample Areas

Cape Henrietta Maria is situated on the north-west corner of James Bay, in the area designated as Polar Bear Provincial Park. The sample area was located on a raised beach system approximately 15 miles south of the Cape and 8 miles inland at Latitude 54°47' N and Longitude 82°23'W. (Fig.1)

This area was chosen partially for its accessability, by air from Moosonee, Ontario and partially because it had been the object of previous study (Ahti 1961, Hustich 1957). Base camp was located at an abandoned (for 7 years) D.E.W. line base, however, by moving a short distance from the site, undisturbed ground could be found.

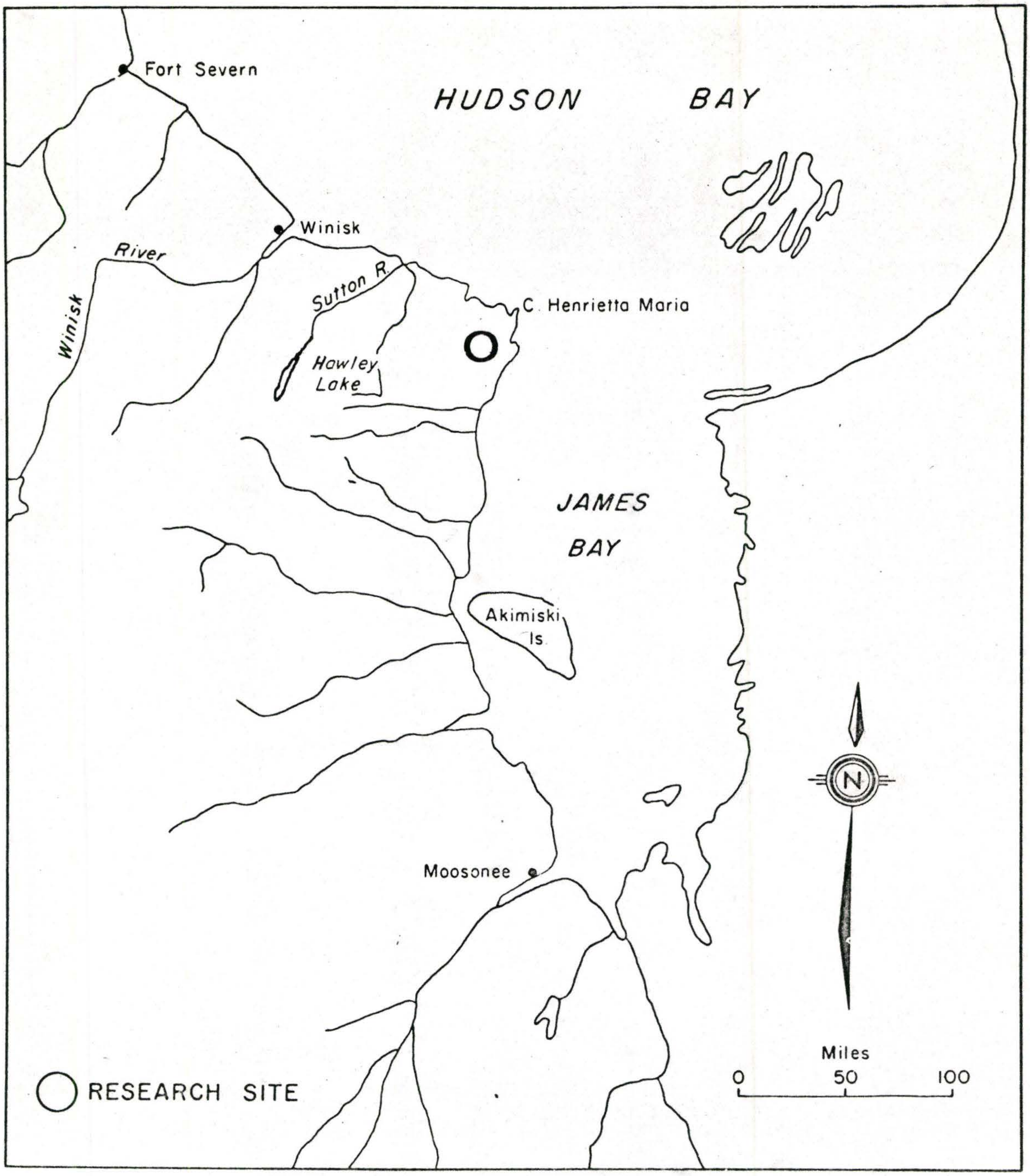


Figure 1. Map of the Cape Henrietta Maria Area.

Plate 1. Aerial Photograph Showing Raised Beach Systems.

Sampling was carried out in five areas, (Fig.2) which were characteristic of the complete Cape Henrietta ridge system.

(1.3) <u>Geology and Geomorphology</u>

The Hudson Bay lowlands, an area about 100 miles in width along the coast of Hudson Bay, are characterized over much of their extent by a series of conspicuous beach ridges, paralleling the coast and extending inland for distances of up to 150 miles (Plate 1). Their origin is related to the effects of the last (Wisconsin) glaciation period.

This ice sheet, with a thickness of 5,000 to 10,000 feet, appears to have been centered in the Hudson Bay area. Previous to the glaciation this area consisted of a low lying plain with its main drainage into the area presently known as Hudson Strait. The weight of this accumulation of ice was so great as to cause a depression in the earth's crust. The maximum extent of this crustal downwarping has been estimated at 1800 feet, and since deglaciation the recovery has been estimated at about 900 feet to date (Flint, 1943). Recent estimates of the rate of uplifting in the Cape Henrietta Maria area have placed it at 1.2 meters per century (Webber, 1970).

This building up of beach ridges is the result of a combination of factors, namely gentle slope (in this

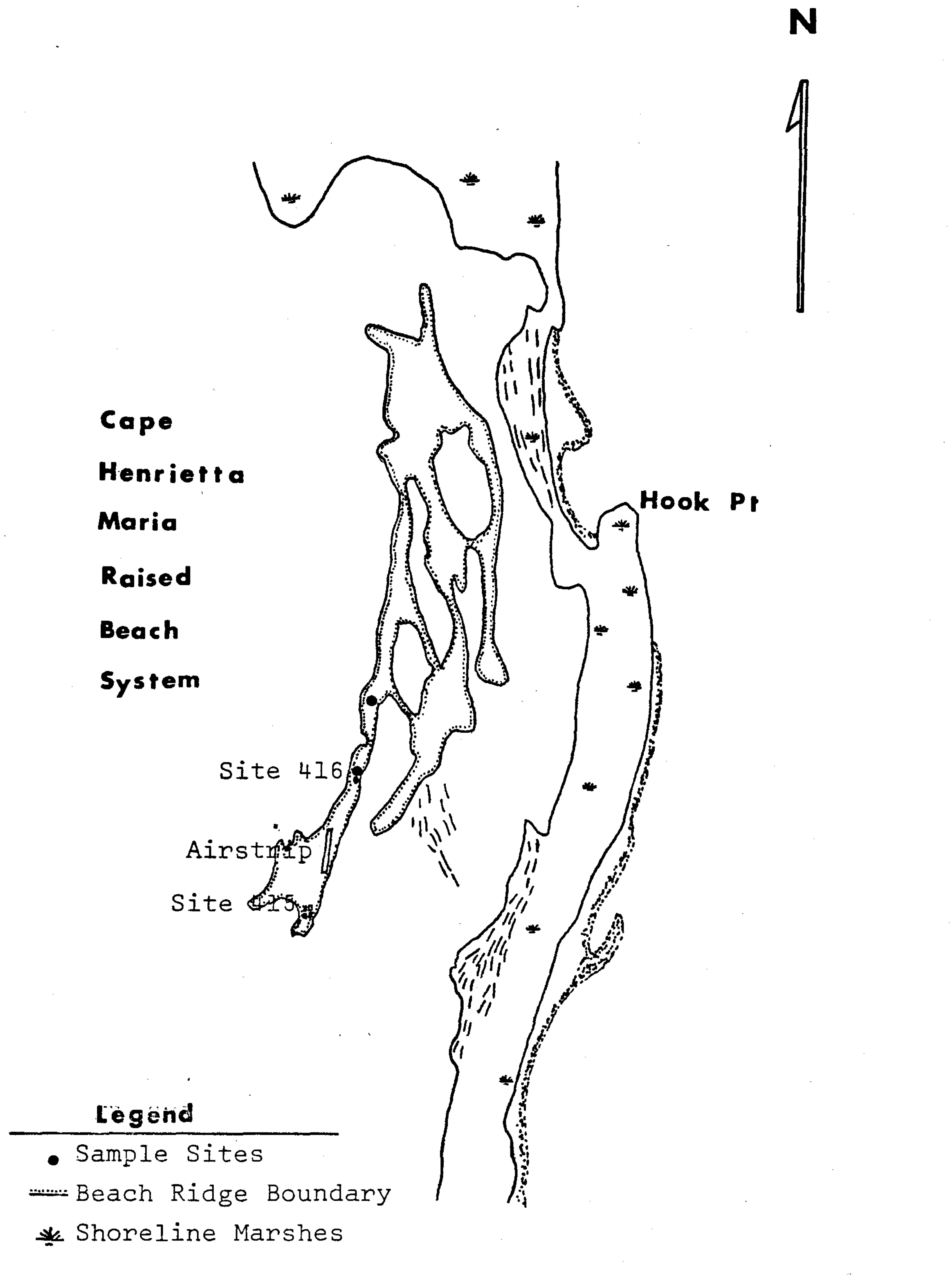

N
Cape
Henrietta
Maria
Raised
Beach
System
Hook Pt
Site 416
Airstrip
Site 415
Legend
Sample Sites
Beach Ridge Boundary
Shoreline Marshes
0
5
miles

Figure 2.

case about 3 feet per mile), onshore winds, an abundance of fine material, and a long straight or gently curving shoreline. Onshore winds cause the formation of waves which carry bottom materials such as silt, clay, sand and pebbles toward the shore where they are deposited. The process of uplift causes these ridges to be gradually removed from the influence of wave action leaving the beach ridge intact. Local processes such as drainage from the interior, local minor differences in relief, ice shove, and variation in sediments have a second order modifying effect resulting in the crowding of ridges, anastomoses, and short discontinuous ridges, superimposed on the basic parallel pattern.

These local effects have been especially important in the Cape area. Because of its situation at the confluence of a northerly and easterly influence, the beach ridges formed here are much wider and more extensive than those to be found elsewhere.

The system studied stretched north and south for about 15 miles with a maximum east - west dimension of 4 miles. Ridges in this system were composed of sand and gravel, with localized accumulations of boulder clay, and covered for the most part with a layer of peat of varying thickness, in places forming peat polygons, characteristic of permafrost zones.

The height of the system reached a maximum of about

Plate 2. (see text)

Plate 3. (see text)

25 feet above the level of the surrounding muskeg. The impression of flatness and uniformity evident in Plates 2 through 6 is due mainly to the size of this particular beach ridge, accentuated by the lack of any obstructions between the viewer and the horizon, and the apparent uniformity of the vegetation (Plate 2). On continued exposure this uniformity breaks down into a number of features of minor relief and a number of readily visible plant communities.

The major slopes of the ridge system are of course those that define the perimeter of the beach ridge. These are designated in Figure 2 by parallel solid and dotted lines. Aspect varies around the compass depending upon the location however the slope is fairly constant at about 20 degrees. Throughout the rest of the system there are smaller slopes that join the more exposed ridge tops with the lower drainage areas. These have variable aspects and angles of slope however none were found with heights of over 10 feet, much less than that of the perimeter slope.

Of the readily visible plant communities the most obvious is that of the low wet areas, probably drainage patterns, that are characterized by *Salix* and *Betula*(Plate 3). Also quite clear are the associations of the peat polygons (Plate 4).

(1.4) Climate

In general with the exception of very cold years the Cape Henrietta Maria area lies inside the often used

Plate 4. (see text)

$10^{\circ}C.$ isotherm, and in a transition zone between the very humid eastern part of the Labrador penninsula and the dry climate of northwestern Canada.

The nearest meterological stations to the research area are located at Churchill, Manitoba, 280 miles north-west, and Moosonee, Ontario, 263 miles south-south-east. Climatic summaries of these two stations are given in Tables 1 and 2 (recopied from Hare,1950). Comparison of these tables indicates that Moosonee has a slightly warmer climate (by $10^{\circ}F.$) and encounters more precipitation than does Churchill (by 4.5 inches). It is difficult to say what the conditions at the Cape should be like, however, assuming that the major variation lies north and south, one might suspect that it is more similar to Churchill. This would give it an annual mean temperature of about $20^{\circ}F.$ and an annual precipitation of about 16 inches which corresponds to values for the Hamilton area of $47.7^{\circ}F.$ and 32.4 inches. Clearly the climate of this area could be considered cold and dry.

x 1938-47	AIR TEMPERATURE (°F)[x] at Station Level								PRECIPITATION (inches)						CLOUDINESS			
		MEAN OF DAILY			MEAN MONTHLY		ABSOLUTE		MEAN OF MONTHLY						MEAN (Tenths)			
MONTH	MEAN DAILY	Maximum	Minimum	Range	Maximum	Minimum	Maximum	Minimum	Precip.	Rainfall	Snowfall	Precip. Days	Rain Days	Snow Days	0130 hrs	0730 hrs	1330 hrs	1930 hrs
January	-14	-7	-20	13	19	-39	32	-50	0.5	-	5	5	-	5	4.5	4.6	4.7	4.9
February	-15	-8	-21	13	17	-36	27	-42	0.6	-	6	6	-	6				
March	-3	5	-10	16	30	-30	40	-41	0.9	0.1	9	6	-	6				
April	11	19	4	16	42	-19	55	25	0.9	0.1	8	6	1	5	4.8	5.9	5.9	6.0
May	29	36	23	13	58	6	72	0	0.9	0.7	2	7	5	2				
June	42	50	35	15	75	25	86	-18	1.9	1.8	1	9	9	1				
July	54	63	45	17	82	36	85	31	2.2	2.2	-	10	10	-	6.1	6.2	6.5	6.3
August	53	59	46	13	79	37	89	32	2.7	2.7	-	12	12	-				
September	43	48	38	10	68	26	84	17	2.3	2.2	2	11	10	1				
October	31	35	26	9	55	9	65	0	1.4	0.6	8	12	5	8	7.8	8.2	8.7	8.5
November	9	15	3	11	34	-18	38	-28	1.0	-	10	9	0	9				
December	-6	0	-12	12	24	-31	34	-35	0.7	-	7	8	0	8				
Annual	20						89	-50	16.0	10.3	57	101	52	51				
Yrs. of Obs.	10	10	10	10	10	10	10	10	30	30	30	10	10	10	10	10	10	10

Table 1. Climatic Summary for Churchill, Manitoba.

MONTH	AIR TEMPERATURE (°F)x at Station Level								PRECIPITATION (inches)						CLOUDINESS			
	MEAN DAILY	MEAN OF DAILY			MEAN MONTHLY		ABSOLUTE		MEAN OF MONTHLY						MEAN (Tenths)			
		Maximum	Minimum	Range	Maximum	Minimum	Maximum	Minimum	Precip.	Rainfall	Snowfall	Precip. Days	Rain Days	Snow Days	0130 hrs	0730 hrs	1330 hrs	1930 hrs
January	-4	7	-15	21	35	-37	45	-44	1.4	-	14		-	17	5.3	6.6	6.0	5.1
February	-1	11	-13	24	33	-42	39	-47	1.1	-	11		-	13				
March	12	24	0	24	47	-30	60	-43	1.3	0.2	11		1	12				
April	26	36	15	21	64	-11	80	-24	1.1	0.5	6		5	7	4.8	6.7	6.5	6.4
May	41	51	31	20	80	15	92	1	1.6	1.3	3		11	3				
June	52	63	41	22	88	26	94	21	2.0	1.9	0.5		14	-				
July	60	71	48	23	89	33	96	29	2.3	2.3	-		14	-	4.7	6.3	7.1	6.4
August	59	69	48	21	85	33	95	30	3.0	3.0	-		16	-				
September	50	60	41	19	81	25	86	21	2.4	2.4	-		17	1				
October	40	48	32	16	70	15	80	3	1.8	1.5	3		13	8	6.3	7.4	8.1	6.4
November	22	29	15	14	51	-14	66	-30	1.1	0.2	8		5	17				
December	5	14	-5	18	36	-31	49	-39	1.4	0.1	13		2	21				
Annual	30						96	-47	20.5		70		98	99				
Yrs. of Obs.	10	10	10	10	10	10	10	10	40		40		10	10	8	10	10	10

Table 2. Climatic Summary for Moosonee, Ont.* * *

* Precipitation Values from Moose Factory, Ontario.

Section II

A PHYTOSOCIOLOGICAL APPROACH

(2.1) Introduction

Central to the phytosociological approach for the analysis of plant associations is the group of concepts and techniques developed by the Braun-Blanquet school in Europe. The Braun-Blanquet system attempts to classify plant communities into associations which are defined as abstractions "conceived from examination of a number of stands found in the field, each of which should have a minimum of characters which personify the association under all circumstances", (Braun-Blanquet 1959) The characters referred to are fidelity, presence, constancy and dominance. Classically the unit of measurement was the 'stand' or rélevé by which was meant the total uniform area sampled where uniformity includes the Braun-Blanquet concept of homogeneity in vegetation.

Poore (1955-56) criticized the classical methods on the grounds that they didn't take into consideration the importance of dominant species, that they over-emphasised fidelity as a character, and that they mis-takenly believed that the associations could be classified as hierarchy. In his subsequent modification of the procedure of association analysis he developed the concept of 'noda' as a term that applies to abstract vegetational units of any category. Implicit in this concept was the idea that although the associations or 'noda' were attempts at classifying units of vegetation, the 'noda' concept also recognised that vegetation in any area is a continuum, with a significant amount of overlap, and that a better type of classification would consist of 'pulling out the peaks'.

In a subsequent paper, Moore (1962) has defended the Braun-Blanquet method, pointing out that in the formation of associations the method does not rely overly much on fidelity "but takes into consideration the ecology, geography and the successional state of the stand." From a practical viewpoint this statement is far from clear.

While this represents an improvement, two important objections remain. Firstly, the Braun-Blanquet sociological method of analysing vegetation is highly subjective. However, balancing this is the fact that it is also a very rapid method of gaining useful information. Secondly, the method involves a circular argument that in choosing a defined homogeneous area to sample, the observer is essentially pre-defining the actual association.

The present study attempts to alleviate this problem by using a more systematic sampling method, but it is to be understood that both criticisms will apply to some extent. This is acceptable in view of the previously defined aims, the modified Braun-Blanquet approach being chosen as a preliminary survey method because of its speed and freedom from the necessity of using large quantities of complex equipment.

(2.2) <u>Methods</u>

The sample areas were chosen on the basis of aspect, slope, exposure, and terrain type. Transects were then laid out from a random start position in these areas in a direction that would optimize the sampling. Along each transect, sample plots 1m. x 1m. were laid out in a random fashion using a set of two co-ordinates in the range 0 to 5, the first co-ordinate designating the distance along the transect from the end of the last plot, the second, the distance away from the transect axis. Right or left was chosen by flipping a coin.

Within each sample plot, 50 quadrates, 5 cm. X 5 cm., were located again using a random co-ordinate system. The presence of each species in the quadrat was recorded. In the first five quadrats, a frame of 10 pins was established and the hits recorded to give an estimate of cover. Both the size of the quadrats and the size of the sample plots were chosen with reference to the type of vegetation under examination on the basis of the morphology of the plants.

The DOMIN (dominance) scale (Table 3) of X to 10 was used as a composite measure of cover and abundance with reference to the sample plots, since it is somewhat easier to use and more specific than the X to 5 scale of the Braun-Blanquet school. Although a subjective technique, it was found that four different people obtained the same sample values with only minor exceptions in the range of 6 to 8. It was therefore felt that these results would be fairly reproducable.

Table 3 (recopied from Kershaw, 1964)

TABLE OF DOMIN SCALE VALUES

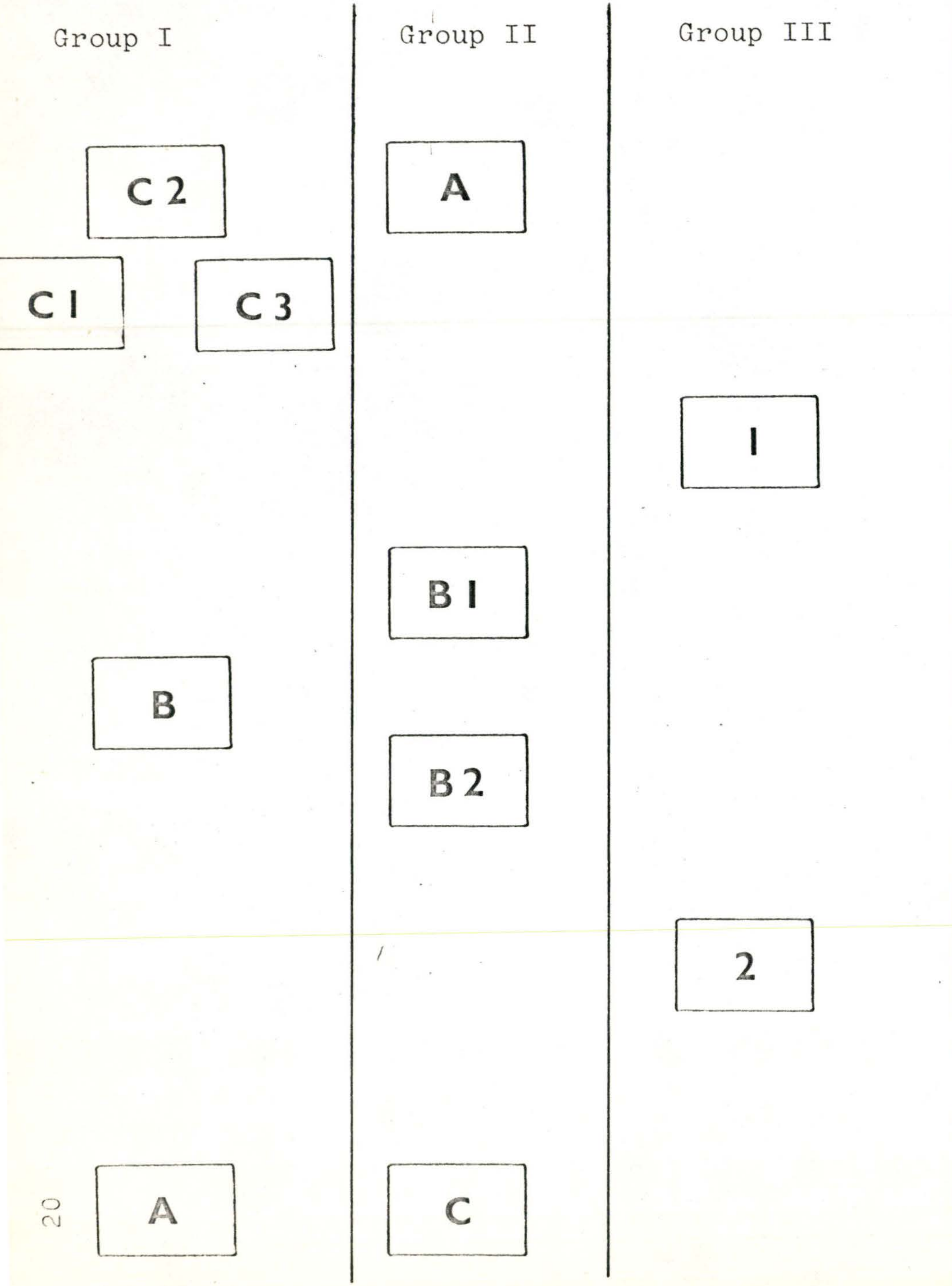
	Domin Value
Cover about 100 percent	10
Cover 75 percent	9
Cover 50 - 75 percent	8
Cover 33 - 50 percent	7
Cover 25 - 33 percent	6
Abundant, cover about 20 percent	5
Abundant, cover about 5 percent	4
Scattered, cover small	3
Very scattered, cover small	2
Scarce, cover small	1
Isolated, cover small	X

Extraction of the associations was carried out by grouping the releves (the data being punched on computer cards) according to their sample areas. Using the listing facility of IBM 407 accounting machine these groups were either sorted or merged on successive runs to achieve a final collection which optimized the similarity of stands within the groups and their dissimilarity without. This synthetic stage of the Braun-Blanquet method has been referred to by Moore et al (1970) as a "polythetic, subdivisive classification of releves, which achieves a quasi-statistical treatment of a large amount of descriptive information, not by mathematical methods, but by visual detection of correlated species occurances, and by a repeated re-writing of the table until a satisfactory visual pattern of 'blocks' of species entries appears."

The random location of the plots in this study follows the system established by Kershaw (1968) when extracting association units from vegetation. This sampling procedure does however tend to reduce the distinctness of the associations compared to those derived from standard Braun-Blanquet methods.

In addition to the subjective description of each plot, the following objective measures were taken to confirm and amplify the field notes. Equal volume soil samples were taken in each plot and placed in sealed plastic bags for analysis in the laboratory. These procedures were carried out four weeks later. The measurements chosen were pH and soil moisture, because of their simplicity and the fact that it was expected that soil moisture might show a correlation with the Group 2 associations, or that pH might show correlations with the Group 1 and Group 3 associations. The methods of analysis were as described in Metson (1961). pH was measured on the air-dry fraction after rehydration and equilibration of 24 hours. Soil moisture values were based on oven-dry weight after 24 hours. The moisture loss values were calculated both by weight and by volume, however the 'by volume' measure was used as it was considered more acceptable. Although some error is certainly expected in these analyses, it is considered that this is less than the natural variation between samples in the field.

Figure 3. Block Diagram of Original Braun-Blanquet Associations.



CORRESPONDING ASSOCIATIONS

IC2 Cladonia rangiferina, Empetrum nigrum, Vaccinium uliginosum.

IC1 Cladonia rangiferina, Empetrum nigrum, Alectoria ochroleuca.

IC3 Cladonia rangiferina, Alectoria ochroleuca, Vaccinium uliginosum.

IB Alectoria ochroleuca, Cladonia rangiferina, C. alpestris, Empetrum nigrum.

IA Cladonia alpestris, Cladonia rangiferina, Empetrum nigrum.

IIA Dryas integrifolia, Hedysarum Mackenzii.

IIB1 Cladonia rangiferina, C. arbuscula, Rhododendron lapponicum, Dryas integrifolia.

IIB2 Cladonia rangiferina, C. arbuscula, Cetraria nivalis, Dryas integrifolia.

IIC Vaccinium uliginosum, Rhododendron lapponicum, Dryas integrifolia.

III1 Cladonia rangiferina, C. arbuscula, Cetraria nivalis, Cornicularia divergans.

III2 Cladonia rangiferina, Empetrum nigrum, Vaccinium Vitis-Idaea, Rubus Chamaemorus.

(2.3) The Plant Associations -

The eleven plant associations extracted from the data on the basis of their floristic similarity are presented schematically in the block diagram shown below (Fig. 3), and in the tables to follow. The columns of the tables represent the species spectrum with associated cover/abundance values. It is worth stressing that this arrangement is only provisional and subject to revision on the basis of the objective analytical procedures to follow.

As seen from the diagram there are three basic groups. Group I is comprised of five associations that lie for the most part on slopes toward low, wetter areas. Group II consists of four associations that exist over a wide range of moisture regimes, but could be characterized by their location on fairly flat ground. Group III has only two associations, related by their occurrence together in an area of peat polygons underlaid by a layer of clay.

GROUP I - The Slope Associations

A) Bottom Slope - Cladonia alpestris, Cladonia rangiferina, Empetrum nigrum (Table 4)

The species composition of this association (Plate 5) could be provisionally related to a 'late snow lie' zone or a difference in microclimate, or the effect of peat accumulation and pH, or a combination of these. Sheltered at the bottom of the slope, this area has a fairly thick accumulation of peat, presenting an acid substratum. Work by Ahti (1961), Mattick (1932), and Dahl (1956), indicates that these factors provide favourable conditions for the growth of these species.

Table 4

Cladonia alpestris-Cladonia rangiferina-Empetrum nigrum Association

Cladonia alpestris	9	6	7	6	8	9	6	7	9	9	9
Cladonia rangiferina	x	1	3	8	6	5	7	4	2	4	4
Empetrum nigrum	x	7	4	4	4	3	5	5	4	4	4
Vaccinium uliginosum	3	4	5	3	3	3	3	4	5	6	1
Cetraria islandica	4	4	4	2	2	1	4	2	2	2	2
Vaccinium Vitis - Idaea	2	3	3	3	2	2	2	2	1	2	1
Cladonia arbuscula	1	3	3	3	5	2	3			3	x
Ptilidium ciliare	x	3	2	2	2	x	1	2	x	1	
Arctostaphylos rubra		3	3	1	3			6		x	
Andromeda polifolia	3	2	3					2	1	2	
Salix reticulata		1			1	1	3		2	1	2
Cetraria nivalis	1	3	1	2	x		4				x
Cladonia gracilis var. gracilis	2	2	1	1	x	1	2				
Cladonia amaurocraea			x	2	2		3				x
Pedicularis flammea	1	1			1		1	1	1		
Dryas integrifolia		x	1	1			3				
Alectoria ochroleuca		x		2			2				x
Stereocaulon alpinum				1				2			x
Cetraria cuculata				1		x	2				
Dactylina arctica			1	x				1			
Cladonia mitis					1					2	
Tortella tortuosa		1	x	x			x	x			x
Hylocomium splendens		1						x	x		x
Arenaria rubella					2		x				
Shepherdia canadensis	x		2								
Poa glauca											2
Stereocaulon paschale	1		x								
Peltigera aphthosa		1							x		
Thamnolia vermicularis				1			x				
Cladonia rangiferina f. humilis					x		1				
Spherophorus globosus							1				
Rhododendron lapponicum				1							
Anemone Richardsonii											1
Carex scirpoidea	x			x						x	
Campylopus flexuosus					x			x			
Carex rupestris											x
Peltigera canina var. rufescens			x								
Ochrolechia frigida							x				
Alectoria nigricans							x				
Cladonia coccifera	x										
Cladonia chlorophaea	x										
Cladonia gracilis var. dilitata	x										
Betula nana							x				

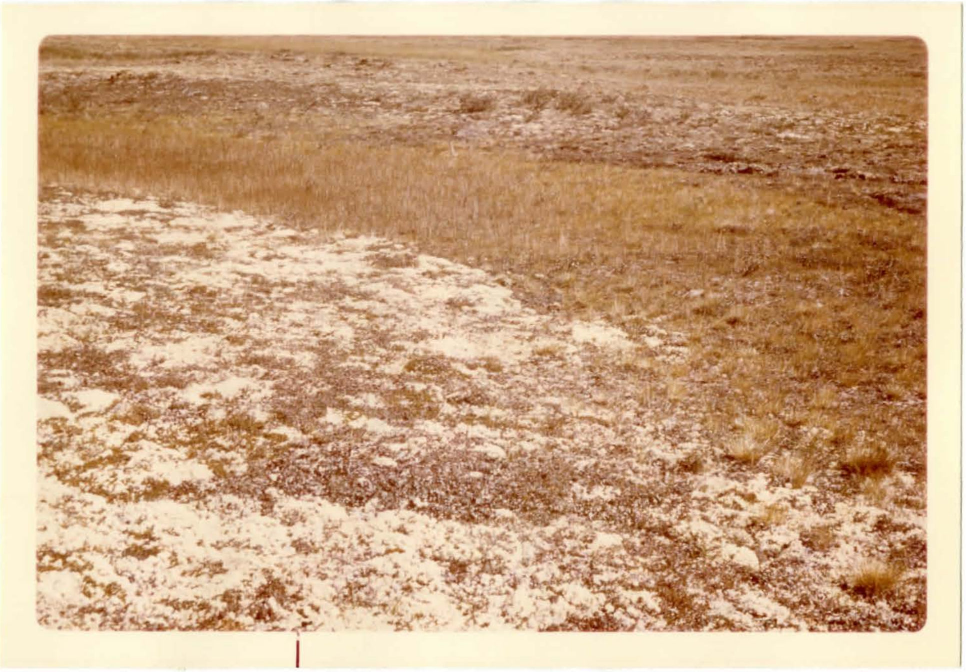


Plate 5. (see text)

The presence of Cladonia rangiferina is not necessarily significant in that it has a wide ecological tolerance. For example C. rangiferina is the last lichen to survive among C. alpestris in the so-called second reindeer lichen phase (Ahti 1959).

B) Intermediate Slope (Table 5) - Alectoria ochroleuca, Cladonia alpestris, Empetrum nigrum.

This association, characterized by the dominance of Alectoria ochroleuca was found in locations of moderate slope usually just up from the bottom slope association mentioned above. It is clearly related to this plant community as seen in the presence of the former's dominant species. Most likely this intermediate association is also intermediate in the same gradient of conditions, that is, snow lie and peat accumulation, responsible for the other associations of the slopes.

C) Upper Slope (Tables 6 - 8)

On a floristic basis alone it is possible to separate out three associations that characterize the upper slopes, namely:

1) Cladonia rangiferina, Empetrum nigrum, Vaccinium uliginosum.
2) Cladonia rangiferina, Empetrum nigrum, Alectoria ochroleuca.
3) Cladonia rangiferina, Alectoria ochroleuca, Vaccinium uliginosum.

Alectoria ochroleuca-Cladonia rangiferina-Cladonia alpestris-Empetrum nigrum Association

Alectoria ochroleuca	8	7	7	7	7	6	7	7
Cladonia rangiferina	5	5	6	6	6	5	4	5
Cladonia alpestris	6	7	7	5	6	7	6	6
Empetrum nigrum	4	5	5	4	5	4	5	5
Cetraria islandica	2	2	3	3	3	3	3	1
Vaccinium uliginosum	3	1	3	2	2	3	2	1
Vaccinium Vitis - Idaea	2	x	2	2	2	3	2	2
Cetraria nivalis	1	x	2	3	1	1	2	2
Cornicularia divergans	3	3	3	2	2	2	4	6
Cladonia arbuscula	2	1	1	1	1	x	2	2
Cetraria cuculata	2	1	1	2	1	1	2	2
Rhododendron lapponicum	3		3	3				
Dryas integrifolia	2		2	2		3		1
Poa glauca			3	2	2	1	2	
Hylocomium splendens	1					2		
Campylopus flexuosus					2		1	2
Dactylina arctica			x	x	x		x	
Ptilidium ciliare			x	2	x			
Alectoria nitidula	x				x		1	1
Alectoria nigricans				1			1	1
Cladonia amaurocraea					x			x
Ledum decumbens							3	
Pyrola grandiflora	3							
Isothecium myurum							1	
Polytrichum juniperinum			x	2				
Tortella tortuosa	x			1	x	x		
Cladonia rangiferina f. humilis	1	x			x		x	x
Carex scirpoidea	x					x		
Arenaria rubella				1				
Sphaerophorus globosus				x			x	
Thamnolia vermicularis						x		

Table 6

Cladonia rangiferina-Empetrum nigrum-Vaccinium uliginosum Association

Cladonia rangiferina	5	5	5	8	6	6	6
Empetrum nigrum	2	7	3	5	3	4	4
Vaccinium uliginosum	6	5	3	4	5	2	2
Cladonia alpestris	3	6	4	3	x	1	3
Cladonia arbuscula	4	1	1	6	4	3	3
Vaccinium Vitis - Idaea	3	4	3	4	4	3	2
Cetraria islandica	3	4	4	3	4	3	2
Alectoria ochroleuca	2	2	3	2	2	6	6
Cetraria cuculata	2	2	3	2	1	2	3
Cetraria nivalis		2	2	3	7	3	3
Cornicularia divergans		1	1	x	1	5	5
Isothecium myurum	1	1	2	1	x	x	1
Rhododendron lapponicum		2	x	1	1	2	1
Hylocomium splendens	4	x	x	1			
Dryas integrifolia		2		2	x	3	x
Thamnolia vermicularis	1	1	x	1	1	x	
Dactylina arctica		x	x	2	x	1	
Cladonia gracilis var. gracilis	2		x	x	x	x	
Campylopus flexuosus			x	x	2	1	
Arctostaphylos rubra			2		2		
Tortella tortuosa	3			1			
Equisitum variagatum	1		1		x		
Cladonia amaurocraea	1			1			
Poa glauca			1	1			
Pedicularis flammea	x	x	1		x		
Salix calcicola	x	3	x				
Sphaerophorus globosus			x	x	x	1	x
Salix reticulata	2		x				
Dicranum scoparium	x	x	x	x			
Cladonia pyxidata			x	x	x		
Ochrolechia frigida				x	2		
Carex scirpoidea	2						
Ptilidium ciliare	x		x				
Silene acaulis	x				x		
Polygonum viviparum	x						
Arenaria rubella					x		
Astragalus alpinus						x	
Carex arctogena			x				
Carex rupestris				x			
Peltigera aphthosa			x				
Bilimbia sabuletorum				x			
Cladonia chlorophaea	x						
Cladonia coccifera					x		

Cladonia rangiferina-Empetrum nigrum-Alectoria ochroleuca Association

Cladonia rangiferina	7	6	7	7	8	6	6	7
Empetrum nigrum	5	7	5	6	3	1	3	5
Alectoria ochroleuca	5	4	3	3	4	4	5	3
Cladonia arbuscula	4	4	4	4	4	3	3	3
Rhododendron lapponicum	4	4	x	3	3	6	2	4
Cladonia alpestris	3	4	3	3	4	3	2	5
Cetraria islandica	4	4	3	2	2	2	3	3
Vaccinium uliginosum	3	4	4	3	3	4	2	3
Cetraria nivalis	3	2	4	3	3	3	4	3
Cetraria cuculata	3	3	3	3	3	3	3	2
Vaccinium Vitis - Idaea	3	3	2	3	3	3	3	3
Cornicularia divergans	1	2	2	2	2	2	4	
Isothecium myurum	1	3	1	2	2	2	3	2
Dryas integrifolia	2	3	x	2	1	1	3	2
Thamnolia vermicularis	1	2	2	2	2	2	1	
Sphaerophorus globosus	2	2	2	2	1	1	1	
Alectoria nigricans	x	2	1	2	1	1	2	
Alectoria nitidula	x	x	x	2	3	3	2	x
Dactylina arctica	1	x	1	3	2	2	x	1
Ptilidium ciliare	2	2	2	2	1			2
Equisetum variegatum			4		2	2		
Tortella tortuosa	1	1	x	x	1	1	x	x
Campylopus flexuosus	x		2	x	x	2		x
Peltigera rufescens	x	1	2					
Arctostaphylos rubra			1			2		
Polytrichum juniperinum						2	1	
Rhacomitrium lanuginosum					3			
Cladonia uncialis	3							2
Ochrolechia frigida			2		x	x		
Cladonia rangiferina f. humilis					x	1	1	
Hylocomium splendens	1		x		x			4
Stereocaulon alpinum			2					
Peltigera aphthosa	x			1				
Pertusaria dactylina			1					
Cladonia gracilis var. gracilis	x	x	x	x	x	x		
Cladonia chlorophaea			x		x	x		
Pedicularis flammea	x		x	x				
Cladonia coccifera			x					
Ochrolechia upsaliensis					x			
Bilimbia sabuletorum					x			
Pertusaria coriacea			x					
Carex rupestris	x							
Carex capillaris						x		
Carex scirpoidea	x							1
Hedysarum Mackenzii		x						2
Salix reticulata			x					

Cladonia rangiferina-Alectoria ochroleuca-Vaccinium uliginosum Association

Cladonia rangiferina	5	8	3	6	5	7	4	6	6	5	6	5	6	5
Alectoria ochroleuca	6	4	6	7	5	5	4	7	7	6	5	8	5	6
Vaccinium uliginosum	3	4	3	5	3	5	4	4	3	2	4	4	5	3
Vaccinium Vitis - Idaea	3	2	3	3	4	3	3	3	3	3	3	3	4	3
Cladonia arbuscula	l	6	6	3	l	x	l	3	3	l	4	2	2	2
Cetraria islandica	2	3	3	3	2	3	4	3	3	3	3	3	2	3
Dryas integrifolia	2	3	l	4	x	2	2	2	3	2	2	4	x	2
Cetraria cuculata	l	3	2	3	2	2	3	2	2	2	3	3	3	2
Cetraria nivalis	3	l	l	l	l	2	3	2	3	l	3	l	2	3
Empetrum nigrum	4	2	4		4	x		2	5				4	4
Rhododendron lapponicum	2	l	3		3	3	3	x	3	3			4	4
Equisetum variegatum	l	l		x	3	2	2	l			x		2	2
Ptilidium ciliare	2	l	l		x	l			l	x		2		l
Arctostaphylos rubra	x	x		2	3	3	3		2		x	l	l	4
Isothecium myurum			x	l	4	3	2	x	l	2	2	l	2	3
Hylocomium splendens		x	2	x	l	l	l		l	x			l	l
Cladonia gracilis var. gracilis		l	l	l		l	x	x			x	l	l	x
Thamnolia vermicularis	l		x		2	l	2		l		x	x	2	l
Dactylina arctica	l		x	x	l	l	x	l	l	l	x	x	l	2
Cornicularia divergans	l		l	x		l	3	l	3	l	5	3	l	3
Pyrola grandiflora		x	l			l							x	l
Poa glauca			x	x	x	2	x	l	2	l	l	l	l	l
Salix reticulata	x	x		l			l	x	l	2		x		
Pedicularis flammea		2			x		x			x	x	x		x
Cladonia amaurocraea			x	l								x		
Tortella tortuosa				x	x	x	l		x		x	l	x	x
Dicranum scoparium	x	x		x			l		x	x				
Campylopus flexuosus		x		x		x	x		x		l	x	l	
Arenaria rubella		x		x		x					x			
Ledum decumbens	l										x			
Carex saxatilis		l												
Peltigera rufescens	x					x				x				
Polygonum viviparum			x	x			x					l		
Cladonia alpestris			x							x				
Cladonia coccifera				x			x							
Ochrolechia frigida					x							x		
Peltigera aphthosa	x						x			x				
Stereocaulon alpinum					x			x					x	x
Carex rupestris			x				l							
Salix calcicola						x				3				
Ranunculus lapponicus		x												
Cladonia gracilis var. dilitata		x										x		

Plate 6. (see text)

The interrelations between the above 'noda' are obvious at least in terms of their dominant species. From their common location on the upper regions of the slopes it is tempting to group them together into one large association, however, they are different enough in terms of the dominance and fidelity of their species to deserve separation at this point, at least in the Braun-Blanquet sense. Aspect suggests itself as a possible explanation for their differences but there is no consistent enough pattern to provide a reliable basis for this argument. Other possibilities such as differences in substrata may underly their disparity but again lack of evidence makes it necessary to leave these groups as they are until the results of the objective analyses are available.

GROUP II - The Central Associations

A) Exposed Ridges - Dryas integrifolia, Hedysarum Mackenzii. (Table 9)

The lack of protection from wind stress and scouring, on the tops of the ridges and knolls, of the beach ridge system, prohibits the establishment of any but the most hardy species. Both Dryas integrifolia and Hedysarum Mackenzii are characteristic pioneer species, on frost-heaved, calcareous, gravelly and rocky barrens (Porsild 1964). The factors controlling the species composition of this association (Plate 6) thus appear to

Dryas integrifolia-Hedysarum Mackenzii Association

Dryas integrifolia	9	8	7	9	7	8	6	8	9	9	9	9
Hedysarum Mackenzii	5	5	6	6	5	6	5	5	6	6	7	6
Cetraria islandica	3	4	3	3	3	3	3	3	2	3	4	4
Thamnolia vermicularis	3	3	3	3	3	3	3	2	3	3	3	3
Isothecium myurum	2	2	4	3	l	2	3	l	2	2	3	3
Carex rupestris	3	2	3	2	3	3	2	2	2	2	3	3
Alectoria ochroleuca	3	3	3	3	2	2	3	2	2	3	2	2
Cetraria cuculata	3	3	2	2	l	2	2	2	l	2	3	3
Ochrolechia frigida	3	x	4	x	2	2	x	4	2	2		x
Vaccinium uliginosum	2	3	5		l	4	5	x	x			
Oxytropis hudsonica	x		2	l	3	3	l	2	3	2	x	x
Physcia muscigena	2	2	2	l	2	2	x	2	3	2	l	2
Cetraria nivalis	2	2	2	x	l	l	2	2	l	l	l	2
Alectoria nitidula	2	4	2	l		x	3	l	x		l	l
Alectoria nigricans	l	2	2	l		x	3	x	l		l	l
Cladonia gracilis var. gracilis	l	x	l	l		x	2	x	x		2	3
Cornicularia divergans	l	l	l	l		l	l	l	l	l	l	l
Campylopus flexuosus	l	x	l		3	2		l	2	l		
Tortella tortuosa	x	3	l	x		l		l	l	l		l
Rhododendran lapponicum	l	3	4				3	l				
Anthelia julacea		l				x		l	l	l	l	2
Astragalis alpinus	l	2		l			2	l			l	
Caloplaca subolivacea			l		2	l		2	l	2		
Bryum inclinatum		l		l	x	x		l	l	l	l	l
Lecanora epibryon						l		2	2	l		
Cladonia rangiferina	l	2	x	x		x	l	x	x		x	x
Parmelia physodes	x		l	x	x	x	x	x			l	x
Dactylina arctica	2	l	2	x	x	l					l	l
Cladonia arbuscula	x	l			x	l					x	x
Bilimbia sabuletorum	x		l		x	x		l	l	x		
Caloplaca elegans			x			x		l	l	x		
Stereocaulon paschale	l						x				x	2
Pertusaria dactylina						x		l	l			
Pertusaria coriacea	x		l					x				
Cladonia chlorophaea		l	x									
Cladonia gracilis var. dilitata		2										
Vaccinium Vitis - Idaea							l					
Polytrichum juniperinum		l										
Hylocomium splendens		x					x		x	x		
Peltigera canina var. rufescens									x			
Cladonia amaurocraea				x								
Cladonia pyxidata									x			

be the ability of the species to colonize and grow on an exposed site, and a tolerance for fairly high pH levels. A further factor involved may be the dry nature of the tops of these ridges. The vegetation type would necessarily be one with a low water requirement. These conditions are born out by the presence of these two species colonizing the edge of a road that had been scraped out with a bulldozer during construction of the base about 1953.

B) The Central Lichen Heath Associations (Tables 10, 11)

Two associations were extracted from the data that fit into this category; these are the associations characterized by:

1) Cladonia rangiferina, Cladonia arbuscula, Rhododendron lapponicum, Dryas integrifolia, Vaccinium uliginosum, Hedysarum Mackenzii.

2) Cladonia rangiferina, Cladonia arbuscula, Cetraria nivalis, Dryas integrifolia.

This vegetation type was the most common of the lichen dominated, raised beach system, covering an estimated 40 percent of the total beach area. Although closely related, the two associations appear to represent a topographic gradient. The first association, including Hedysarum Mackenzii, consisted mainly of stands situated centrally on a low rise in the ground, (slope approximately 6 degrees), while the second association, in which Hedysarum Mackenzii was lacking, but which included Cetraria nivalis, consisted of plots that

Table 10

Cladonia rangiferina-Cladonia arbuscula-Rhododendron lapponicum-Dryas integrifolia-Vaccinium uliginosum-Hedysarum Mackenzii Association

Cladonia rangiferina	8	7	4	3	8	7	7	7	4	4	5	5	7	7	6	6	7	4	4	4
Cladonia arbuscula	x	6	2	3	6	6	3	3	l	4	4	3	5	4	4	5	6	3	2	3
Rhododendron lapponicum	5	6	2	3	3	2	2	2	2	2	3	3	2	4	3	3	6	4	3	4
Dryas integrifolia	4	l	3	2	3	2	3	4	4	4	2	4	4	4	4	5	5	3	7	6
Vaccinium uliginosum	l	2	4	3	4	2	3	2	3	3	3	4	3	4	5	l	2	3	l	4
Hedysarum Mackenzii	5	2	4	2	x	l	4	x	l	4	2	3	l	x	2	3	x	4	3	4
Cetraria nivalis	3	3	4	2	2	2	3	4	2	3	3	3	3	3	3	5	5	2	l	l
Alectoria ochroleuca	4	4	4	4	4	2	4	3	3	4	3	3	3	3	3	3	5	3	4	3
Cornicularia divergans	4	4	2	2	2	2	4	4	2	3	2	3	3	4	4	3	3	2	2	l
Cetraria islandica	2	2	3	2	2	2	3	3	2	3	3	4	3	2	3	4	4	3	2	2
Empetrum nigrum	x	4	3	2	2	6	2	4	x	2	3	x	x	2	3	x	l	2		
Cetraria cuculata	l	l	3	3	2	3	2	2	2	3	3	3	3	3	3	l	l	x	2	2
Vaccinium Vitis - Idaea	l	3	l	x	2	2	2	3	3	2	3	2	3	2	2	l	2	2	2	l
Alectoria nigricans	4	x	l	2	3	3	l	2	x	l	l	l	l	l	l				x	3
Carex rupestris	5	l	3	2	2	l	l	l	l		x		l		l	3	3	2	3	l
Thamnolia vermicularis	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Spherophorus globosus	2	l	x	x	l	l	l	2	2	2	l	2	2	3	2	2	l	l	x	x
Dactylina arctica	l	l	x	l	l	l	l	l	l	l	l	l	l	l	l	x	l	l	x	l
Campylopus flexuosus	l	l	x	x	l	l	l		l	l	l		2		l	x		l	x	l
Isothecium myurum		2	l	l	l		l		2	x	l		l	2		x	x	l	l	2
Ochrolechia frigida		x		2		l	x	2	3	l	l	l	l	x	x		2	2		
Alectoria nitidula														3	3					
Kobresia simpliciuscula									2	2	x									
Salix calcicola										2	2									
Dicranum scoparium									2		x							x		
Carex scirpoidea		l	x						x		x	l				x	x	x		
Tofieldia pusilla								x			l				x			l		
Cladonia gracilis var. gracilis													x	l	l					
Cladonia chlorophaea		x		x		x	x		x			l								
Pertusaria coriacea						x	x	x								l		x		
Astragalus alpinus							x		x	x								l		x
Cladonia pyxidata									x		x		l							
Caloplaca elegans									l							x	x			
Tortella tortuosa					x				l	x				x						
Carex capillaris		x				l					x									
Pedicularis flammea										x				l						
Andromeda polifolia										l										
Cladonia mitis										l										
Cladonia coccifera				x		x	x									x				
Parmelia physodes	x		x																	x
Bilimbia sabuletorum		x							x									x		
Polygonum viviparum							x													
Cladonia alpestris				x																
Cladonia amaurocraea														x						
Pertusaria dactylina							x													
Physcia muscigena										x										
Hylocomium splendens														x						
Oxytropis hudsonica													x							
Cladonia gracilis var. dilitata																		x		

Cladonia rangiferina-Cladonia arbuscula-Cetraria nivalus-Dryas integrifolia Association

Cladonia rangiferina	7	7	6	7	6	8	6	8	5	5	7	9	6	5	9	7	7	8	5	7	6
Cladonia arbuscula	6	5	4	5	5	5	3	7	4	4	6	7	2	4	6	3	6	6	3	4	6
Cetraria nivalus	5	3	3	3	3	3	3	3	3	6	4	3	5	4	4	5	4	4	4	3	4
Dryas integrifolia	5	5	4	2	5	3	4	4	2	2	4	1	2	x	3	3	3	1	4	4	4
Cornicularia divergans	3	3	3	3	4	4	3	2	2	2	2	1	3	1	4	5	3	2	4	4	4
Alectoria ochroleuca	4	4	4	3	3	4	4	3	3	2	3	2	4	1	1	2	3	2	3	3	3
Vaccinium uliginosum	3	2	1	2	2	3	3	2	3	2	2	4	1	4	5	4	4	4	3	4	5
Vaccinium Vitis - Idaea	3	2	3	3	4	2	2	3	1	5	3	3	4	3	2	3	2	2	3	2	2
Cetraria islandica	3	2	3	3	2	3	3	3	3	3	3	3	4	4	2	3	3	3	3	2	3
Cetraria cuculatta	1	1	2	2	2	3	2	3	2	3	1	2	2	3	3	4	3	3	3	3	3
Rhododendron lapponicum	2	2	3	2	3	2	3	3	3	2	x	x	1	3	1	2	2	3	3	4	3
Sphaerophorus globosus	2	1	1	2	3	1	1	2	2	3	2	x	1	1	3	3	3	3	3	3	2
Empetrum nigrum			4	4	1	2	x			6	4	3	4	5		x		3	4	2	2
Carex rupestris	3	3	2	1	3	2	3	3	4		1						2	x		1	1
Thamnolia vermicularis	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	2	2	1	2	3
Dactylina arctica	1	1	1	x	x	1	1	1	1	1	1	1	2	1	x	1	1	1	x		1
Alectoria nitidula													1	x	3	4	4	3	3	3	3
Alectoria nigricans						2	2	2				x			x	1	2	2	2	1	1
Ochrolechia frigida	1	1	2	1	2		1	2		1		x	1	1				x		x	x
Cladonia gracilis var. gracilis				x										x	1	1	2	2	2	1	1
Cladonia amaurocraeae									x						1	2	1	3		x	
Campylopus flexuosus	1	1		x	x		x	1				x			x	1	x	1	1		1
Isothecium myurum				1		x	x		1	x	x	x	x	x	1	1		x	4	2	
Pertusaria dactylina			1	1	1					x											
Polytrichum juniperinum											x		x			x	1	x	1		
Tortella tortuosa						x		1	x		x							1			
Pedicularis flammea											x				3			x	1		
Astragalus alpinus		1		x	x		x	x	1												
Dicranum scoparium										1		x	x	x							
Cladonia chlorophaea								1	x			x		x							
Oxytropis hudsonica									1								2				x
Ptilidium ciliare										x	2	1	x	x							
Tofieldia pusilla							x		x					x							x
Hylocomium splendens										x		x	x							x	
Caloplaca elegans	x																x				
Ochrolechia upsaliensis																		x			
Parmelia physodes																	x				
Physica muscigena																			x		
Bilimbia sabuletorum																		x			
Peltigera aphthosa																			x		
Stereocaulon paschale													x								
Carex capillaris																		x			
Arenaria rubella														x							
Cladonia crispata								x													
Cladonia gracilis var. dilitata									x						x						
Poa glauca												x									

were located to the sides of this central rise. As with the intermediate slope associations, it appears that here also a gradient exists that has one extreme in the dry, calcareous, Dryas - Hedysarum association of the exposed ridges, and proceeds to a moist calcareous association described as follows:--

C) The Depression Areas - Vaccinium uliginosum, Rhododendron lapponicum, Dryas integrifolia. (Table 12)

The whole raised beach system is marked by a series of low or depressed areas which appear to provide some drainage between the numerous shallow lakes. Although most of these are low and wet enough to support areas of Salix spp and Betula, with a number of grass and sedge species, many other areas are characterized by the above mentioned association. It would appear that the factors controlling the distribution of this vegetation type are a high water availability, and a sandy substratum with a high pH. However, the fact that all these species are found in other associations would indicate a wide ecological tolerance for them, plus some other factor that controls their establishment in this particular location.

GROUP III - The peat Polygon Area (Tables 13,14)

The two associations indicated in this group:

1) Cladonia rangiferina, Cladonia arbuscula, Cetraria nivalis, Cornicularia divergens.

Table 12

Vaccinium uliginosum-Rhododendron lapponicum-Dryas integrifolia Association

Vaccinium uliginosum	5	6	8	7	5	7	8	7	4	7	6	6	6	4
Rhododendron lapponicum	4	4	5	4	3	4	3	3	2	3	3	3	4	3
Dryas integrifolia	5	6	x	4	3	3	1	4	2	x	5	4	5	3
Arctostaphylos rubra	x	5	1	3	5	2	2	4	2	x	1	1	3	x
Isothecium myurum	4	3	x	3	3	1	4	2	1	2	2	1	2	2
Dicranum scoparium	4	3	1	3	3	2	2	2	x	3	3	x	3	3
Carex capillaris	2	2	2	3	2	3	3	3	3	2	3	1	2	2
Carex scirpoidea	2	2	3	2	1	1	x	1	2	2	2	4	2	1
Carex repestris	3	3	x	2	3	1	3	4	2	2	4	2	x	x
Tofielda pusilla	2	3	2	2	2	3	3	3	2	1	3	x	3	2
Campylopus flexuosus	1	1	6		x	1	2	3	3	1	2	2	x	4
Tortella tortuosa	1	1	x	1	2	x	1	1	x	1	1	x	x	x
Hylocomium splendens	2	1	x	2	1	1	1	1	x	1	x	1	2	1
Astragalus alpinus	3	2		3	1	1	3	3	2	2	2	2	2	x
Bilimbia sabulatorum	1	1	2	x	1	2	x	2			x			
Ochrolechia frigida	2	1	1	3		1	2	2	1	x	1	1	1	
Scirpus caespitosus	1	2	1		1	3	1	2	6	1	x			3
Cladonia gracilis var. dilitata	2	1		2	2	2	2	2		1	2		1	1
Rhacomitrium lanuginosum	3	x		1		1		2		1	3	1	4	1
Salix reticulata	1		2			1	2	x	1	2		3		
Salix calcicola			x	1	4		x		5			4		x
Silene acaulis				3	x	1	3	x	1	x	x	x	3	2
Carex arctogena	x	1	2	1	x	2			1	2		x		
Pedicularis flammea	x		x	1		1	2	2	1	1	1	2	2	1
Polygonum viviparum		x		1	x	x	1	1	1	x	1	2	2	2
Lecanora epibryon	1	x	2	1		1	2	1						
Cetraria islandica	1	x	x	2	2			x				x	4	
Empetrum nigrum	x	x		x		x	x	2		x	x	2	x	1
Cladonia chlorophaea	x	x	x			2		1		2	1		2	
Cetraria nivalis	1		x	1			x	x				x	4	
Thamnolia vermicularis	1			2		x		1					1	
Oxytropis hudsonica		1		x	x	1					1	1		
Cladonia rangiferina	x			x	2								1	
Andromeda polifolia					1							1		
Arenaria rubella											2			
Kobresia simpliciuscula								1	x		x			2
Physcia muscigena							1							
Dactylina arctica					1									
Pertusaria dactylina	x				1	x				x				
Equisetum variegatum												1	2	1
Caloplaca elegans	x		x		x	x		x						
Cetraria cuculata	x			x	x							x	3	2
Hedysarum Mackenzii		x			x							x	x	
Cornicularia divergens	x				x			x					2	
Pinguicula vulgaris									1					
Sphaerophorus globosus				x									x	
Carex rariflora	x													
Cladonia arbuscula									x				x	
Poa glauca												x	x	

Cladonia rangiferina-Cladonia arbuscula-Cetraria nivalis-Cornicularia divergens Association

Cladonia rangiferina	6	6	8	8	7	7	5	8	6	8
Cladonia arbuscula	5	5	7	6	6	6	5	6	6	2
Cetraria nivalis	4	3	4	4	3	3	3	4	3	4
Cornicularia divergens	5	2	2	4	3	4	2	4	5	3
Empetrum nigrum	4	7	4	2	x	2	6	4	x	4
Alectoria nitidula	6	3	3	4	2	2	l	2	3	3
Ledum decumbens		2	5	3	4	4	l	4	6	3
Cetraria cuculata	3	3	3	3	3	3	3	3	3	3
Vaccinium Vitis - Idaea	3	3	3	3	3	3	3	3	3	3
Alectoria ochroleuca	3	l	2	2	3	3	3	3	4	5
Vaccinium uliginosum	2	2	3	3	3	3	3	2	4	3
Cetraria islandica	2	l	2	2	2	2	3	3	2	3
Poa glauca	2	3	3	2	2	l	2	x	l	3
Sphaerophorus globosus	3	2	l	2	2	2	l	l	l	l
Ochrolechia frigida	x	x		2	2	2	x	2	l	
Campylopus flexuosus		x	l	l	l		2	2	l	2
Dactylina arctica	x			x	l	x	2	l	l	2
Cladonia amaurocraea	l	l	l			l	x			l
Ptilidium ciliare		2	2	x	l		3			
Rubus chamaemoris					x	3	2	x	x	l
Thamnolia vermicularis	l	l	x	l	x	l	x	x	x	l
Cladonia gracilis var. gracilis	2	2	l	l	l	l	l	x		x
Polytrichum juniperinum	x	x			2	l	x			2
Alectoria nigricans					x	l	2	2	x	
Dryas integrifolia	2		x				2	x	x	
Tortella tortuosa	x	l	l	x			2	x		
Isothecium myurum	x	x					2			2
Arenaria rubella	2	l	x		l					
Cladonia chlorophaea	x	x			2	l				x
Cladonia coccifera				x	x			l	x	x
Salix planifolia		x	x		x		l			
Hylocomium splendens	x			x			l			
Salix reticulata							3			
Rhododendron lapponicum	3									
Cladonia rangiferina f. humilis									3	
Peltigera aphthosa	l						x			
Pedicularis flammea	l									
Cladonia pyxidata	x			x						
Dicranum scoparium	x						x			
Polygonum viviparum	x						x			
Carex scirpoidea					x					

Cladonia rangiferina-Empetrum nigrum-Vaccinium Vitis - Idaea Rubus Chammaemorus Association

Cladonia rangiferina	5	7	4	7	3	6
Empetrum nigrum	6	7	9	5	5	8
Vaccinium Vitis - Idaea	3	3	5	4	4	4
Rubus Chammaemorus	4	5	3	4	5	3
Ledum decumbens	5	2	1	4	4	4
Isothecium myurum	3	4	4	3	3	4
Cetraria islandica	2	2	3	3	4	4
Cetraria cuculata	2	2	3	3	4	3
Tortella tortuosa	3	2	3	2	4	3
Alectoria ochroleuca	2	3	3	4	4	1
Cetraria nivalis	2	1	2	2	3	3
Polytrichum juniperinum	3	4	3	4	4	x
Campylopus flexuosus	1		1	3	5	6
Poa glauca	2	2	1	2	2	2
Dactylina arctica	1	1	1	1	2	1
Cladonia amaurocraea	x	x	4	x	1	3
Cladonia alpestris	2		x		x	x
Cladonia arbuscula	x	x	x	x	x	1
Hylocomium splendens	x	1	2			1
Thamnolia vermicularis	1	1	x	x		1
Ranunculus lapponicus		x	2		x	x
Peltigera apthosa		2	x	x		x
Ochrolechia frigida	2	x	1		1	
Cladonia coccifera	x	x		x		
Vaccinium uliginosum					1	1
Cladonia gracilis var. gracilis			1			1
Cladonia chlorophaea			1			x
Cladonia rangiferina f. humilis	x	x				
Cornicularia divergens			x		1	
Dicranum scoparium					1	
Peltigera canina var. rufescens			x			
Sphaerophorus globosus						x
Salix planifolia						x

2) Cladonia rangiferina, Empetrum nigrum, Vaccinium Vitis-Idaea, Rubus Chamaemorus

each have a marked resemblance to associations in the preceding groups, but small differences in species composition, plus the obvious differences in the geography of their location, indicated that they should be separate. The presence of the polygon formation indicates a different microclimate, that might alter conditions somewhat from the flatter areas of the central associations. In addition the presence of clay under the area, although 8 to 12 inches down, may be significant.

Whereas the peat polygon formation is fairly dry, especially on the tops of the polygons, the whole area slopes down to a wetter depression, characterized by the second association. The slow breakdown of the mossy substratum, (Sphagnum spp.) leads to a rather low pH, which provides optimum conditions for the establishment of Rubus Chamaemorus (Porsild, 1964) and Empetrum nigrum.

SECTION III AN OBJECTIVE APPROACH TO ASSOCIATION ANALYSIS . . .ORDINATION

(3.1) Introduction

The subjective nature of the Braun-Blanquet and related techniques of extracting plant associations has led to many attempts at finding objective methods of accomplishing these aims. Whereas, subjectively, one can group releves into associations by rearranging them so that the pattern they present to the eye expresses the within-group similarity, while showing the dissimilarity between groups; to derive such a solution in objective terms requires two main components. First an index which measures the similarity-dissimilarity between individuals, and secondly an algorithm or set of operations which organizes the individuals on the basis of this index. This set of operations must lie on some mathematical model which sets up criteria upon which the organization is carried out.

Ordination, loosely defined as any method in which given phytosociological entities (species or plots), as abstract spatial points, are ordered according to one or several of their properties, in such a manner that their arrangement will reveal some useful information about their relationships, (Orlocci, 1972), is a technique which satisfies these criteria.

The present availability of large, high-speed, digital computers has had a great deal of influence on the type of procedures carried out in phytosociological research. Although the trend has turned toward the more sophisticated methods, there are a number of simpler methods that have much to warrant their consideration. There are also more sophisticated methods developed in other fields that appear interesting to the phytosociologist but have not been examined in detail or applied to an ecological situation.

Polar ordination techniques were first developed and used by Curtis and his associates in the study of Wisconsin vegetation, (Brown and Curtis, 1952; Curtis and McIntosh, 1950; Bray and Curtis, 1957). The term polar refers to the choice of the end stands for the ordination. The original version given by Curtis and McIntosh, used an importance value based on a number of vegetational measurements to describe the stands. The stands were placed in a continuum of specific composition by the assignment of climax adaptation numbers. Later versions used similarity coefficients to describe the relations between stands, and permitted the ordination of multiple axes.

An approximation of the principal components method, but computationally more simple, is the technique known as position vectors ordination. The position vector of a quadrat is defined as the line which connects the centroid of the sample space with the quadrat as a spatial point, (Orlocci, 1972). As the criterion for choosing this vector, the sum of squared projections of all possible vectors is calculated, and the maximum vector is chosen as the first ordination axis. Further calculation of residual matrices is used to pick out subsequent axes.

The major advantage of both of these methods is the possibility of doing the calculations without the aid of a computer. However, in both cases further sophistication in terms of similarity coefficients, and the extraction of multiple axes, along with the application of the methods to large matrices of data, soon makes the computer an essential tool to the analysis. A further criticism of the Curtis method is the assignment of climax adaptation numbers.

Although they may be useful in some cases, the fact that more sophisticated methods are available that are easily applied if a computer is available, tends to eliminate these techniques from consideration.

Two further techniques for ordinating vegetational data are worthy of consideration. The first is the method of principal axes ordination (van der Maarel, 1969; Gower, 1966), which may be defined as the extraction of cartesian co-ordinates from any given resemblance matrix, which need not be metric. Although van der Maarel (1969) states that a computer is not required, the method still involves the extraction of eigenvalues and eigenvectors from a matrix, which, if large, would be an inordinately time consuming and tedious process. This combined with the possible distortion resulting from the use of non-metric, non-Euclidian resemblance measures puts this method in a doubtful position.

The last method, Kruskal's non-metric multi-dimensional scaling, involves the representation of n objects geometrically by n points, so that the interpoint distances correspond in some sense to the experimental dissimilarities between objects, (Kruskal 1964a, 1964b). The scaling process is carried out to compute the configuration of points that optimizes goodness of fit. Orlocci (1972), points out that although there appears to have been no recorded instance of the use of this technique in phyto-sociology, the method is attractive in its flexibility and the choice of a range of possible regression models to allow for the ordination of non-linear data. Hopefully with more research, this method might provide a useful ordination technique.

(3.2) Why Principal Component Analysis?

Of the ordinations described in the ecological literature two methods occur more than any others. These are the simple polar ordination methods developed by Curtis and his associates and the method of principal components analysis. Polar ordination is preferred by some for the simplicity of its technique or the fact that it can sometimes be carried out without the aid of a computer. It appears to suffer, however, from its own simplicity in that it is relatively insensitive and prone to misplacing stands on the ecological gradient set up.

Principal component analysis, although requiring the use of a computer to carry out the calculations, has been well received, both because of its efficiency and the reliability of the results produced. The technique also carries the advantage, over other complex multivariate methods in use, of being fairly elegant mathematically. Perhaps this advantage will disappear as methods such as factor analysis and multidimensional scaling are explored further. At present, component analysis provides the highest degree of sophistication while maintaining a solid mathematical background, especially when the use of non-normally distributed data is contemplated. For this report this method was adopted for the objective analysis of the Cape Henrietta Maria data.

In the sections to follow the mathematical principles of component analysis will be discussed, especially with reference to its similarities with a particular version of the factor analysis model.

One of the better sources of information on these techniques is the book by Harman (Harman, 1967) and this reference has been relied upon heavily in developing the mathematical basis for this method.

(3.3) The Ordination Model

In order to develop the concept of species association, consider a situation in which there are three stands or plots each composed of two species in quantities that may vary from complete absence to complete presence. We shall define the elements of the problem, either species or plots, as entities. These entities may be either individuals or attributes. In this case we shall consider the plots as individuals and the species they are composed of as attributes. As the plots are characterized by the species they contain, so the individuals are defined in the attribute space. Those attributes which vary among the individuals, called variates, can be used to effectively describe the individuals.

Geometrically this simple case can be represented as in (Fig. 4). The individuals are fixed points in space (x_{11}, x_{32}, x_{23}) whose positions are determined by the size or state of the attributes they possess, i.e. (I & J).

These attributes are regarded as the axes of a reference system. This system with all of its properties constitutes the sample space. In this case, since there are

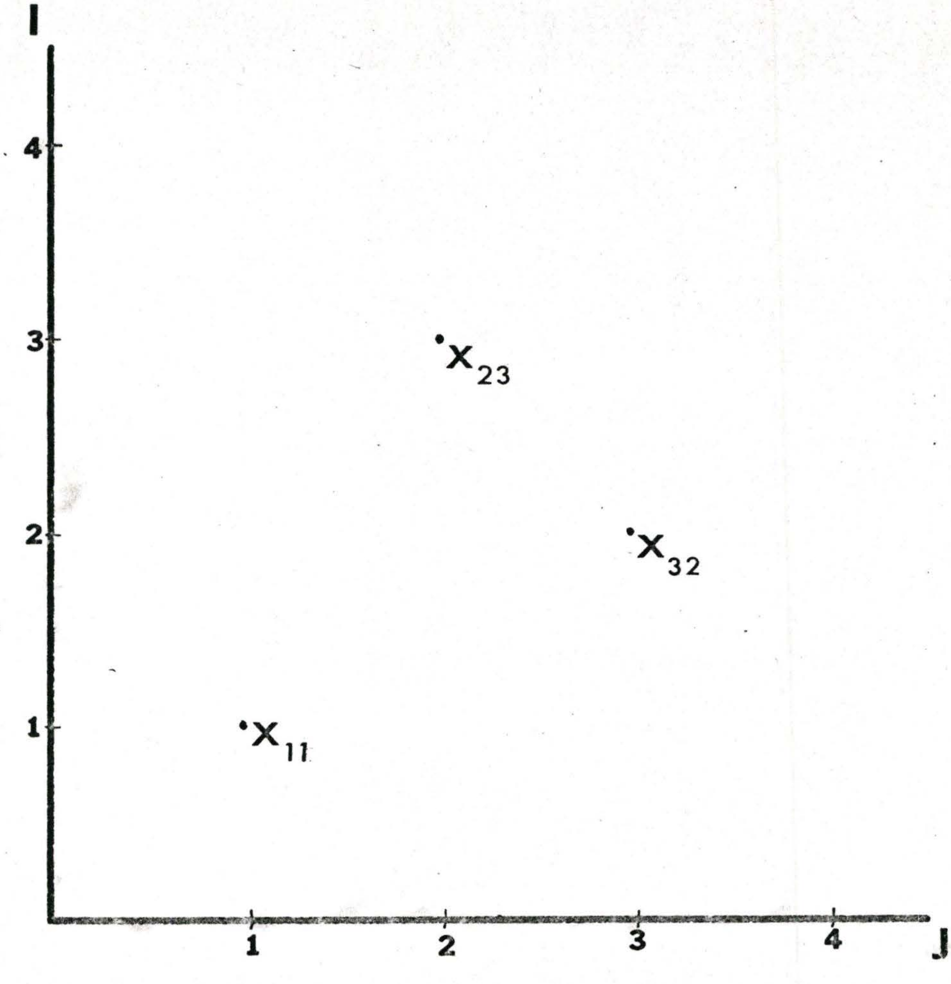


Figure 4. (see text)

two variables, the system can be defined in two dimensions, or referred to as a 2-space.

In general terms, this system could be defined as a collection X (sample population) of c individuals in a p-variate space, or in short, as a system of individuals in attribute space. The converse is also possible where species become the individuals and the plots become the attributes, so that the geometric model of the system becomes one of species in plot-space.

In carrying out the ordination of this system we are concerned with the similarity or dissimilarity between any given pair of individuals, ie. (x_1 & x_2). This resemblance can be defined in terms of an Euclidian distance. The set of all these resemblances can be put in terms of an Euclidian matrix which defines a sample space having the following metric properties:

(a) the metric function defining the distance between the two points cannot be negative.

(b) it must be symetric so that it will not be affected by the order in which the individual points are compared.

(c) it must possess the triangle inequality property, implying that given three individuals as points in a sample space, the sum of the length of any two sides of the triangle they define, is not less than the third side.

In addition an Euclidian sample space is distinguishable from other metric spaces by the fact that it is only the Euclidian sample space where a scalar product of vectors exists. (Orlocci, 1972)

Continuing with our example then, the set of individuals in Fig. 4 could be described by a data matrix:

$$X = \begin{bmatrix} x_{11} & x_{12} \\ x_{21} & x_{22} \\ x_{31} & x_{32} \end{bmatrix} = \begin{bmatrix} 1 & 1 \\ 3 & 2 \\ 2 & 3 \end{bmatrix}$$

Each entry x_{ij} in this matrix represents the quantity of a species in a given quadrat. Sample means for the species could be represented by:

$$\bar{X} = \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 2 \\ 2 \end{bmatrix}$$

For the purposes of example we shall define a very simple resemblance function: $a_{ij} = (x_{ij} - x_j)/S_j$ where for reasons of simplicity $S_j = 1$. S_j represents a standardization factor chosen by the phytosociologist.

Assuming that the sample contains p species and c individuals where i = 1, 2,...., c and j = 1, 2,..., p, we can derive a p x c matrix A from this resemblance function, such that;

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \\ a_{31} & a_{32} \end{bmatrix} = \begin{bmatrix} -1 & -1 \\ 1 & 0 \\ 0 & 1 \end{bmatrix}$$

Using this we can generate a (p x p) matrix of scalar products called R from the relation R = A'A where A' is the transpose of A:

$$R = A'A = \begin{bmatrix} -1 & 1 & 0 \\ -1 & 0 & 1 \end{bmatrix} \begin{bmatrix} -1 & -1 \\ 1 & 0 \\ 0 & 1 \end{bmatrix} = \begin{bmatrix} 2 & 1 \\ 1 & 2 \end{bmatrix}$$

The elements of R relate the species in pairs.

The collection X of c individuals described on the basis of p variates, and the resemblance function 'f' which generates the resemblance matrix R from X, represent the first two components of our model.

The third component is a set of statements specifying the steps in the analysis.

(3.4) <u>Principal Components Analysis vs Factor Analysis</u>

Much confusion can be found in the literature as to what principal components is and does, especially when referred to along with the technique of factor analysis. The discrepancies between the two methods are at the same time both large and yet not so large, depending on how the situation is viewed.

Both of these ordination techniques could be loosely classified under the term 'factor analysis', but whereas the method of principal components or component analysis is aimed at the summarization of the total variance in the sample, classical factor analysis is an attempt to elicit the common covariance structure of a given population in terms of m common factors. Emphasizing the confusion is the fact that the most commonly used method of factor analysis (in the classical sense), the principal factors solution, closely parallels the techniques used in component analysis.

In order to clarify the above consider the following two linear models:

Model (1)

$$z_j = a_{j1}F_1 + a_{j2}F_2 + \ldots + a_{jn}F_n \qquad (j = 1,2,\ldots,n)$$

Model (2)

$$z_j = a_{j1}F_1 + a_{j2}F_2 + \ldots + a_{jm}F_m + d_jU_j \qquad (j = 1,2,\ldots,n)$$

The objective of model one is to extract the maxiumum variance, ie, component analysis. Each of n observed variables, z_j's, is described in terms of n new uncorrelated components. It should be noted that although only some of the components may be retained, nevertheless, all the components are required to reproduce the correlations.

The objective of model two might be stated; to "best" reproduce the observed correlations. Each of the n observed variables is described linearly in terms of m (usually smaller than n) common factors and a unique factor. The common factors account for the correlations among the variables, while each unique factor accounts for the remaining variance.

In both models the a's represent the factor loadings, while the F's represent the common factors or new uncorrelated components, however, there is no relation between the a's and F's in the two models.

Linear Dependence

The set of co-ordinates $(x_1, x_2, \ldots, x_N)$ which represents a point P in an N-space may be considered as a vector which joins the origin 0 to the point P, that is, a radius vector. Any linear combination of m points may be defined by combining the following operations:

(a) if $P = (x_1, x_2, \ldots, x_N)$ then

$$cP = (cx_1, cx_2, \ldots, cx_N)$$

and (b) $P_1 + P_2$ is

$$(x_{11} + x_{21}, x_{12} + x_{22}, \ldots, x_{1N} + x_{2N})$$

resulting in

$$t_1P_1 + t_2P_2 + \ldots + t_mP_m.$$

Any of the new points P(t) is said to be linearly independent on the original points $P_1, P_2 \ldots, P_n$.

For example if $P_1 = (1,3,4)$ and $P_2 = (2,1,5)$ and $t_1 = 1$, and $t_2 = 2$ then P (t) is given by $x_1 = 5$, $x_2 = 5$, $x_3 = 14$.

These principles form the basis of a theorem which may be stated as follows.

If m is the rank of a matrix X, the points P_1, P_2, ..., P_n are all dependent upon m of them, which are themselves independent. In other words, the example given above could be expressed in matrix form as follows:

$$\begin{bmatrix} 1 & 3 & 4 \\ 2 & 1 & 5 \\ 5 & 5 & 14 \end{bmatrix}$$

This matrix is of rank two since the three column vectors are dependent on the first two of them which are themselves independent, that is, the third column can be constructed as a linear combination of the first two of them, as was done by adding and multiplying in the above example.

It should be clear that in a given matrix of biological data the composition of some species may be controlled by that of other species in the sample area, or that some species may be linearly dependent on others. Hence the rank of the generated resemblence matrix may be less than its order.

It becomes necessary at this point to enter the concept of subspaces. If P_1, P_2, ..., P_k are a set of k linearly independent points, the set of all points linearly dependent on them is called a linear k-space. Related to this is a theorem in algebra which states the following:

If m is the rank of a matrix X, the points P_1, P_2, ..., P_n are all contained in a linear m-space but not in a linear u-space, where u is less than m. (Harman,1967)

The point of the above arguements is that a set of correlations based on n variables, hence n dimensions, may be contained in a space defined by m n factors, that is,in a space of smaller dimension than the original. However, these m factors represent the smallest number of dimensions that will represent the original data.

The whole basis for the difference between the analysis of principal components and the technique of factor analysis lies on these arguements. In a principal component solution the observed correlations are represented in a cluster of the same number of dimensions as there are original variables. In factor analysis, the assumption is made that some of the variables are dependent on others so that the information contained in the cluster can be represented in few dimensions. Basically the model sets up a hypothesis that the information can be represented by m factors, or in m dimensions, so that in essence the technique reconstructs a sample space based on the correlations calculated by the model on the basis of these assumptions. In summary, the n variables can be expressed as linear functions of not less than m factors, where m is the rank of the correlation matrix. It should be kept in mind, however, that the correlations reproduced by this method, will approximate the observed correlations only to the extent that the mathematical models of the variables are adequate.

As mentioned below the second program used (BMD03M) is documented as a 'factor analysis' routine, however, only the principal components form of the model was used. The decision against using a factor analysis approach (in the strict sense) was made on the following criteria: (a) factor analysis may only be used where the data is multivariate normal or close to it; (b) there is some doubt as to how the existing factor analysis programs operate; and (c) the mathematics of the various factor analysis procedures are not sufficiently well developed to allow their use without a great deal of further research. This situation is unfortunate in view of the obvious advantages and it is hoped that the problems will be cleared up in the near future.

Composition of Variance

Before leaving this topic it is worthwhile to mention the composition of variance in these models. The variance of a variable can be expressed in terms of the factor model as follows:

$$s_j^2=1=a_{j1}^2+ a_{j2}^2+ \ldots + a_{jm}^2 +d_j^2 \quad \text{(Harman, 1967)}$$

The terms on the right represent the portions of unit variance accounted for by the common factors, ie. a_{j2}^2 is is the contribution of factor F_2 to the total variance of z_j.

This argument leads to the introduction of two major concepts of factor analysis. Firstly the communality, h_j^2, of a variable z_j is given by the sum of squares of the common factor coefficients, ie.

$$h_j^2 = a_{j1}^2 + a_{j2}^2 + \ldots + a_{jm}^2$$

Secondly, the uniqueness, d_j^2, or the contribution of the unique factor, (d_jU_j), which indicates the extent to which the common factors fail to account for the total unit variance of the variable. The uniqueness can be further broken down into the <u>specificity</u>, that is, the possibility that the addition of further variables might necessitate the postulation of further common factors, and the <u>error variance</u> or <u>unreliability</u>, or the variance due to imperfections in measurements. With these considerations in mind the factor analysis model could be represented as follows:

$$z_j = a_{j1}F_1 + a_{j2}F_2 + \ldots a_{jm}F_m + b_jS_j + e_jE_j.$$

The composition of variance in the model can then be said to be composed of the communality + the uniqueness + the unreliability, or:

$$s_j^2 + h_j^2 + d_j^2 + h_j^2 + b_j^2 + e_j^2.$$

If the reliability is defined as the one complement of the unreliability, ie.

$$e_j^2 = 1 - r_jj$$

then the composition of variance may be summarized as follows:

Total Variance = 1

Reliability = r_jj

Communality = h_j^2

Uniqueness = d_j^2

Specificity = b_j^2

Error Variance = e_j^2

A very important point can be made here. If the communalities are specified as unity then the uniqueness disappears. In other words, if the communality is set to one, the total observed variance is expressed in terms of m = n factors. This version of the factor analysis model, ie.

$$z_j = a_{j1}F_j + a_{j2}F_2 + \ldots a_{jm}F_m$$

is equivalent to the principal component model discussed previously, where m is equal to n, the number of original variables.

A word of caution must be inserted here. This approach to the analysis of principal components bears some discrepancies with the method to be discussed below. It is hoped that these differences will become apparent in the discussion to follow.

(3.5) The Principal Components Technique

It has been stated that the object of the principal components model (Model 1) was to extract the maximum variance from the observed correlations by representing the n observed variables in terms of n new uncorrelated variables the effect of which is to summarize the original data.

To make this concept more clear consider the following analogy. . . The diagram in Fig. 5 might represent a cluster of points in a 2-space, the shape of the cluster being extremely variable. If one's aim was to summarize this cluster, an apt question would be, "what property can be found that expresses the shape of the cluster." One such property is variance.

By drawing two axes through the cluster at right angles, it is possible to represent the major components of the variance of the cluster. It can be seen that these axes form the basis of an ellipse, (Fig. 6), which represents the two most important properties of the shape of the cluster, its length and its width, but leaves out all the minor variations that we have assumed are not important. In essence then, we have summarized the system, so that we can represent an approximation of it by two properties.

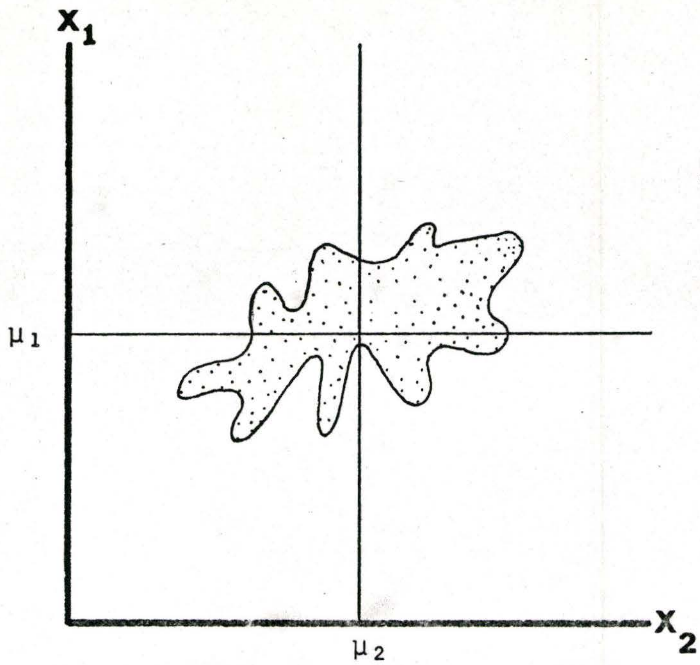


Figure 5. (see text)

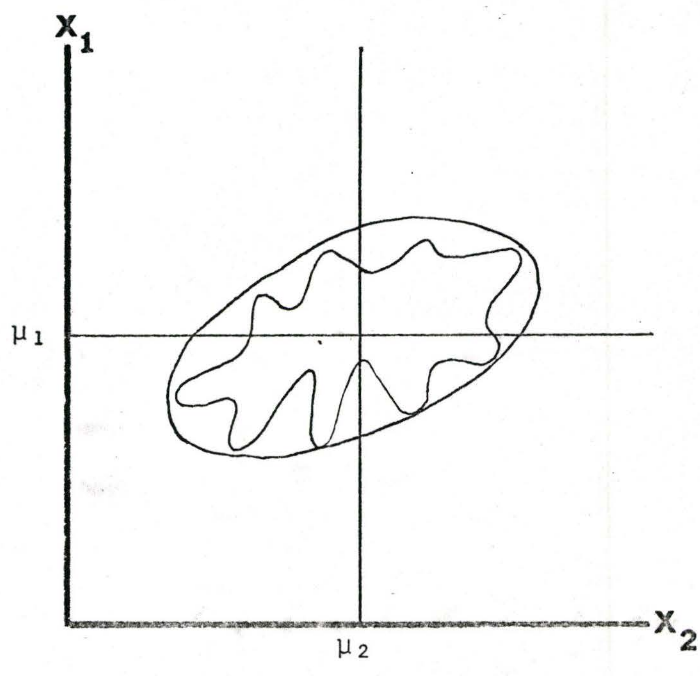


Figure 6. (see text)

If we look at the ellipse in terms of its reference axes, X_1 and X_2 (Fig. 7) and consider any point P on the circumference, it can be seen that the distribution of X_1 with respect to u_1 is not symetrical at the point P, for a given value of X_2. Similarly the distribution of X_2 with respect to u_2 is non-symetrical for a given value of X_1. In other words, the distribution of one is being influenced by that of the other, hence the two reference axes, or variables, are correlated with respect to the points in the cluster.

If the two reference axes were rotated counter-clockwise through α degrees, we would end up with a set of uncorrelated axes, Y_1 and Y_2, as in (Fig. 8).

Using the same sort of argument it can be seen that the distributions at a given point P, in a cluster of higher dimension are non-symetrical. The most important point here is that it is only in their uncorrelated position that these axes represent the maximum amount of variance in the cluster, or, only when the axes are uncorrelated and orthogonal do we get an efficient summarization of the cluster.

This is essentially what the principal components technique does. It rotates the system of reference axes to a position such that they are uncorrelated and linearly orthogonal. The points in the cluster are then defined by a new system of co-ordinates which have their reference

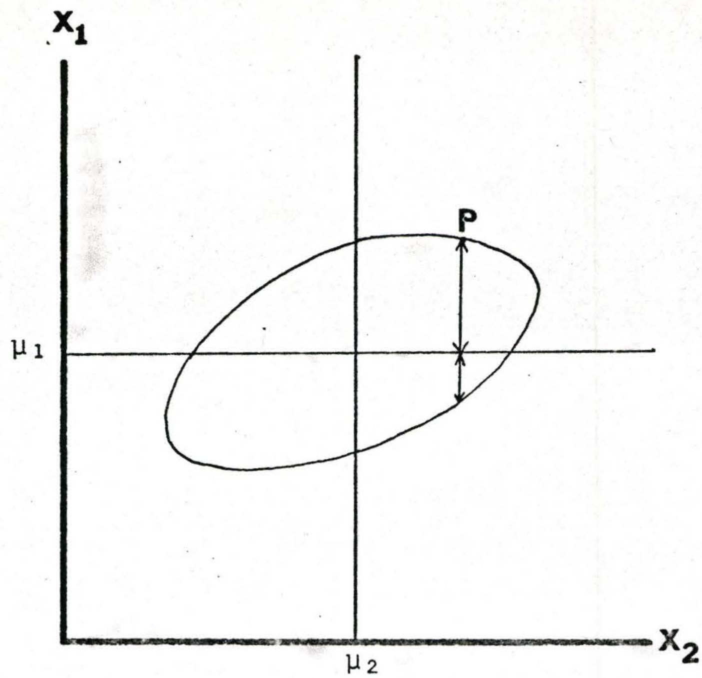


Figure 7. (see text)

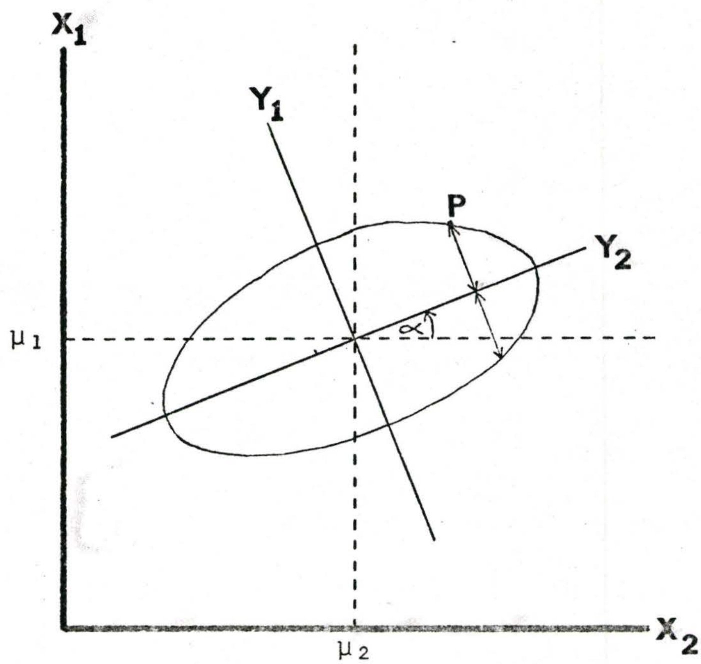


Figure 8. (see text)

points on this new set of axes.

This technique of orthogonal transformation refers to one which leaves the distances between points unaltered, that is, one which carries straight lines into straight lines. In mathematical terms such a transformation is one in which any point $P_1(x_{1i})$ is carried into $Q_1(y_{1i})$ and $P_2(x_{2i})$ is carried into $Q_2(x_{2i})$ with the property that:

$$\Sigma\ (x_{1i} - x_{2i})^2 = \Sigma(y_{1i} - y_{2i})^2$$

If the transformation is linear...

$$y_{ji} = \sum_{k=1}^{N} \alpha_{ik}x_{jk} + c_i \quad \text{where} \quad (i = 1,2,\ldots,N \text{ and } j = 1,2,3,\ldots$$

In this case the first equation becomes...

$$\sum_{i=1}^{N} (x_{1i} - x_{2i})^2 = \sum_{i=1}^{N} [\sum_{k=1}^{N} \alpha_{ik}(x_{ik} - x_{2k})]^2$$

The problem is then to find a value of α to satisfy the equation. This value then specifies the most general transformation that will retain the distances.

In order to achieve a linear orthogonal transformation we make use of the condition that $T\,T' = I$, where T represents the transformation matrix and I represents the identity matrix. If R is the correlation matrix of observed variables then the correlation matrix of the transformed variables is $T\,R\,T'$. Given Λ, a diagonal matrix with elements $(\lambda_1,\lambda_2,\ldots\lambda_n)$ which represent the variances of the new uncorrelated variables then $T\,R\,T' = \Lambda$. The values

$\lambda_1, \lambda_2, \ldots, \lambda_n$ are termed the eigenvalues or latent roots of the resemblance matrix R and can be found by solving the terminental equation

$$|R - \lambda I| = 0$$

If the equation $T R T' = \Lambda$ is post-multiplied by T the result is

$$T R = \Lambda T.$$

Using the equation in this form the values of the eigenvectors corresponding to the values of λ in Λ can be found. The elements of these eigenvectors specify the co-ordinates of the transformed variables.

A measure of the efficiency of each new principal component in accounting for a proportion of the variance in the original cluster is the ratio of each eigenvalue to the sum of the eigenvalues, ie.

$$E = \frac{\lambda_i}{\sum_{i=1}^{n} \lambda_i}$$

The usual expression of this ratio is in terms of the per cent variance extracted by the components, with the method usually being set up to give principal components of decreasing value.

With the high-speed computer the principal components technique has been the method of choice in much of the phytosociological work in the literature. Table 15 gives an abbreviated list of references pertaining to the use of principal components analysis in an ecological context, subdivided into sections according to whether the paper was

Table 15

Applications of Principal Component Analysis to Plant Ecology

Method Comparison	Methodologies	Applications to Phytosociology
Anderson, A. J. B. J. Ecol. 59 (3) (1971)	Austin & Noy-Meir J. Ecol. 59 (3) (1971)	Allen, T. F. H. J. Ecol. 59 (3) (1971)
Anderson, D. J. J. Ecol. 53 (2) (1965)	Bannister, P. J. Ecol. 54 (3) (1966)	Austin, M. P. J. Ecol. 56 (3) (1968)
Bannister, P. J. Ecol. 56 (1) (1968)	Ivimey-Cook et al. J. Ecol. 57 (3) (1969)	Austin & Greig-Smith J. Ecol. 56 (3) (1968)
Austin & Orlocci J. Ecol. 54 (1) (1966)	Orlocci, L. J. Ecol. 54 (1) (1966)	Greig-Smith et al. J. Ecol. 55 (2) (1967)
Ivimey-Cook & Proctor J. Ecol. 55 (2) (1967)	Orlocci, L. Syst. Zool. 16 (3) (1967)	Kershaw, K. A. J. Ecol. 56 (2) (1968)
Moore et al. Vegetatio 20 (1970)	Swan, J. M. A. Ecology 51 (1970)	Yarranton, G. A. Can. J. Bot. 45 (1967a)
Webb et al. J. Ecol. 55 (1) (1967)	Yarranton, G. A. Can. J. Bot. 45 (1967b)	

orientated toward the methodology of component analysis, the comparison of component analysis with other methods, or the application to the extraction of ecological information.

The analysis of these papers yields the following important points and limitations...

(i) Effect of Outliers

Anderson (Anderson, A.J.B., 1971) points out that the interpretation of a principal component solution may present difficulties if (statistically) outlying quadrats are present in the data set. These quadrats lie relatively far from the main cluster and can cause one or both of the following situations to occur:

(a) The principal axes extracted are very different from those defined by the main cluster, whose quadrats are therefore badly represented.

(b) Outliers can appear in the midst of the main cluster unless an inflated value for q (the number of dimensions) is used.

The first situation can be detected visually and the outliers removed for a second analysis, however the second case is more difficult and requires elimination of the quadrats on the basis of the Mahalanobis distance. These conclusions are born out by Austin (1968) who states that the principal components technique has most to offer in a homogeneous situation. This effect was also predicted by Greig-Smith (1964) and Whittaker (1967). Swan (1970) helps to clarify the basis of the problem using simulated vegetation data in an ordination. These models were constructed to simulate numerical changes along a single environmental gradient. The ordination was found to be successful when the data were drawn from a short length of the gradient but became progressively less so as larger lengths of the environmental gradient were involved in the data. This effect was found to parallel an increase in the number of stands from which each species is absent in the total data set. Swan hypothesizes that the zero values tend to mask ecological information, finding that the assignment of a "degree of absence" value helps to eliminate the problem.

(ii) Non-centering versus Centering Coefficients

Orlocci (1966a, 1966b) has pointed out that the orientation of the principal axes extracted by the P.C.A. technique, with respect to the point cluster, is entirely dependent on the coefficient which defines the spatial relationships between ecological entities. The coefficient must therefore be such that the principal axes obtained are the major axes of an ellipsoid. He goes on to derive a "weighted similarity coefficient" which satisfies these conditions. The product moment correlation coefficient, with modifications for the two types of models, is also satisfactory, and has the additional effect of introducing a standardization which makes the variance of every species equal to unity. This is useful in ordinating data based upon a number of scales of measurement, as pointed out by Austin (1968).

Principal component ordinations carried out by Austin and Greig-Smith (1968) using a number of standardizations have indicated that the effect of standardizing is not important in ordinations of temperate vegetation, but is more important with data where there are numerous rare species, such as tropical rain forest.

(iii) The R/Q Problem

One of the most frustrating problems in ordination has been the apparent inability of various researchers in the field to get together on a system of terminology. The most important aspect here has been the confusion over normal and inverse ordination, R and Q techniques and matrices, A and I models etc. Some clarification is presented by Williams and Dale (1965) who recommend the following system: the symbols R and Q refer to the resemblance matrix and the symbols A and I refer to the two types of models.

It is recommended here, in accordance with Ivimy-Cook et al (1969) that these systems of terminology be dropped altogether in preference to an explicit statement of the analysis system used.

(iv) The Use of Subjective Measures of Vegetation

The advantages of using subjective measures of cover-abundance in terms of time required to collect the data have been discussed in an earlier section. Use of methods such as the Domin scale in ordinations is discussed in a paper by Bannister (1966). When the Domin scale is examined with respect to cover or frequency alone or to combinations of these estimates, a non-linear relationship is found particularly in the lower part of the scale. Bannister describes a transformation coefficient which can be used to account for the discrepancy between the two types of measurement.

(v) The Problem of Non-Linearity in Ordinations

The incompatibility of the linear mathematical model of component analysis with the non-linear ecological model of species response to the environment has frequently been mentioned in the literature (Harman, 1967; Austin and Noy-Meir, 1971; Greig-Smith, 1964; and others). Austin and Noy-Meir (1971) examined this problem using a principal components analysis of simulated vegetation data. They found two types of distortion; involution, where extreme stands occur closer to the environmental plane than less extreme stands, and spurious axes which appear in the ordination although they do not represent environmental gradients. Although many types of standardization were applied, no one method could consistently remove these problems. In conclusion they make these recommendations:

(a) To limit the use of ordination to situations with narrow ranges of vegetational and environmental variation, where linearity holds as a first approximation. This is in agreement with the recommendations of Greig-Smith (1964), Ivimy-Cook and Proctor (1966), and Greig-Smith, Austin and Whitmore (1967).

(b) To develop methods for correcting non-linear relationships or explicitly based on them. Previously mentioned have been Swan's (1970) standardization by transformation of zeros and Kruskal's method of multi-dimensional scaling.

(c) To limit detailed interpretation of the ordination to a phytosociological mode with further analysis to determine the direction and trend of the non-linear environmental variation.

(vi) Rotation of Principal Components

The rotation of a principal component solution has been attempted by Ivimy-Cook and Proctor (1967), however the validity of this technique for interpreting ordination results is questionable in the case of the component analysis model. In factor analysis, the solution derived by the extraction of eigenvalues and eigenvectors is mathematically unique, however, an infinity of solutions can be obtained by changing the frame of reference (Harman, 1967). Whether this applies to component analysis also depends of which definition of component analysis one chooses to take. Seal (1964) takes the negative opinion, however, more research into the similarities between P.C.A. and factor analysis is needed before one can say for sure.

(vii) The Combination of Ordination and Classification Techniques.

Mention has been made in the literature, and examples given, of the application of classification techniques to break down a system of vegetational data into units that can then be ordinated more efficiently, (Greig-Smith et al, 1967). This approach corresponds with the attempt to restrict ordinations to homogeneous sets of data. In contrast, however, is the viewpoint that ordination will produce a more meaningful classification with less effort (Greig-Smith, 1957) depending on the scale with which it is used. This sort of use has been successfully applied (Kershaw, 1968) with quite good results. D. J. Anderson (1965) sums up the problem in stating, "the applicability of these procedures to any particular problem depends very largely upon the chosen terms of reference of the investigator concerned: the acid test of any methodology rests on the extent to which it assists us to understand more meaningfully the ecological complexity of the biosphere."

(3.6) Methods

In this study, two different ordination programs were used in the analysis of the data. The first one, referred to as BIGMAT (Elson and Funderlic, 1965), operates on a resemblance matrix R calculated from Orlocci's coefficient of similarity, ie.

$$\sum_{i=1}^{n}(x_{ij} - x_i)(x_{ih} - x_i) \qquad \text{(Orlocci,1966)}$$

This is a non-centering measure of dispersion (Orlocci, 1966). Two versions of this model were used, the first ordinating species in an individual space, the second using the more usual technique of individuals in an attribute space. These are referred to respectively as species ordination and plot ordination.

The second ordination program, referred to as BMDO3M, (Dixon, 1965), operated on a resemblance matrix calculated from the product moment correlation coefficient, ie.

$$\frac{\sum_{i=1}^{n}(x_{ij} - \bar{x}_j)(x_{ih} - \bar{x}_h)}{\sum_{i=1}(x_{ij} - \bar{x}_j)\sum_{i=1}(x_{ih} - \bar{x}_h)}$$

which is a centered measure of dispersion standardized to zero mean and unit variance. This program was run on the basis of a model of individuals in attribute space only. The results of this program were output as factor scores representing the elements of the eigenvectors corresponding to the three largest eigenvalues.

In the case of the first program the final results were represented in graphical form using the program PCAPLOT, whereas the results of BMDO3M were represented by two types of graphical representation, PCAPLOT and a three dimensional routine 3DPLOT (Kershaw and Shepard, in preparation). The input for these plot generation routines were the factor scores of the ordination programs.

The part of the analysis concerned with hypothesis generation was accomplished by overlaying both the abundance of various indicator species, and the values of the environmental factors, pH and soil moisture, derived from the analysis of the soil samples, on the locations of their respective sample areas specified by the co-ordinates on the plot axes. Trends in these overlay values were extracted subjectively by drawing contours at the various levels of the dependent variables, and by the method of trend surface analysis.

(3.7) The Trend Surface Analysis of Dependent Factors

The word trend refers commonly to any systematic changes that are noted on contour type maps, such as structural trends or the 'grain' of a map, (Krumbein and Graybill, 1965). In this context the trend can be defined by means of a polynomial that may contain all or parts of the linear, quadratic and higher terms.

The trend surface model can be represented in the following form:

$$T(U_i, V_j) = \tau(U_i, V_j) + e_{ij}$$

where $T(U_i, V_j)$ is the observed value of the mapped variable, and is equal to the trend $\tau(U_i, V_j)$ plus a random component.

Although the basic trend model is linear, the fact that the variables under study may be expressed in higher order terms, allows the interpretation of non-linear data, within the framework of linear analysis.

Drawing contours through the variations in mapped variables conveys considerable information, but in many cases local fluctuations obscure the underlying, broad, large scale patterns.

The procedure of constructing trend surfaces to represent large-scale variations was applied in this analysis using a multiple regression trend surface program KWIKR8.

In order to use the trend surface program effectively it was necessary to run a set of preliminary analyses, the results of which are shown in Table 17, page136, and in Figures 9 through 14 . pH values were used as the trial dependent variable and the routine was run for first, second and third order trend surfaces. While the first order surface accounted for 47.5 per cent of the large scale variation, the second and third order surfaces accounted for only 6.2 and and 2.6 per cent more variation. These values are for axis 1 with 2, similar results being obtained for the other pairs of axes. The similarity with the principal components solution is apparent here with each higher order accounting for successively smaller amounts of variation. Two problems arise: which order of surface would most efficiently represent the large scale variation present in the data -- (That this variation is not readily visible can be seen in the plot of the original data in Figures 9,11, 13 and with non-normal population statistical measures of significance are not valid. The result is that significance criteria must be set up to fit the occasion. In this case significance has been judged on the following points: (1) ecological interpretation; (2) very highly significant F-Ratio test, (3) appreciable variance extracted; and (4) no significant large scale variation present in a trend surface of the residuals.

Considering the case for axes 1 and 2 the trend surface of the first order shows a broad banded, horizontal pattern increasing down the page (Fig. 9). Although this surface meets the first three criteria mentioned it has two faults. Firstly, there is still a small but significant variation in the residual trends (Fig. 10). The orientation of this surface indicates that there might be a force causing cross-scatter to the original surface direction. Secondly, the trend surface of the first order tends to extrapolate too much. That is, it picks out the trend in the major cluster to the right but neglects to account for the cluster of fairly high values at the left. Looking at Figure 11 it can be seen that the second order surface, in allowing for a curved component in the data has bent down at the left to account for this smaller cluster, otherwise the surface is almost identical. The trend map of residuals in this case did not exhibit any significant large-scale variations (Fig. 12).

One might think that if the second order surface offered improvement, the third order surface might enhance this, however this is not the case. It is worthwhile to note that in applying a statistical procedure such as this we are trying to simplify the data to give a result that is more informative than the original data. Figure 13 showing the third order surface shows a fairly complicated pattern, forming islands and tending to curve to fit around the clusters in the data. Ultimately of course, increases in the order of the surface would bring us close to the original situation where even the minor scatter would be accounted for, and the purpose of the analysis would be defeated.

Similar results were obtained for the other pairs of axes in this analysis of pH trends. (not shown). In the subsequent analyses only the trend surfaces themselves will be shown, however, the same significance criteria were employed.

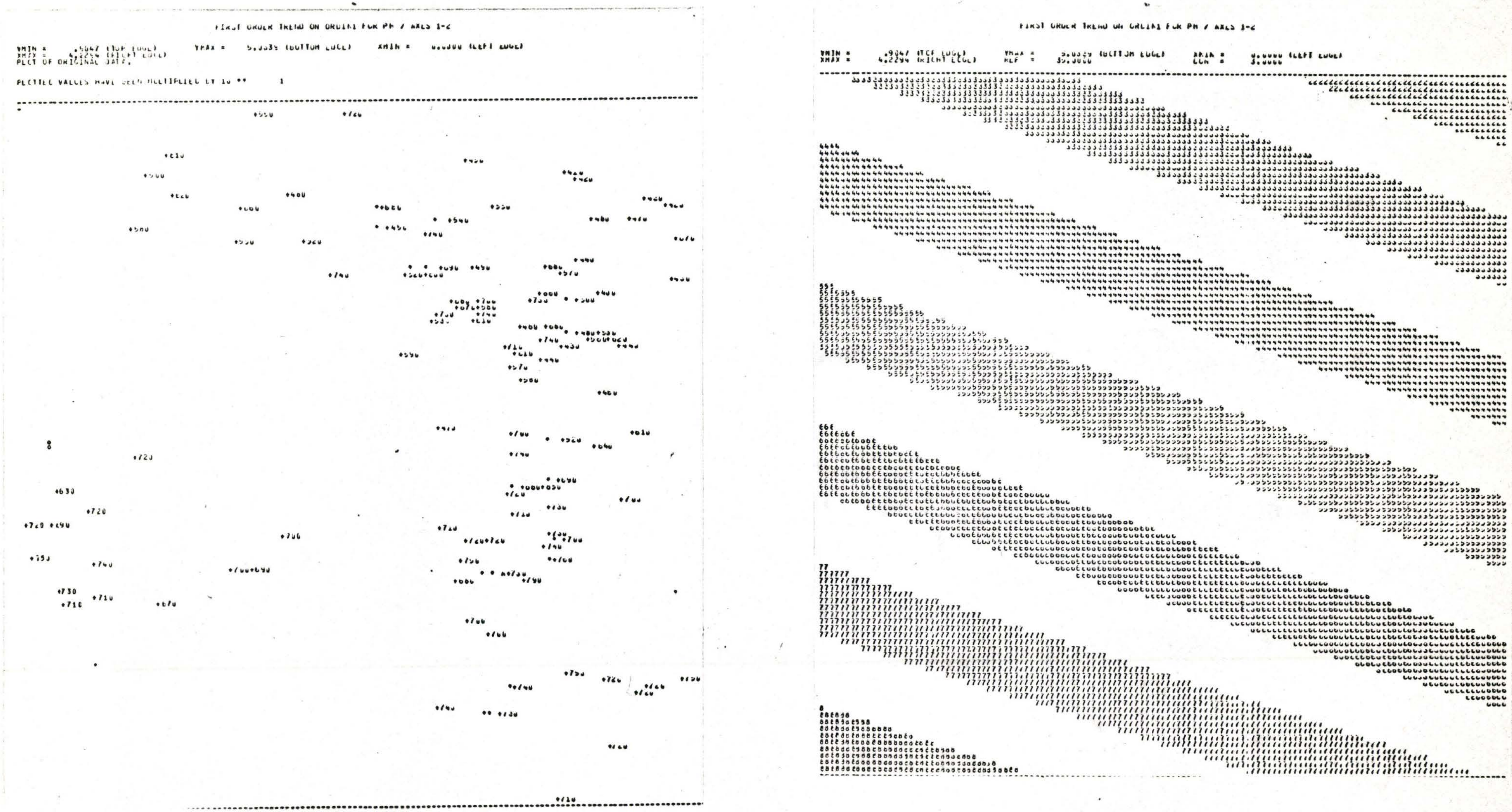


Figure 9. First order trend on ORDIN1 for pH--Axes 1-2

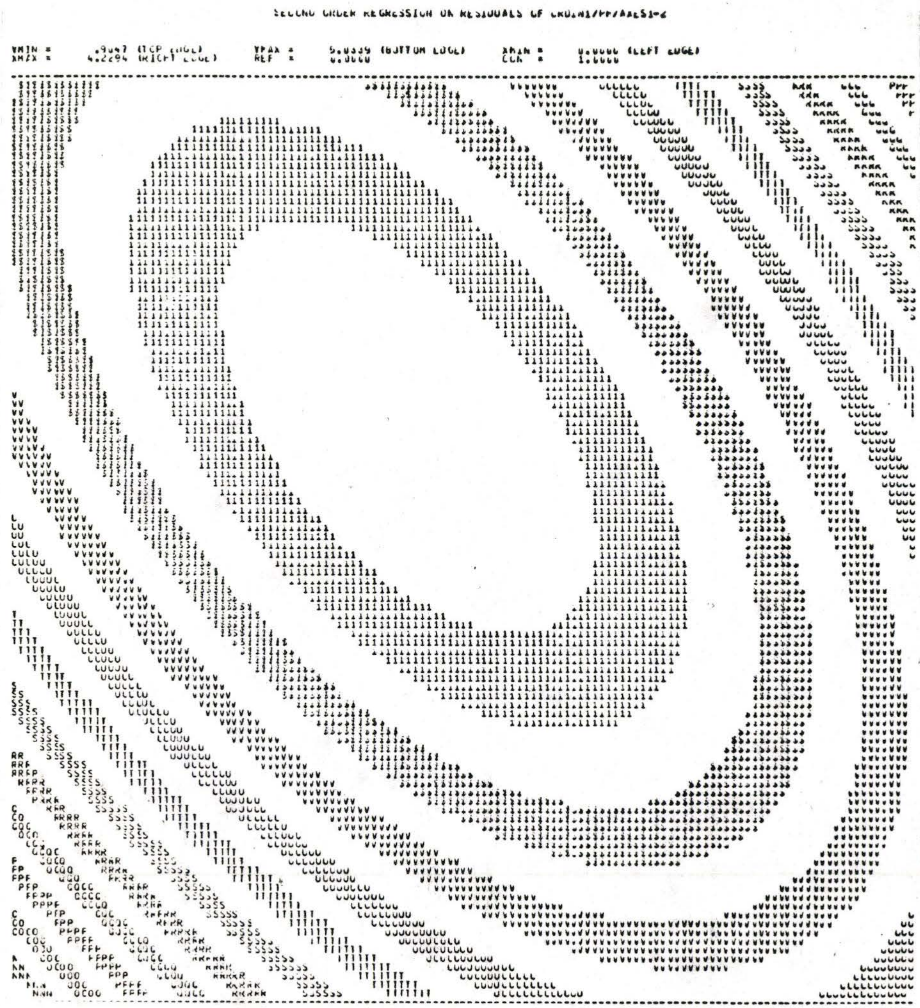


Figure 10. Second order trend on residuals of ORDIN1 for pH--Axes 1-2

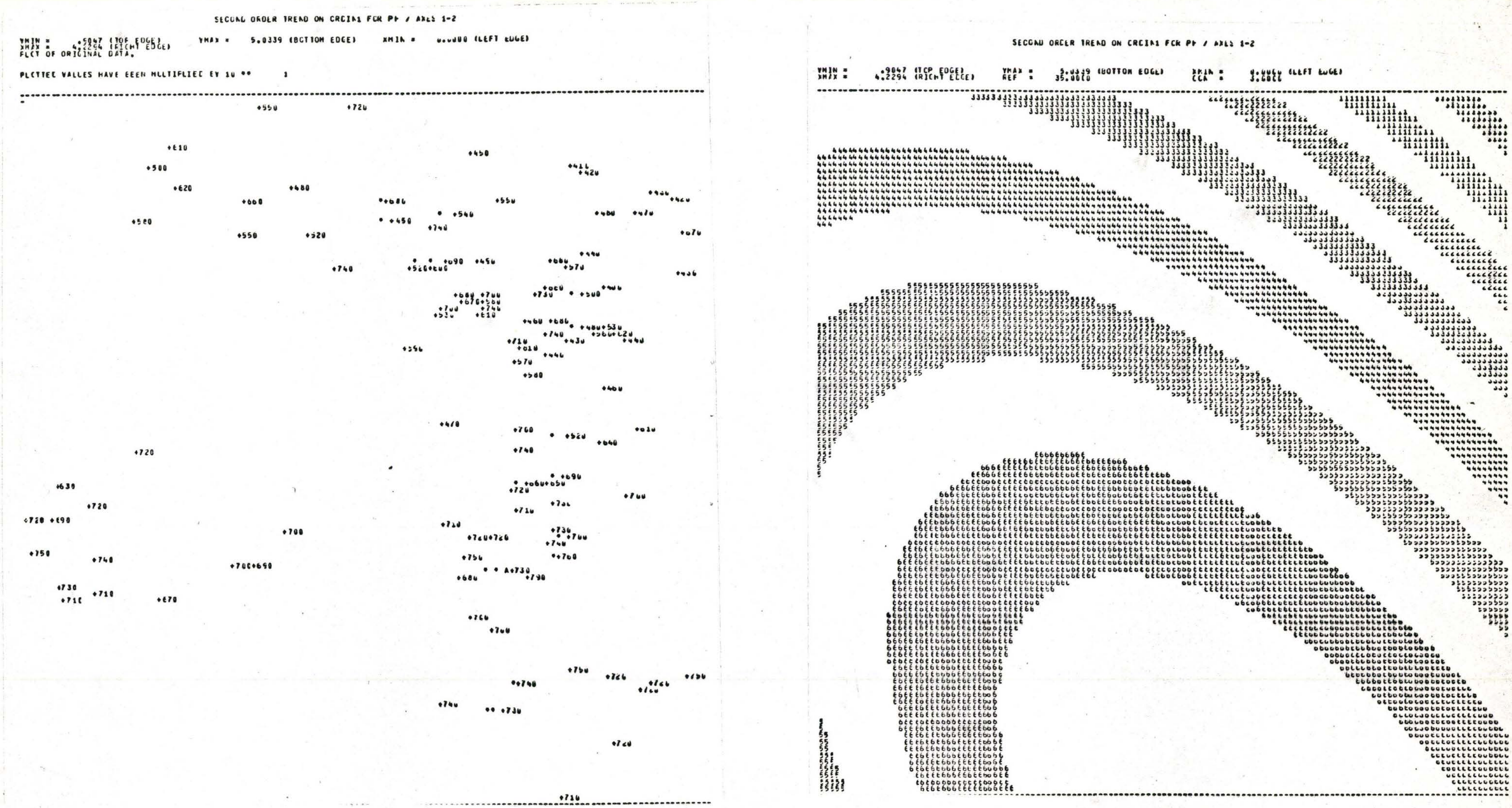


Figure 11. Second order trend on ORDIN1 for pH--Axes 1-2

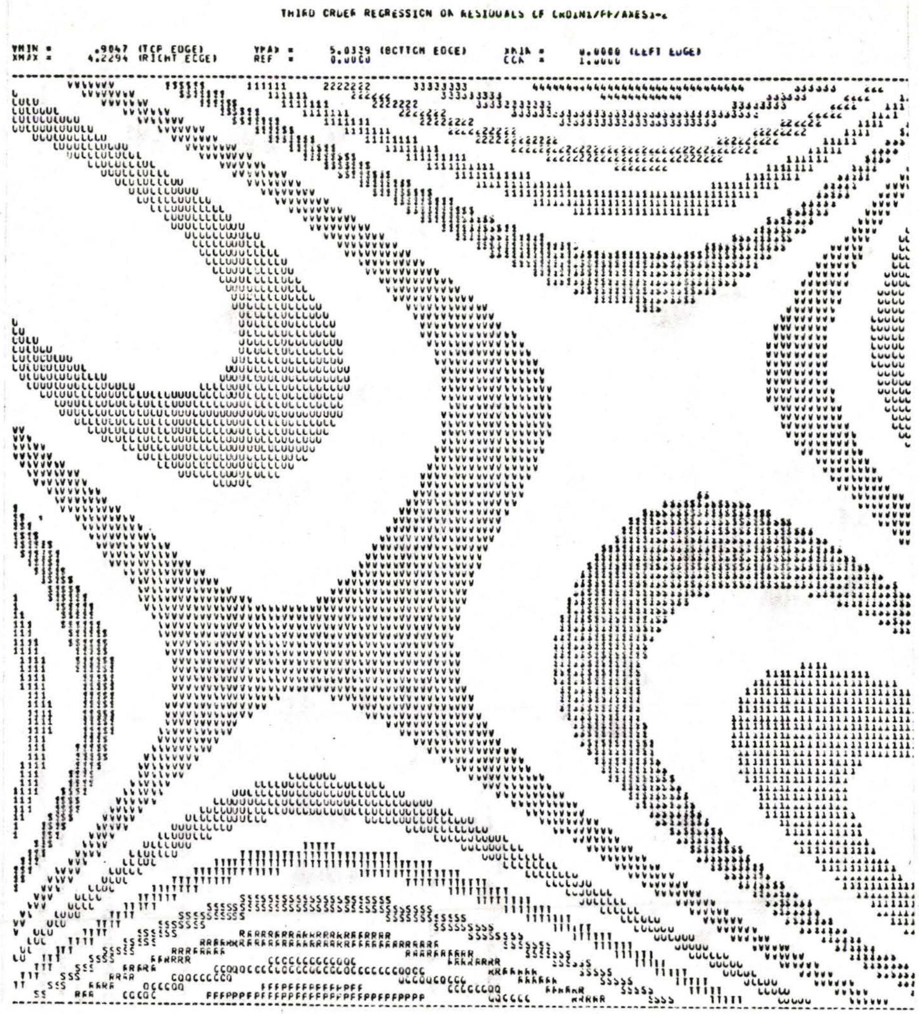


Figure 12. Third order trend on residuals of ORDIN1 for pH--Axes 1-2

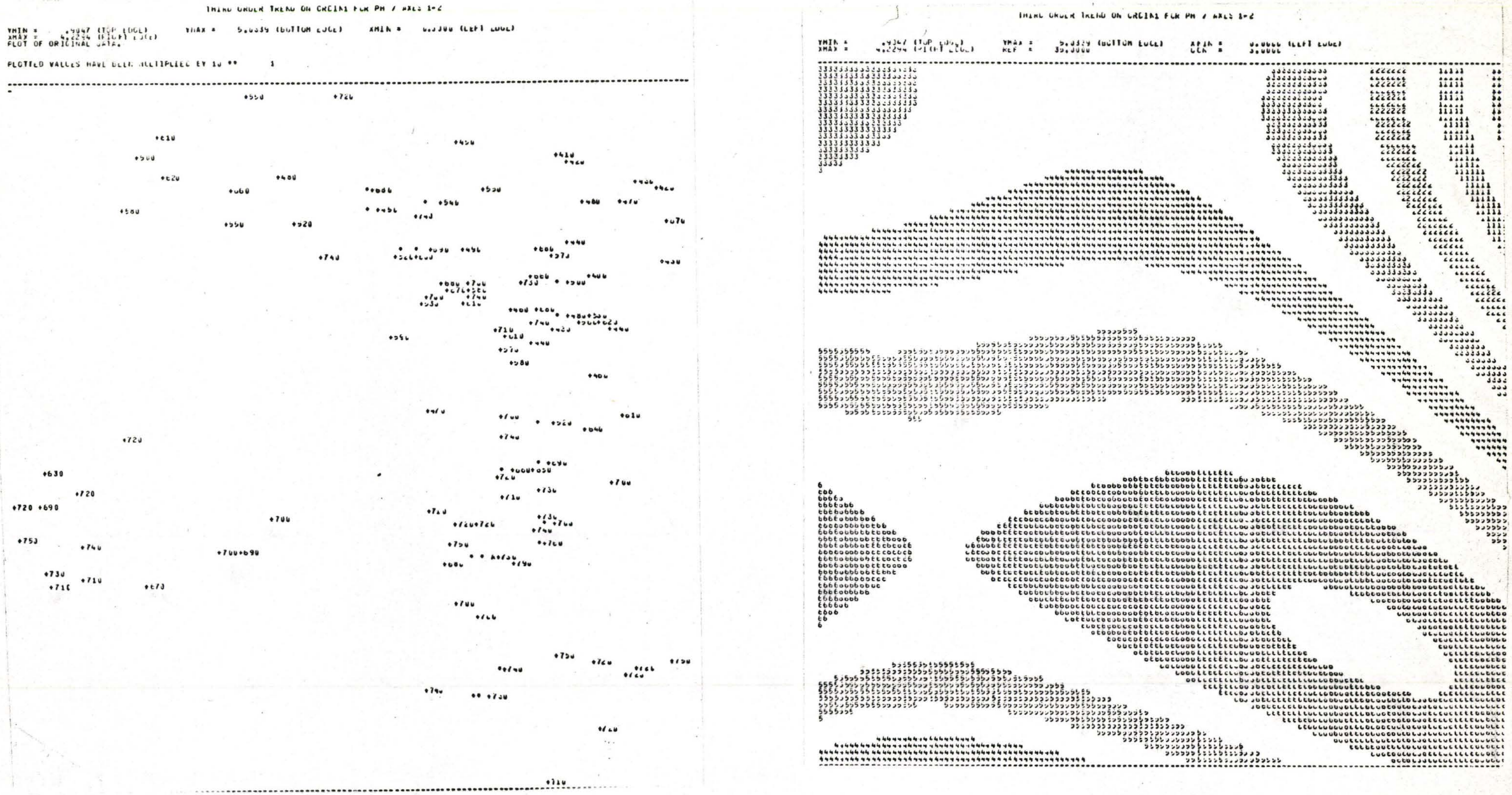


Figure 13. Third order trend on ORDIN1 for pH--Axes 1-2

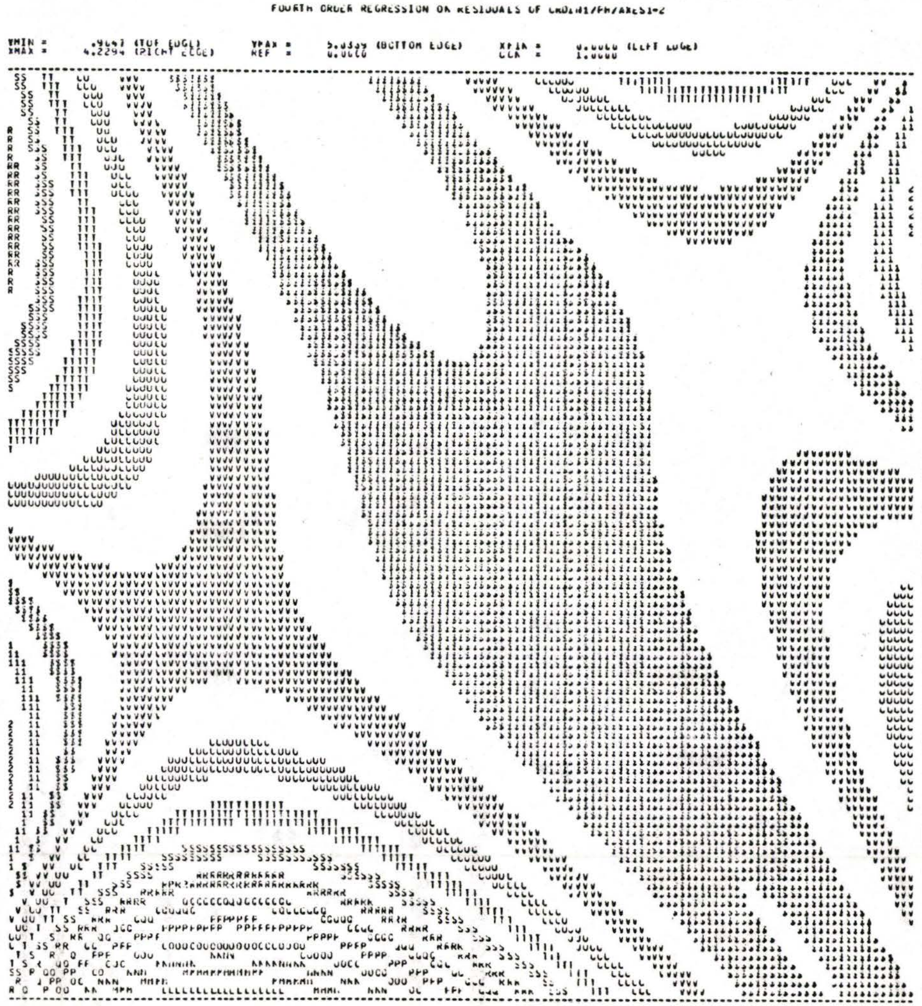


Figure 14. Fourth order trend on residuals of ORDIN1 for pH--Axes 1-2

Section lV

RESULTS

There were two aims to this study, the major one being to delimit the number of associations that would describe the vegetation of this area in terms of a number of vegetational units. The results of the classical Braun-Blanquet method in extracting these units have already been discussed above. The results of the objective methods will now be presented.

(4.1) The Objective Analysis of Plant Associations

Two ordination programs were used on the data collected at the Cape Henrietta Maria site: BIGMAT, an ordination program using Orlocci's weighted similarity coefficient, and the Biomedical program, BMDO3M, which used a product moment correlation coefficient. The results of the analyses carried out using these programs, in terms of the type of data, the numbers of variables and cases, and the variance extracted is presented in Table 16.

When extracting vegetational units it is usual to use the "normal" (in the sense of Williams and Lambert, 1959) ordination employing a model of plots in a species-space. These were termed Plot-Ordinations. Plot-Ordination-1 and Plot-Ordination-2 used the Domin data and extracted

Table 16

SUMMARY OF ORDINATION PROGRAMS

Fig. Ref.	Identification	Data Type	Resemblence Function	No. of Variables	No. of Cases	Components Graphed	Variance, % per Component	Total Var. Extracted %
24	Species Ord.-1 BIGMAT	Domin	Orlocci	130	74	1, 2, 3	53.8 11.3 6.9	71.9
25	Species Ord.-2 BIGMAT	Domin	Orlocci	130	74	2, 3, 4	11.3 6.9 4.5	76.4
26	Species Ord.-3 BIGMAT	Domin	Orlocci	130	30	2, 3, 4	16.1 8.7 6.3	74.2
15	Plot Ord.-1 BIGMAT	Domin	Orlocci	74	130	1, 2, 3	26.0 17.6 9.1	52.7
16	Plot Ord.-2 BIGMAT	Domin	Orlocci	30	130	1, 2, 3	28.1 20.9 9.2	58.2
-	Plot Ord.-3 BIGMAT	Frequency	Orlocci	74	130	1, 2, 3	27.0 18.4 11.3	56.7
-	Plot Ord.-4 BIGMAT	Cover	Orlocci	74	130	1, 2, 3	26.0 20.0 11.1	57.1
17	Plot Ord.-5 BIGMAT	Cover	Orlocci	30	130	1, 2, 3	26.8 20.5 11.4	58.7
18	Plot Ord.-6 BIGMAT	Frequency	Orlocci	30	130	1, 2, 3	28.1 20.2 11.5	59.8
19	ORDIN1 BMDO3M	Domin	P. M. C.	30	130	1, 2, 3	21.9 16.9 7.4	46.2
20	ORDIN2 BMDO3M	Domin	P. M. C.	30	92	1, 2, 3	19.6 12.8 9.5	41.9
-	ORDIN3 BMDO3M	Domin	P. M. C.	60	130	1, 2, 3	21.9 12.8 7.3	42.0

52.7 and 58.2 percent of the total variance respectively (see Fig. 15 and Fig. 16). Plot-Ordination-2 used only the 30 most common species, a technique employed to reduce the variance (Kershaw, 1968). Although producing basically the same ordination pattern, it did tend to produce slightly more dispersion, and was more successful in extracting a larger amount of the total variance, one of the criteria used to judge a successful ordination.

Figure 16 indicates that this ordination successfully extracted three associations, marked A, B, and C, corresponding to the three associations (of Braun-Blanquet extraction) lying at the extremes of the proposed ecological gradients. These are, the *Hedysarum Mackenzii* / *Dryas integrifolia* association of the top of the ridges, the *Vaccinium uliginosum* / *Rhododendron lapponicum* / *Dryas integrifolia* association of the depression areas, and the *Cladonia alpestris* / *Cladonia rangiferina* / *Empetrum nigrum* association of the bottom slopes.

Although there was some suggestion of organization in the remaining plots comprising the central cluster, this was not sufficient to indicate any further discrete associations.

Plot-Ordinations 3 through 6 operated on the same basis, but these employed the two other types of sample data obtained, namely, frequency and cover values. Only numbers 5 and 6, which used only the 30 most common species, are shown in Figures 17 and 18 respectively. Although these

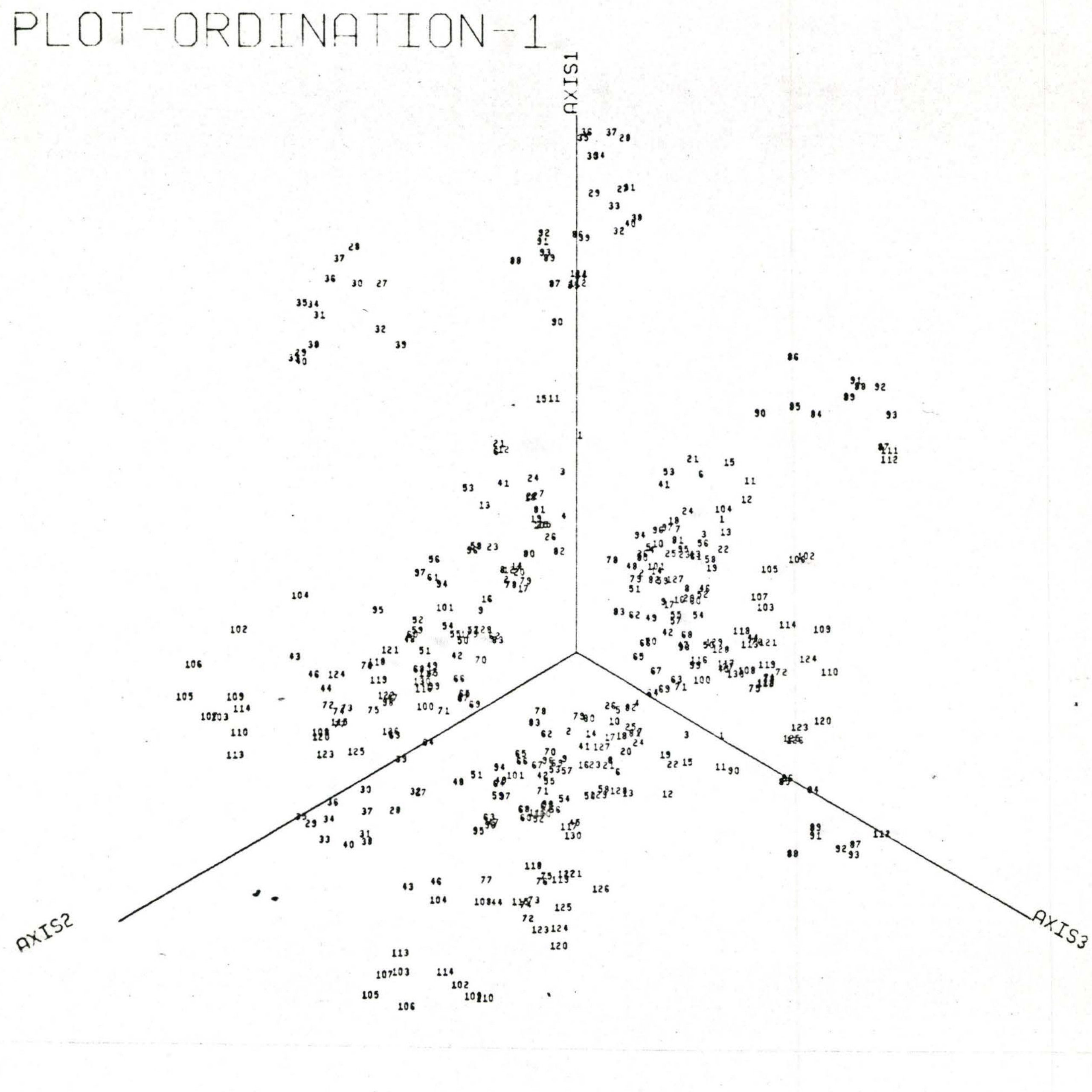


Figure 15. Plot-Ordination for BIGMAT, 74 species, 130 plots. Domin data.

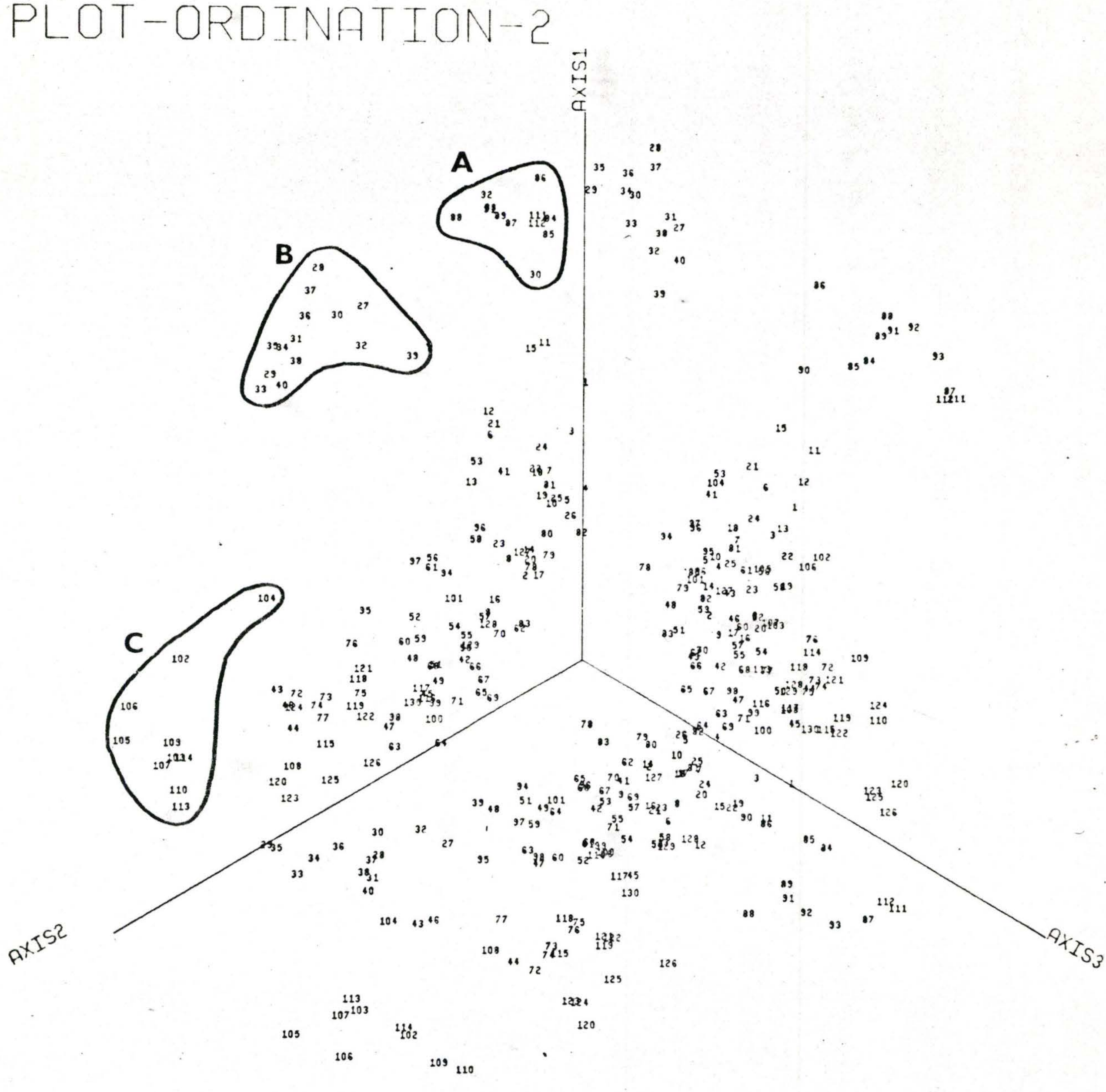


Figure 16. Plot-Ordination for BIGMAT, 30 species, 130 plots. Domin data.

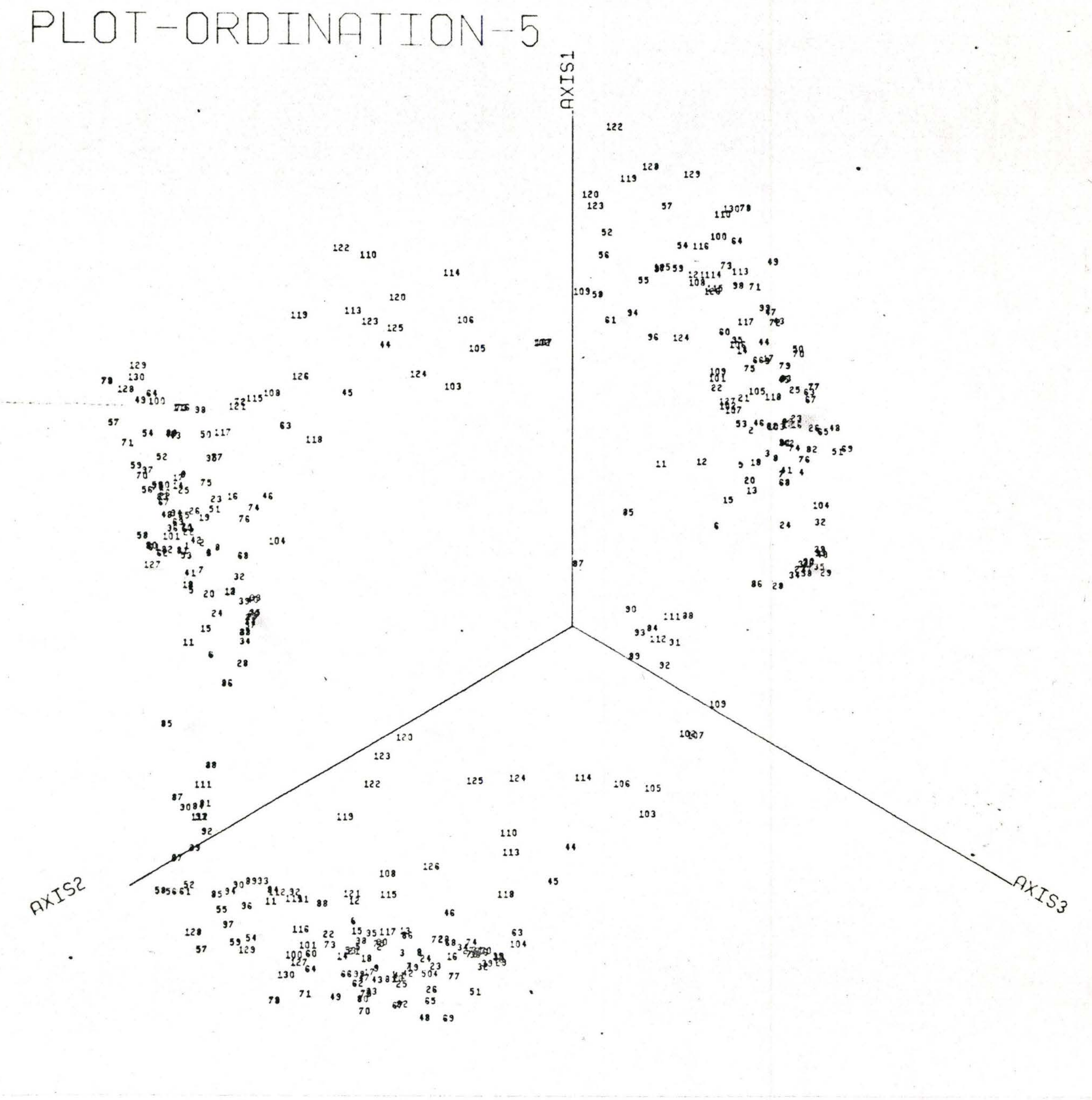


Figure 17. Plot-Ordination for BIGMAT, 30 species, 130 plots. Cover data.

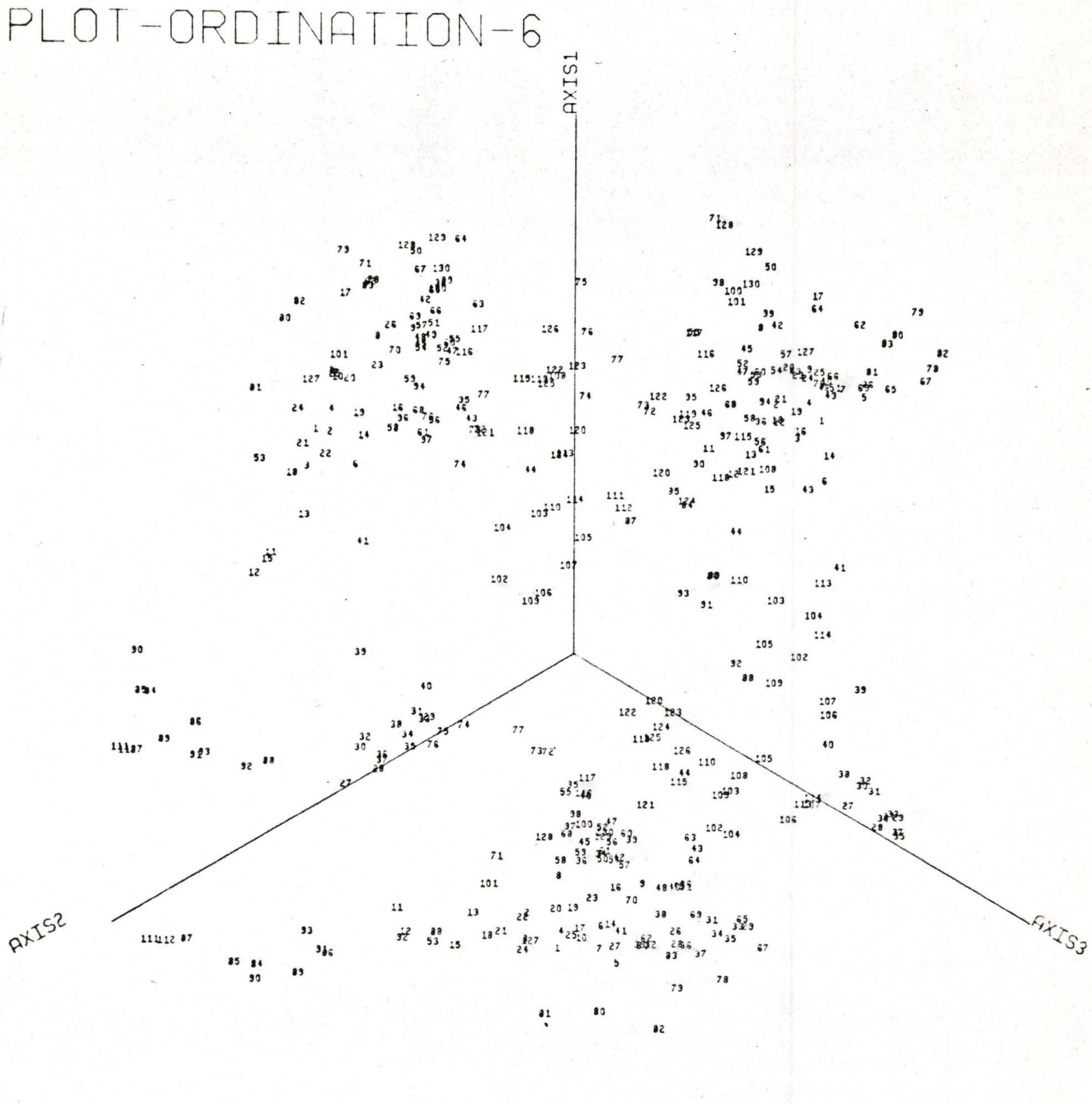


Figure 18. Plot-Ordination for BIGMAT, 30 species, 130 plots. Frequency data.

extracted very slightly more variance than did the Domin ordination, it was found that they did not yield as easily to ecological interpretation as the other type. This may well be a function of the higher total variance associated with numerical measures. (Kershaw, 1968) and in view of the amount of time and expense involved in carrying out further analysis procedures, it was decided to restrict future work to the Domin data.

Subsequent analyses, referred to as ORDIN1, ORDIN2, and ORDIN3 were carried out using the Biomedical program BMD03M (Dixon ed., 1965). Although termed a factor analysis program, it was used with the communalities set to unity (ref. page 55), yielding a principal components solution. Graphical representation of their results are shown in Figure 19 and 20, the results for ORDIN3 being omitted since the large variance involved in ordinating 60 species in this case gave a result which could not be interpreted (See above). In Figure 19, entitled Plot Locations, the three extreme associations are outlined solidly and designated A, B, and C as in the previous case. Five additional, tentative clusters are surrounded by dotted lines. This particular analysis (ORDIN1) ordinated all 130 sample plots. A subsequent analysis (ORDIN2) entitled Outliers Removed gave the results shown in Figure 20. Three additional associations are outlined here, designated D, E, and F. These correspond to the Cladonia rangiferina / Empetrum nigrum / Vaccinium

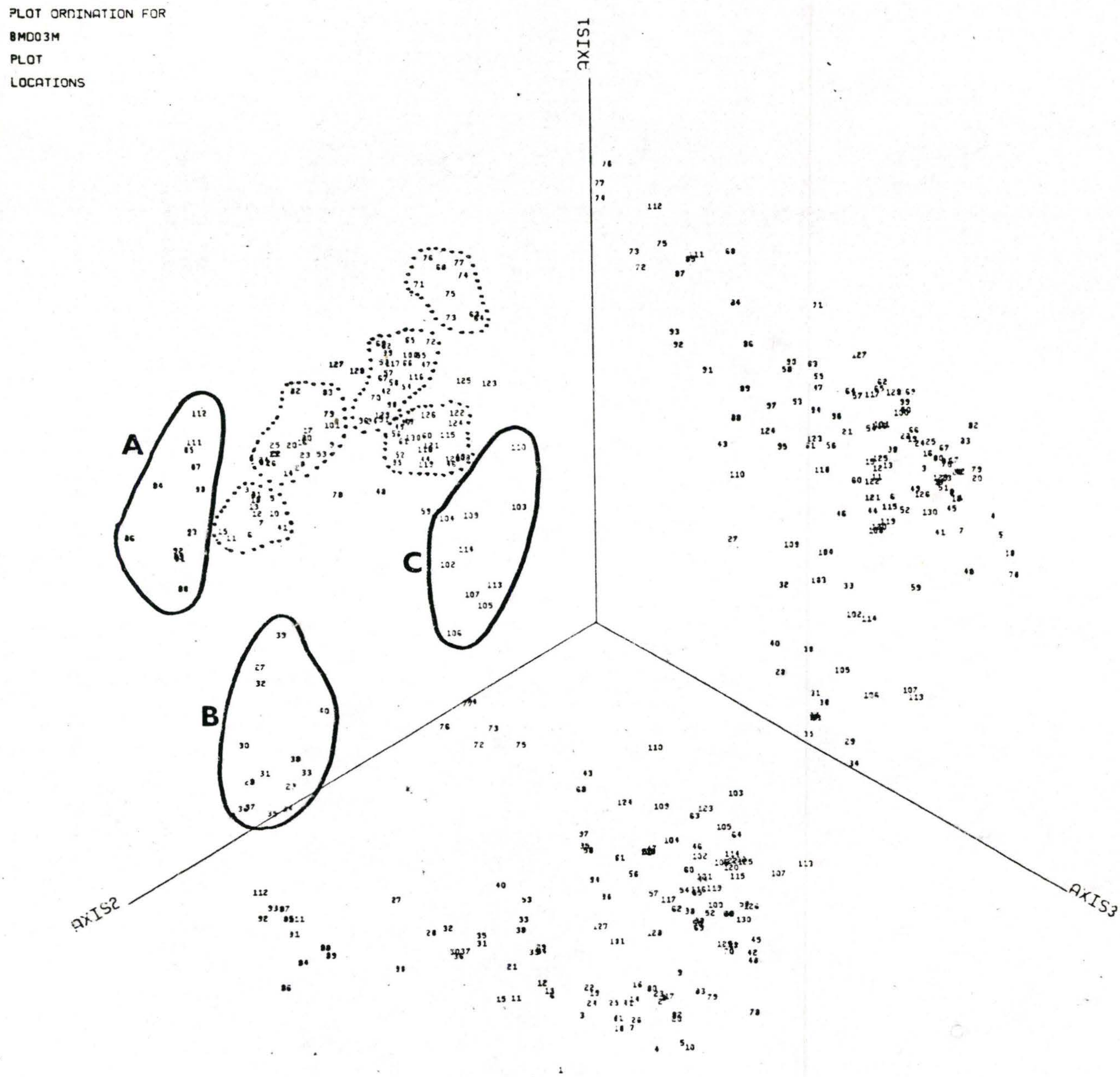


Figure 19. Plot-Ordination for ORDIN1, 30 species, 130 plots. Domin data.

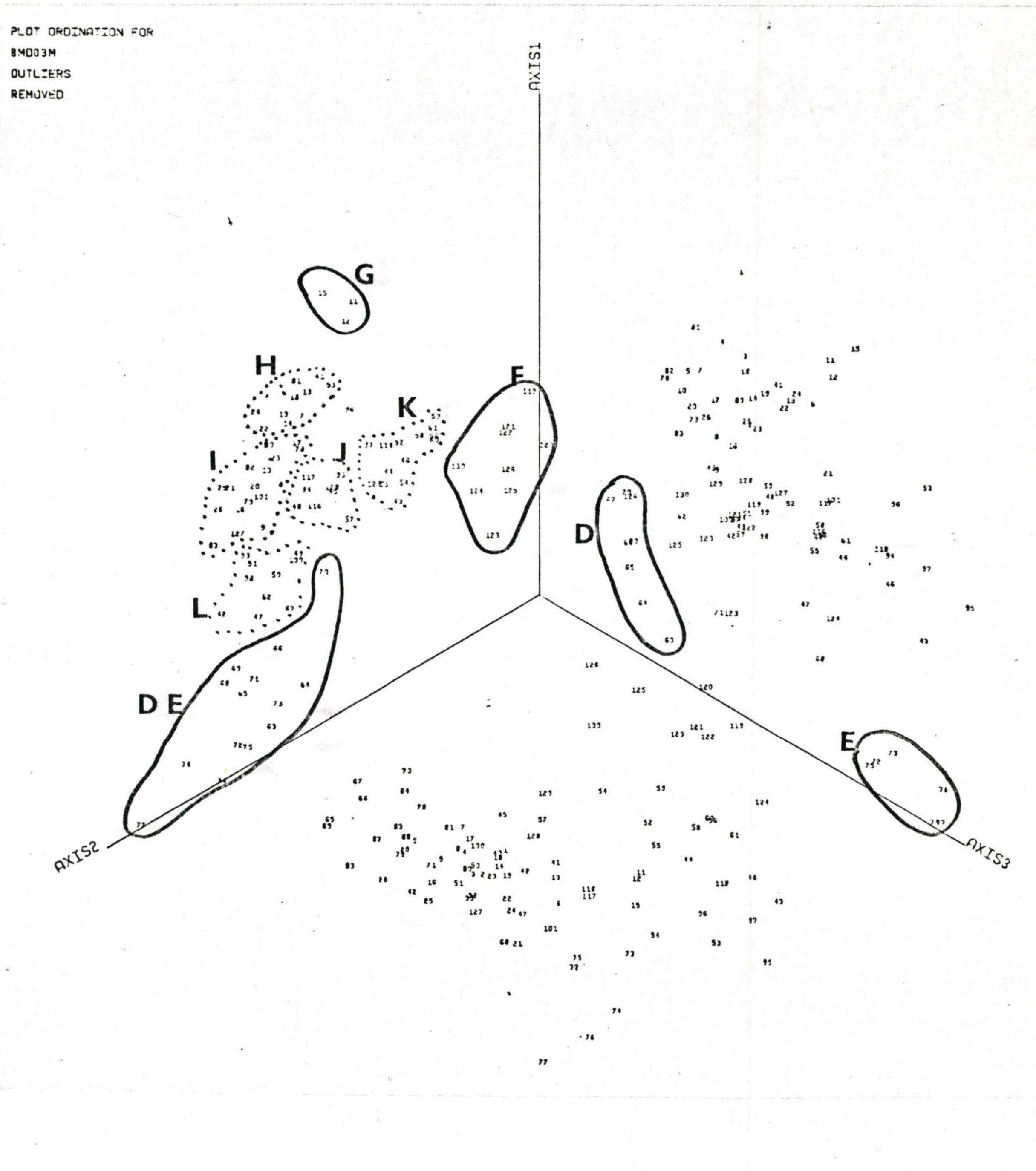


Figure 20. Plot-Ordination for ORDIN2, 30 species, 130 plots. Domin data.

Vitis-Idaea / Rubus Chamaemorus association of the low, mossy, peat-polygon area, the Cladonia rangiferina / Cladonia arbuscula / Cetraria nivalis / Cornicularia divergans association of the higher peat polygon area, and the Alectoria ochroleuca / Cladonia rangiferina / Cladonia alpestris / Empetrum nigrum association of the intermediate slopes.

The remaining sample plots showed little tendency to form groups. Six additional tentative clusters have been indicated and are surrounded by dotted lines. These are designated G, H, I, J, K, and L and show some consistancies with the Braun-Blanquet results. G and H, with relatively few exceptions correspond to the Cladonia rangiferina / Cladonia arbuscula / Rhododendron lapponicum / Dryas integrifolia / Vaccinium uliginosum / Hedysarum Mackenzii association of the central areas. The three plots that separate out as cluster G appear to be marked by being somewhat higher relative to the areas around them. Cluster K expresses a close similarity in composition to the Cladonia rangiferina / Cladonia arbuscula / Cetraria nivalis /Dryas integrifolia association of the central area, the plots of which are marked by a lack of Hedysarum Mackenzii, and a relative abundance of Cetraria nivalis characteristic of sample plots on the slightly sloping parts of the central zone. The rest of the clusters are from the upper slope associations, perhaps indicating that these are not very good associations and that they should be combined into one group.

The results of the three dimensional plot (Fig.21) tend to show the same results with the full compliment of sample plots as did both versions of the planar graphics representation. For example the peat polygon area association has been pulled out at the far top of the diagram. On the other hand the bottom slope association is hidden in this view behind the central cluster. The 3DPLOT program has the capability to rotate the cube containing the clusters of points but as the program is still in the developmental stages further views were not obtainable. Under this situation, the conclusions to follow were based for the most part on the simpler graphical procedures and trend surface analysis.

In summary then, six of the eleven original associations extracted by the Braun-Blanquet technique were retained in identical form in the principal component analysis procedure. Two further associations were present in the ordination results clearly enough to warrant thei retention. The remaining three associations extracted originally did not survive the objective analysis procedures. Considering the doubt attached to them in the Braun-Blanquet analysis these were regrouped to form a broader nodum representing the upper slope areas.

These modified final associations are shown in a block diagram in Figure 22 and their topographic relationships in the sketch in Figure 23.

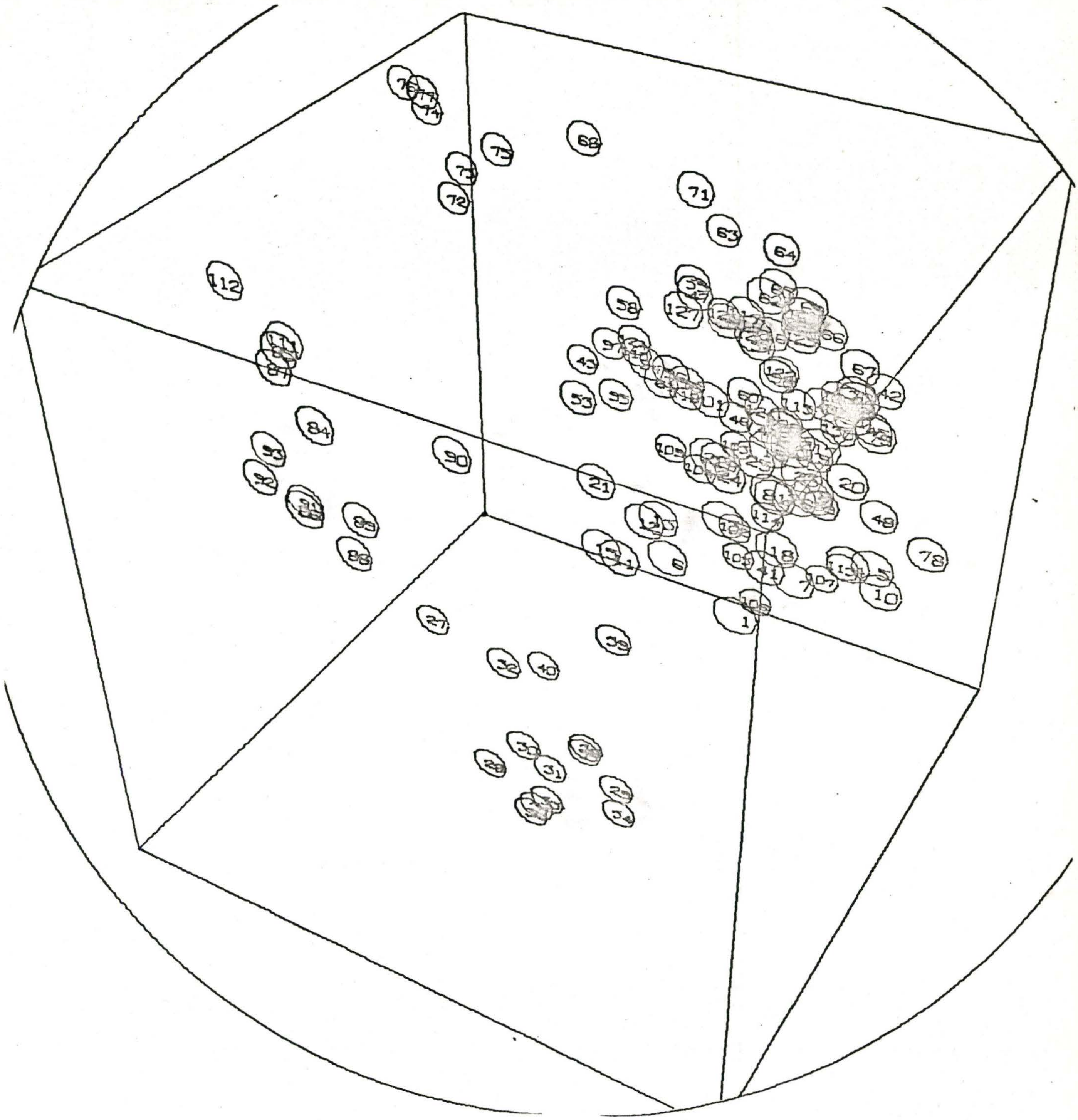
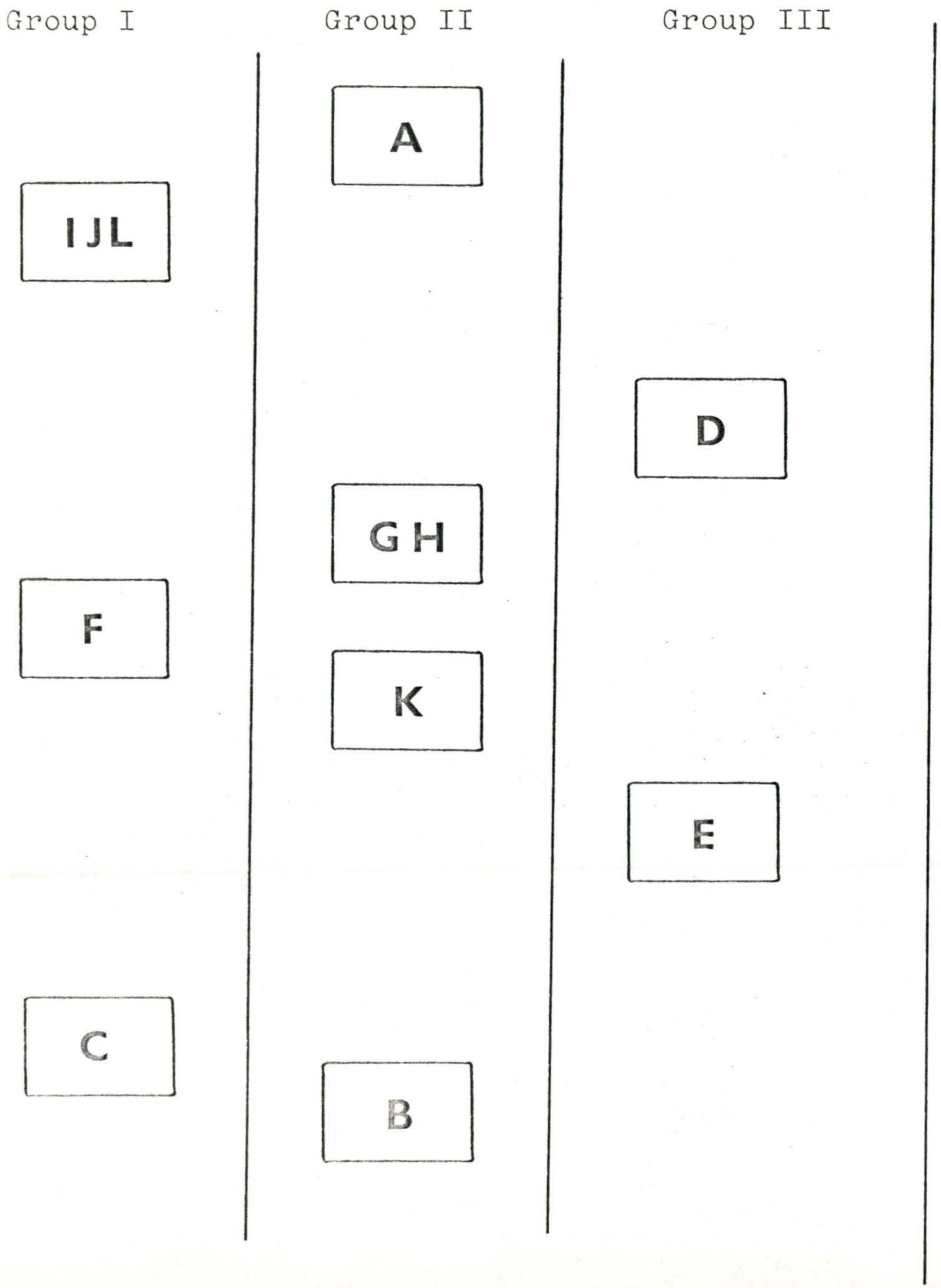


Figure 21. Plot-Ordination for ORDIN1, 30 species, 130 plots.
Domin data.
Three-dimensional representation (3DPLOT).

Figure 22. Block Diagram of Final Plant Associations.



CORRESPONDING ASSOCIATIONS

I,J,L *Cladonia rangiferina, Empetrum nigrum, Alectoria ochroleuca, Vaccinium uliginosum.*

F *Alectoria ochroleuca, Cladonia rangiferina, Cladonia alpestris, Empetrum nigrum.*

C *Cladonia alpestris, Cladonia rangiferina, Empetrum nigrum.*

A *Dryas integrifolia, Hedysarum Mackenzii.*

G,H *Cladonia rangiferina, Cladonia arbuscula, Rhododendron lapponicum, Dryas integrifolia.*

K *Cladonia rangiferina, Cladonia arbuscula, Cetraria nivalis, Dryas integrifolia.*

B *Vaccinium uliginosum, Rhododendron lapponicum, Dryas integrifolia.*

D *Cladonia rangiferina, Cladonia arbuscula, Cetraria nivalis, Cornicularia divergans.*

E *Cladonia rangiferina, Empetrum nigrum, Vaccinium Vitis-Idaea, Rubus Chamaemorus.*

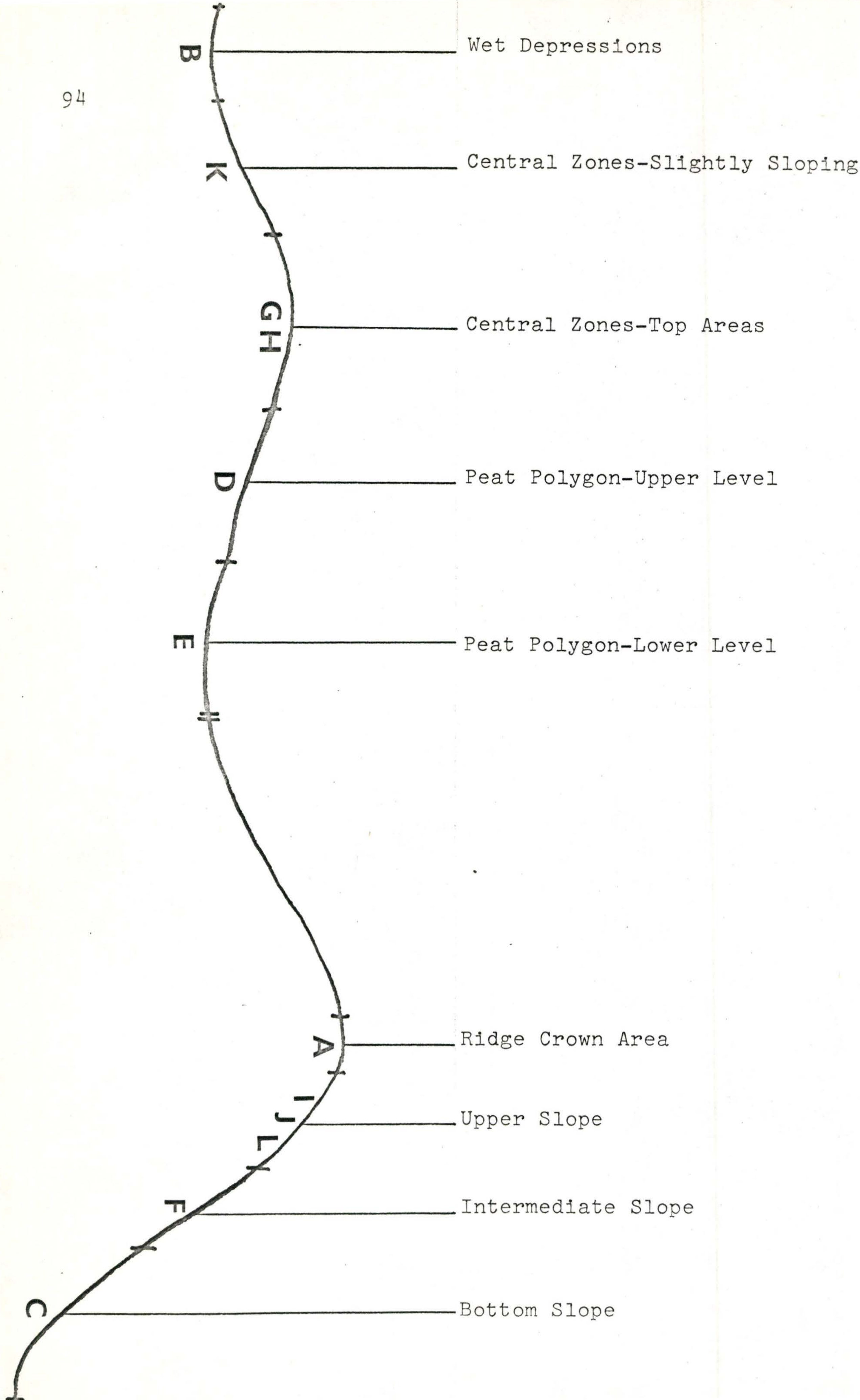


Figure 23. Topographic Relationships of Final Associations.

(4.2) The Analysis of Principal Component Trends

(a) Inverse or Species Ordination

The second major aim of this study was to generate hypotheses concerning the underlying ecological factors controlling the distribution of the vegetation under study. This was accomplished through the use of three different techniques, inverse or species ordination, subjective trend analysis and objective trend surface analysis.

The first type of ordination involves the use of a model which represents the species in a sample space defined by their sample plots. The first analysis, refered to as Species-Ordination-1 (Fig.24) extracted the first three axes. It showed a high loading on the first axis (53 percent) that was related to the relative frequency of the species in the total sample. This effect was expected and has been pointed out in other studies (Kershaw, 1968). Consequently the ordination has been examined in terms of axes 2, 3, and 4, (Species-Ordination-2), but did not yield a clear representation of any but the most abundant species (Fig.25).

A reduction to the 30 most common species (Species-Ordination-3) in order to reduce the variance, was more successful (Fig.26). The extreme species were used as indicators which showed the following characteristics:

The presence of species number 9 and 28 (Dryas integrifolia and Hedysarum Mackenzii) at the extreme end of axis

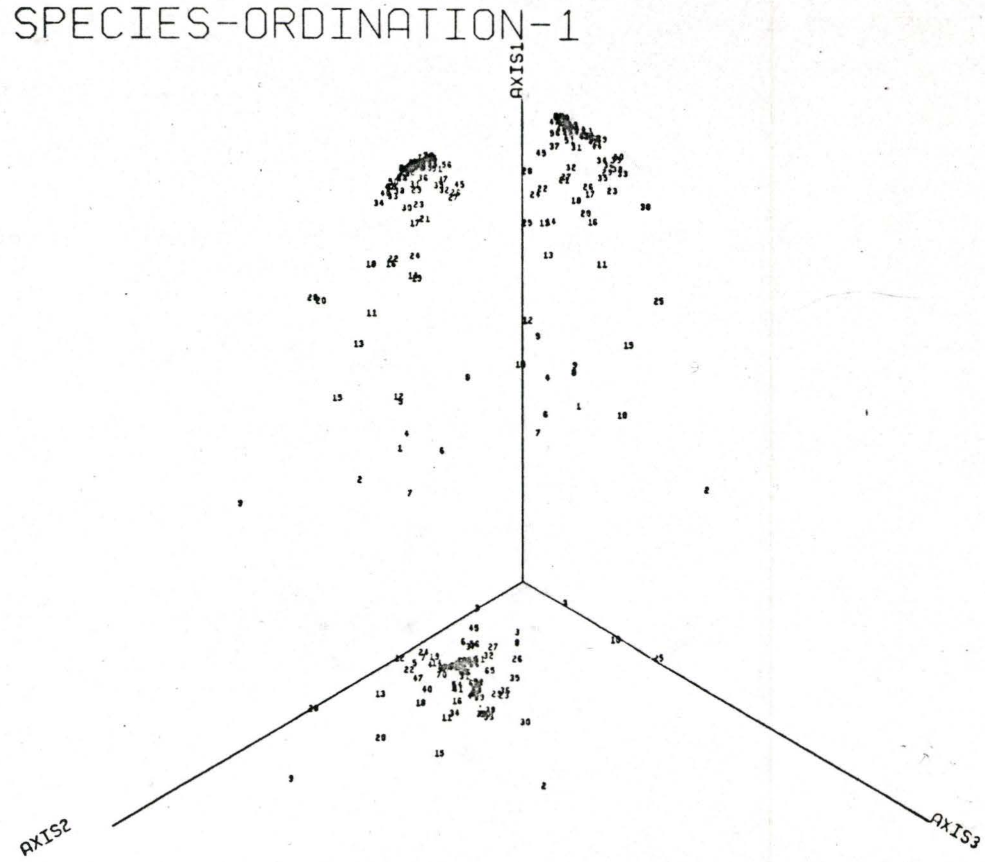


Figure 24. Species-Ordination for BIGMAT, 74 species, 130 plots. Domin data.

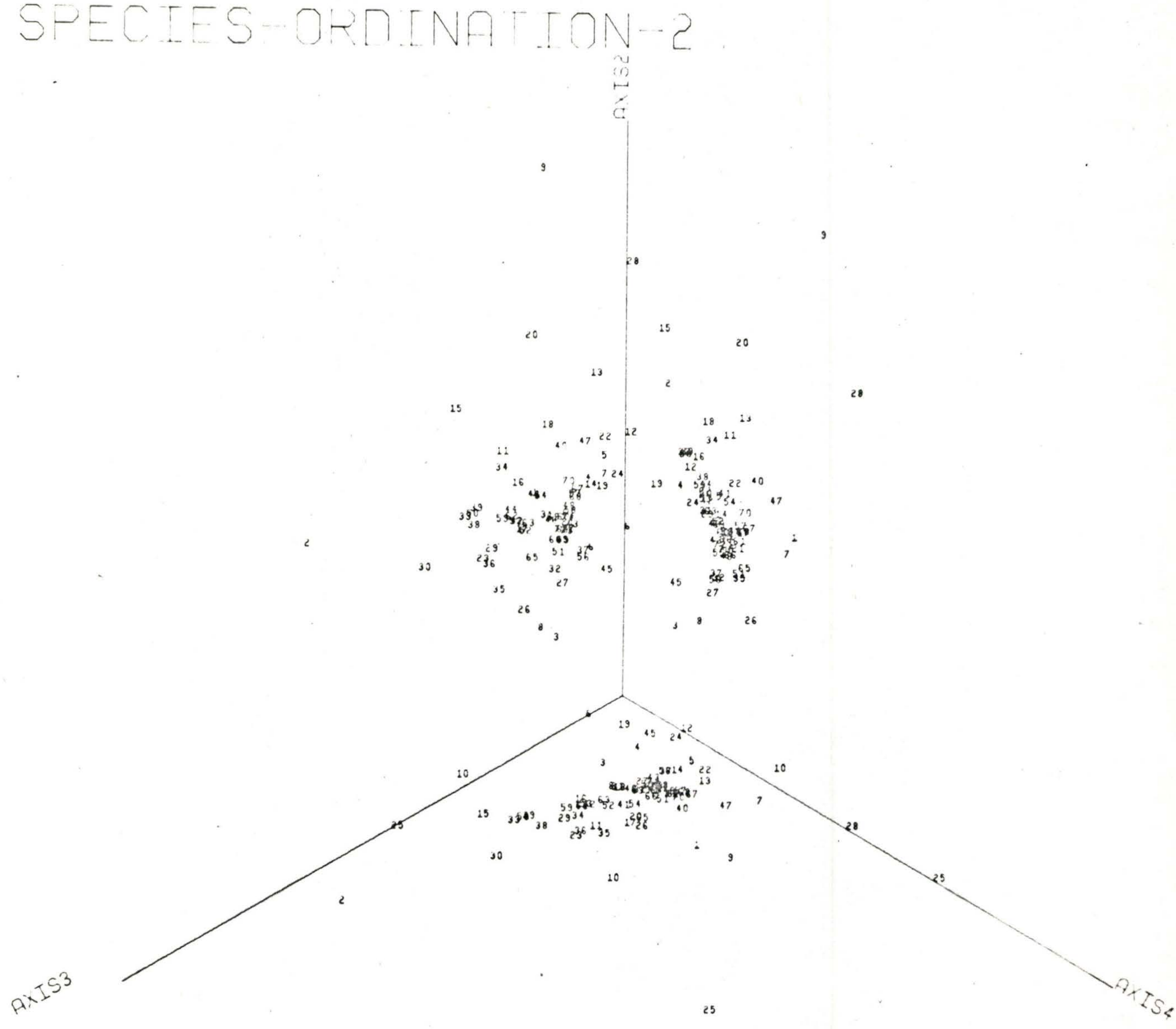


Figure 25. Species-Ordination for BIGMAT, 74 species, 130 plots. Domin data.

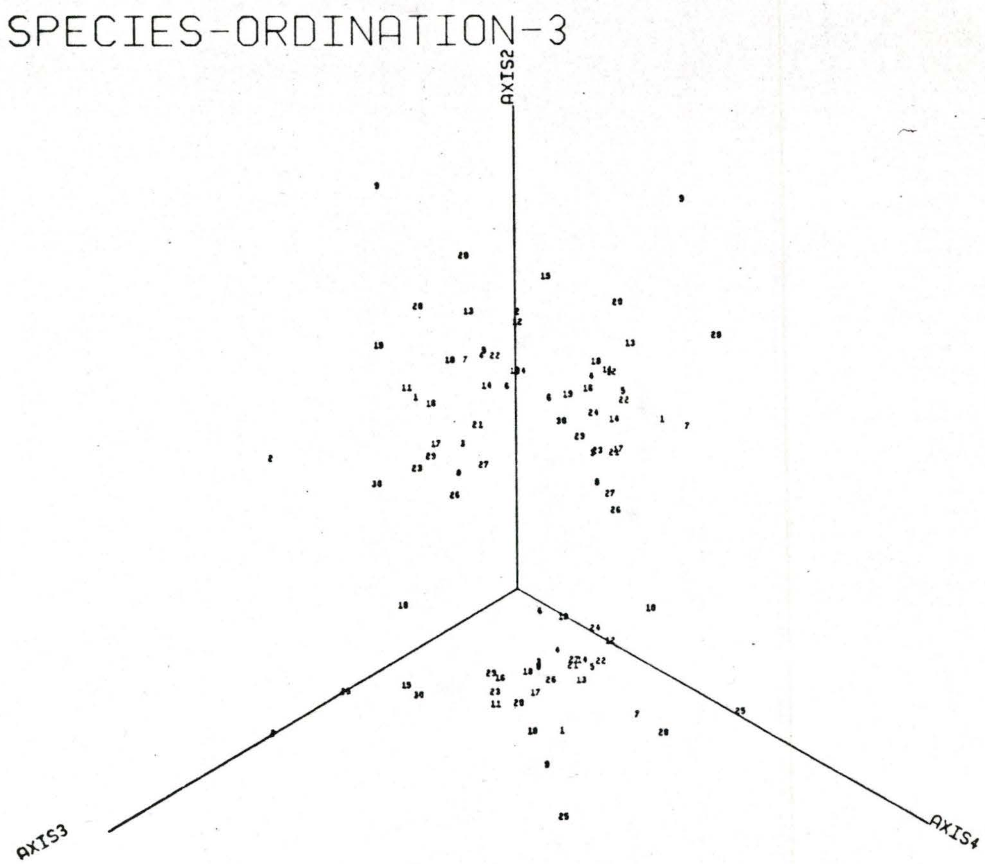


Figure 26. Species-Ordination for BIGMAT, 30 species, 130 plots. Domin data.

2 indicates that this pole may be correlated with an absence of a peaty substratum, or perhaps a high pH value for the soil. This is supported by the presence of species 10 and 25 (Empetrum nigrum and Cladonia alpestris) at the opposite pole of this axis. Empetrum is said to prefer acid substrate (Porsild, 1964) as is Cladonia alpestris (Ahti, 1961). Dryas and Hedysarum are both calcicoles (Porsild, 1964). Loadings on axis 3 show a separation of species 2 (Vaccinium uliginosum) at the extreme and species 12 (Cornicularia divergans) at the origin. Although Vaccinium uliginosum was found fairly commonly throughout the sample area, it did display a preference towards a moist habitat, while Cornicularia was most commonly found on the crests of ridges, in what might be considered a dry habitat. The orientation of species with axis 4 did not display a clear correlation with any obvious factor. This is not surprising in view of the small amount (6.3 percent) of the total variation accounted for by this component, and the lack of detailed ecological information on the species ordinated.

From these observations it is tentatively concluded that there are correlations with the presence/absence of peat or a change in soil pH, and water availability or some factor controling its presence, in the distribution of the species examined.

(b) Analysis of Trend Surfaces

Species overlays were produced for both the full compliment ordination, that is, the ordination of all 130 plots, and also on the ordination with outliers removed. The species chosen were Vaccinium uliginosum, Cladonia rangiferina, Dryas integrifolia, Empetrum nigrum, Alectoria ochroleuca, Cetraria nivalis, Carex rupestris, Hedysarum Mackenzii, Alectoria nigricans, Cladonia alpestris as well as pH and Soil Moisture by Volume. Of these, trend surface analyses were carried out on pH, Soil Moisture, Vaccinium uliginosum, Empetrum nigrum, Dryas integrifolia, Hedysarum Mackenzii, Cladonia alpestris and additionally Cornicularia divergans, however, only for the factor scores derived from the full compliment ordination.

Figure 27 shows a semi-three-dimensional representation of the second order trend surface analysis for pH based on the factor scores of ORDIN1. This corresponds to the overlay diagram shown in Figure 28. Refering to Table 17 it is apparent that the largest amounts of large scale variation were accounted for in the trend surfaces of axes 1 - 2 and 2 -3 with 54.0 and 48.3 percent respectively. These two surfaces have in common axis 2. The trend maps produced by the line printer and combined into the representation in Fig.27 shows a trend along axis 2 and increasing toward the extremity. The axes 1 - 3 plot shows a trend increasing toward the origin in the same direction. These results all appear to indicate that pH has a significant trend of large scale variation on axis 2 increasing away

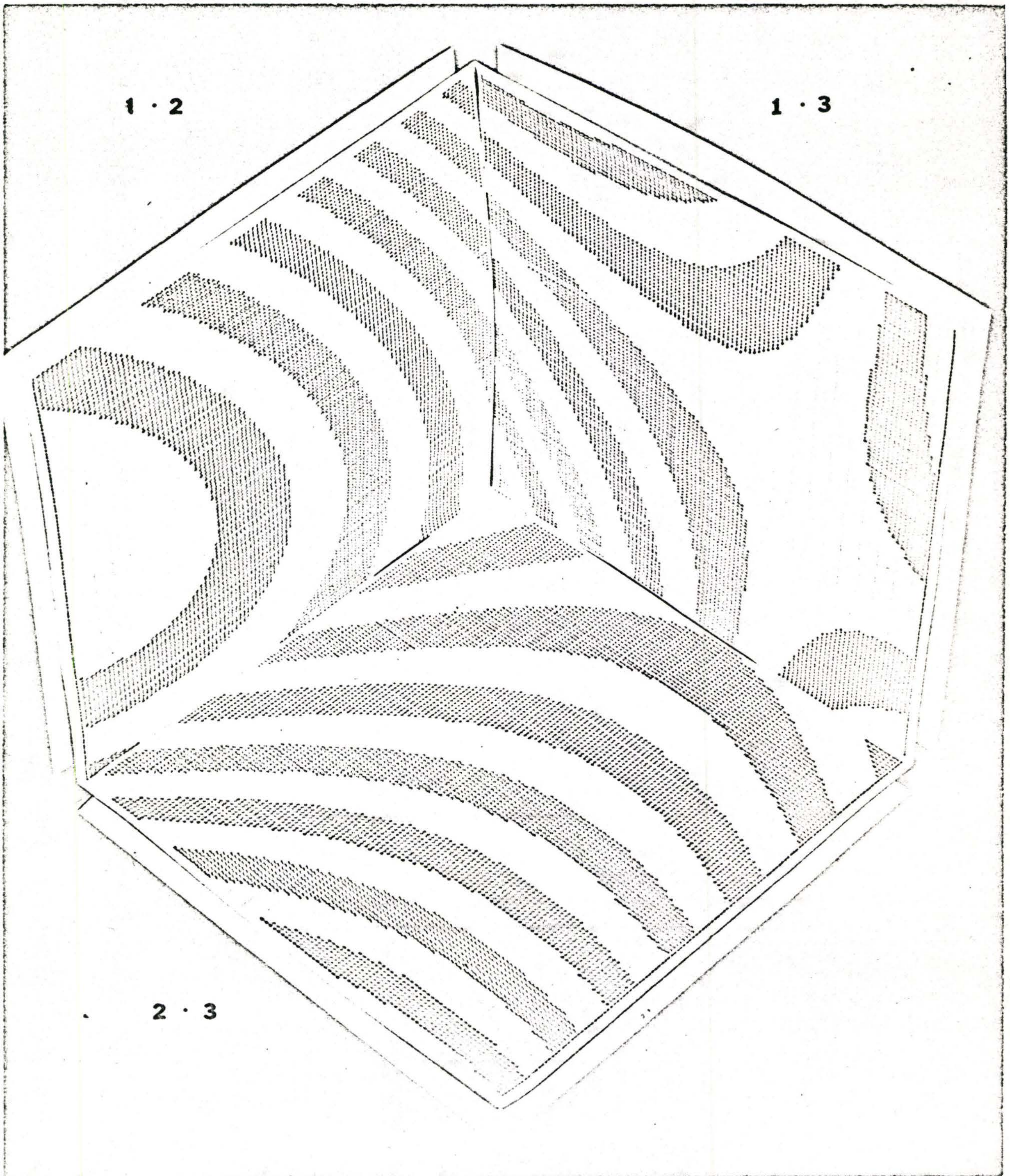


Figure 27. Combined trend surface for pH.

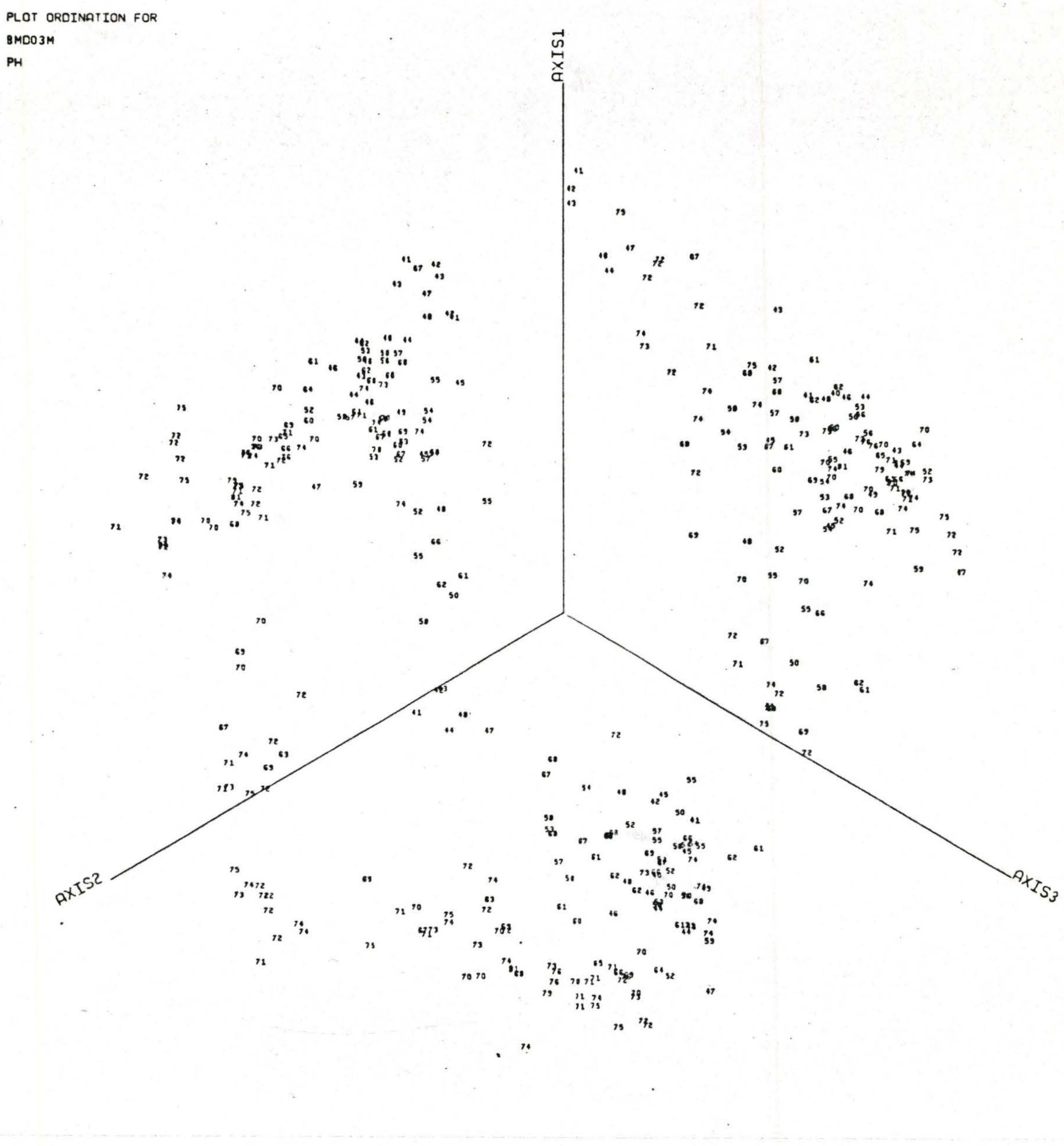


Figure 28. Overlay diagram for pH based on ORDIN1.

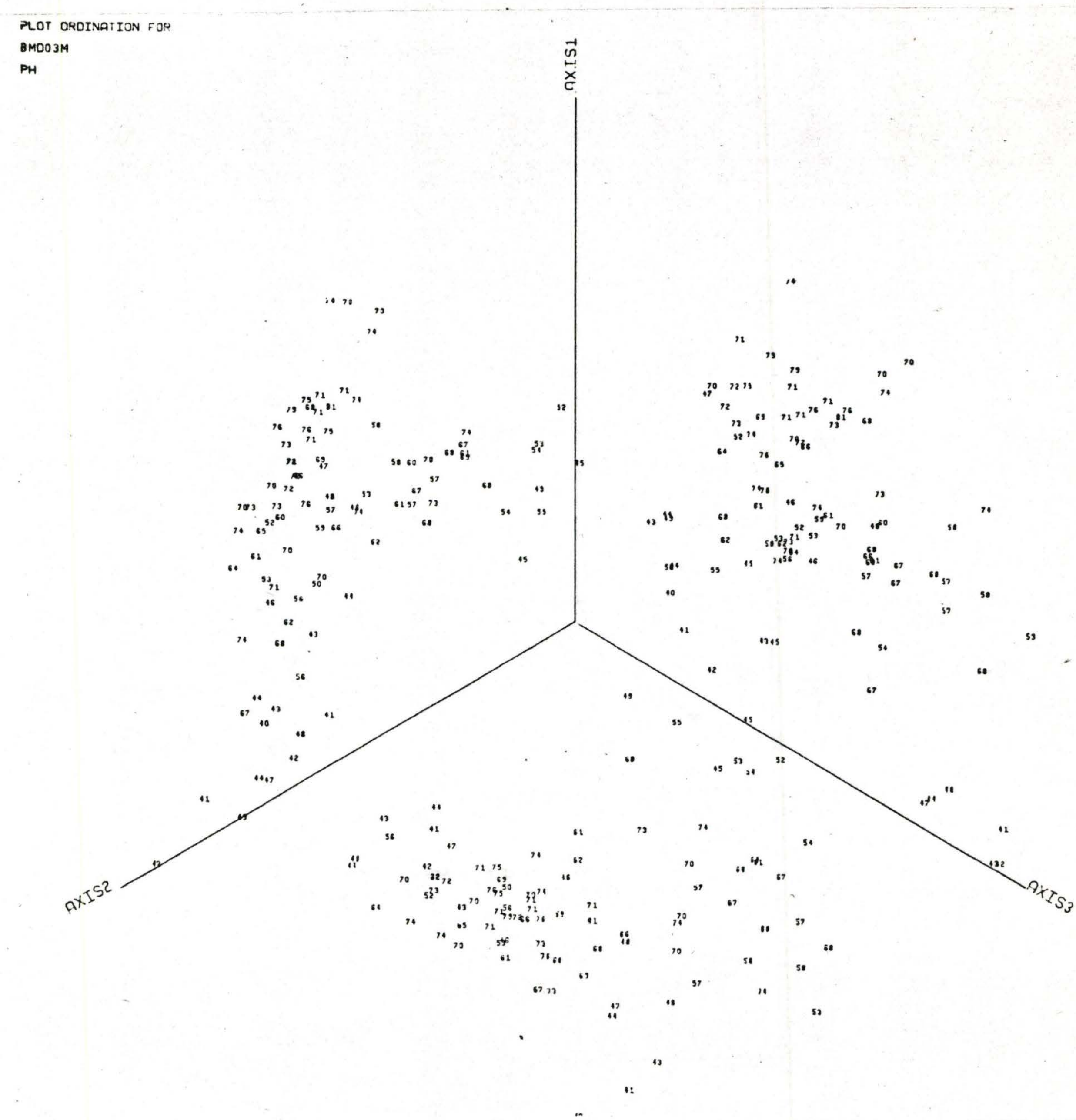


Figure 29. Overlay diagram for pH based on ORDIN2.

from the origin. This observation is in agreement with the subjective trend visible in the overlay diagram in Figure 28.

The overlay diagram of Soil Moisture (Fig.31) does not appear to show any clear direction of trend. Results in terms of variation accounted for are also confusing in that only the axes 1 - 2 map shows a really significant trend. With this in mind the trend map in Figure 30 would appear to indicate that Soil Moisture is correlated with both axes 1 and 2 increasing towards the origin. The axes 2 - 3 plot might be interpreted as showing a bias in the trend towards axis 2. Considering the reverse direction of this trend to that of pH it is not unreasonable to conclude that since the measurement of both pH and Soil Moisture are related to the amount of peat in the soil sample they might well be correlated with each other. The reverse directions are logical in that a sample with more peat will have a lower, more acid pH, but will retain more soil water.

The overlay and trend surface of species abundance for Dryas integrifolia (Figs.33 and 34) shows a very clear correlation with axis 2 increasing along its length.

Empetrum nigrum is also clearly correlated with axis 2 as shown in the results of Figures 36 and 37 and Table 17. Its trend however, shows an increase toward the origin.

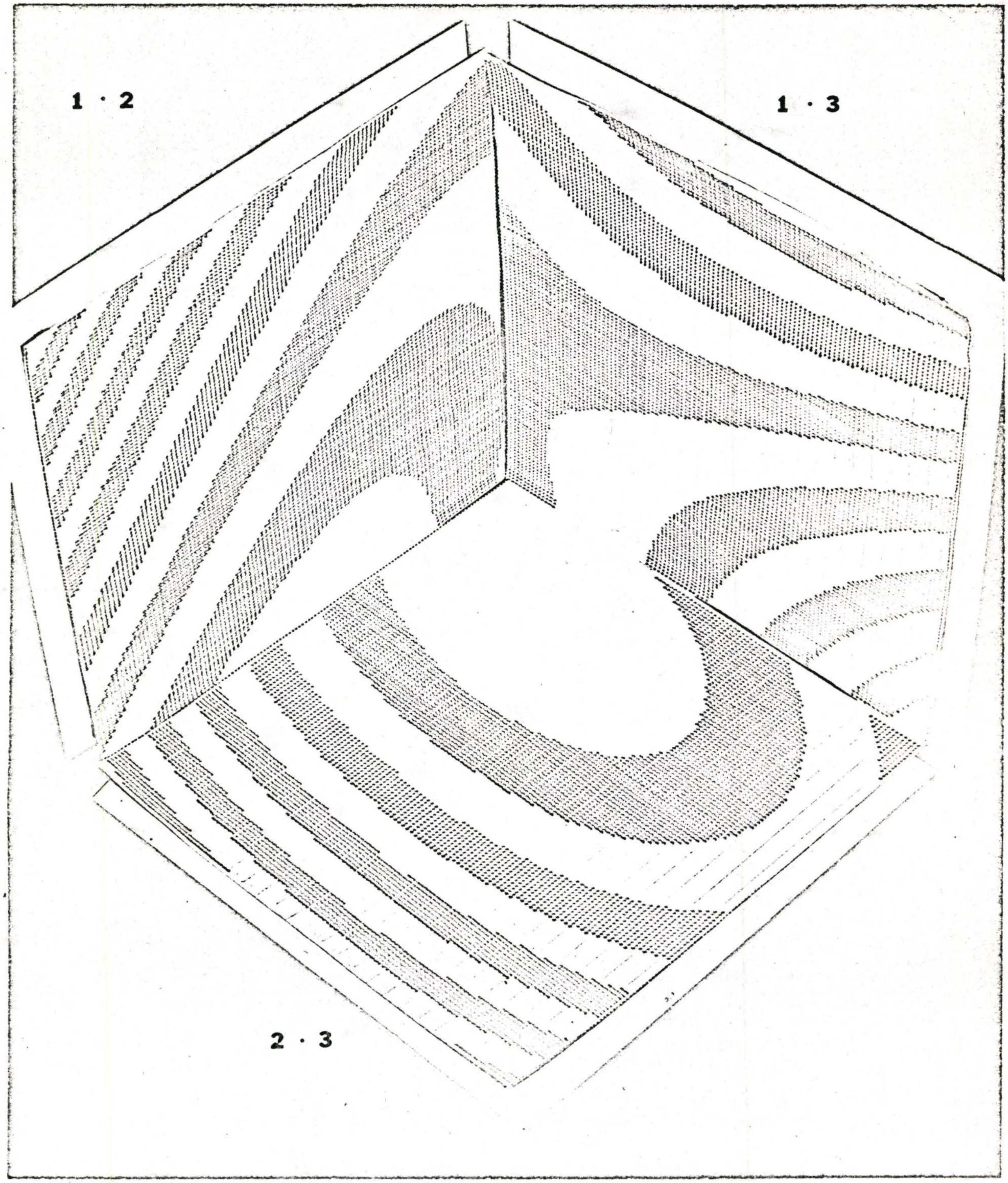


Figure 30. Combined trend surface for Soil Moisture.

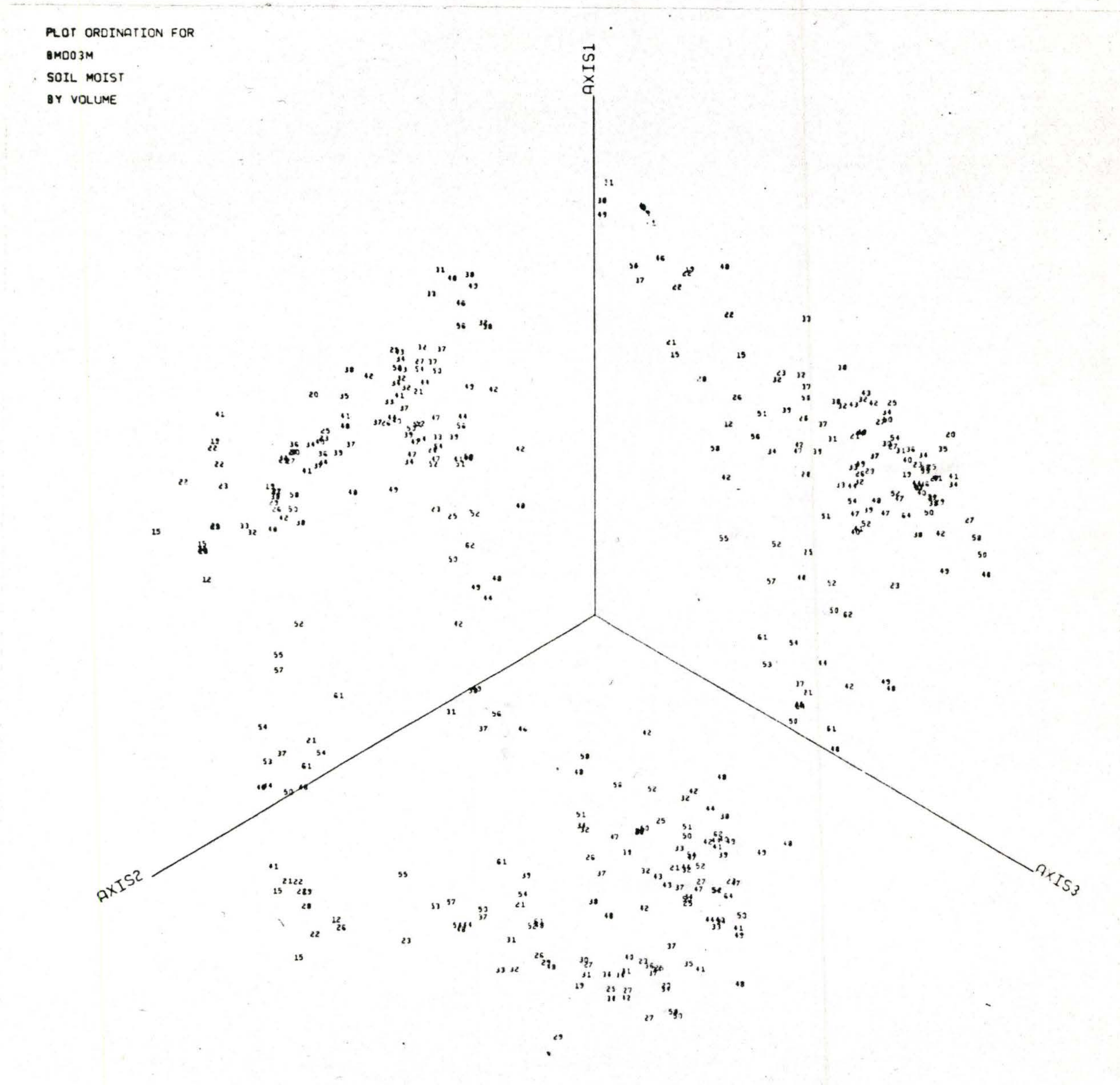


Figure 31. Overlay diagram for Soil Moisture based on ORDIN1.

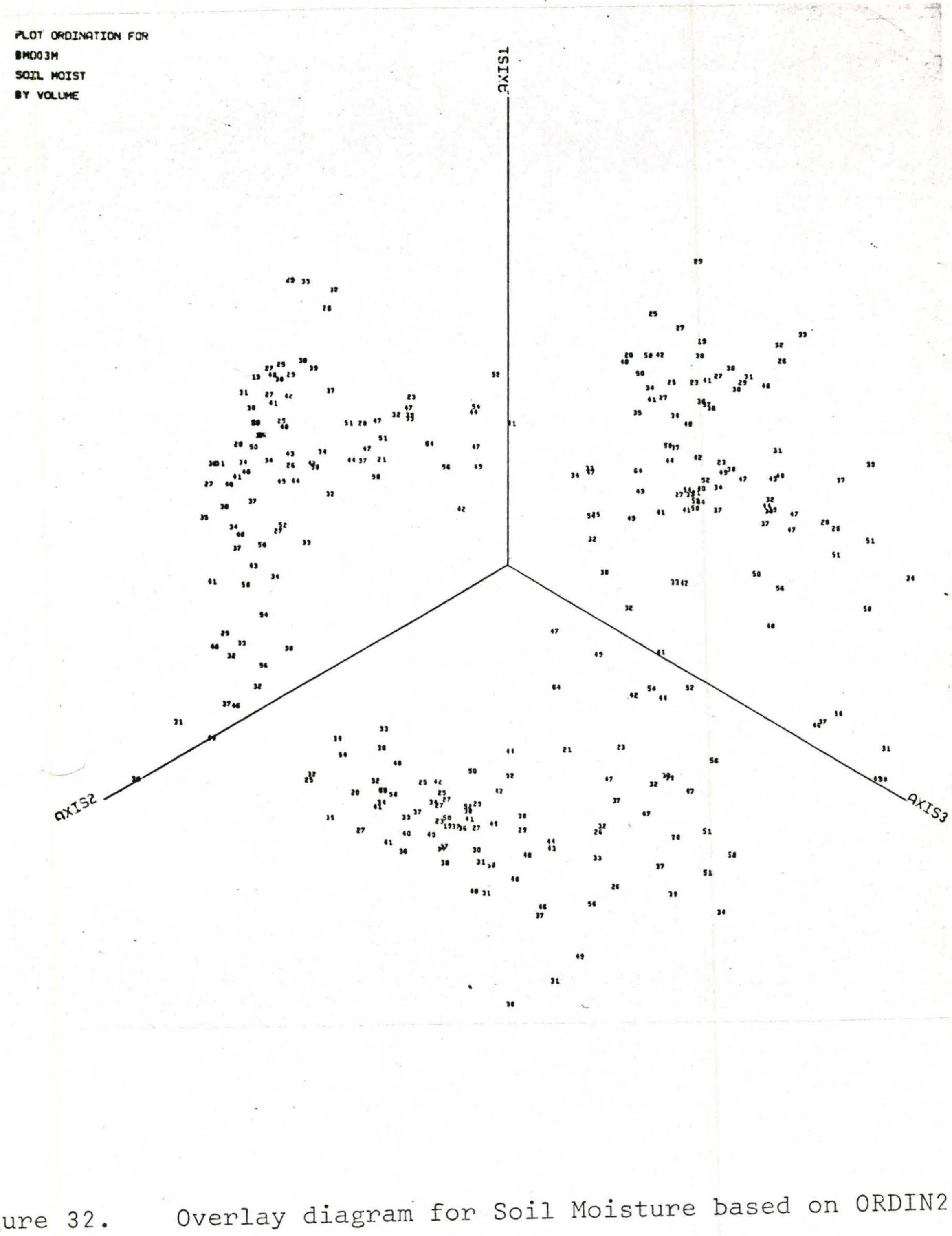


Figure 32. Overlay diagram for Soil Moisture based on ORDIN2.

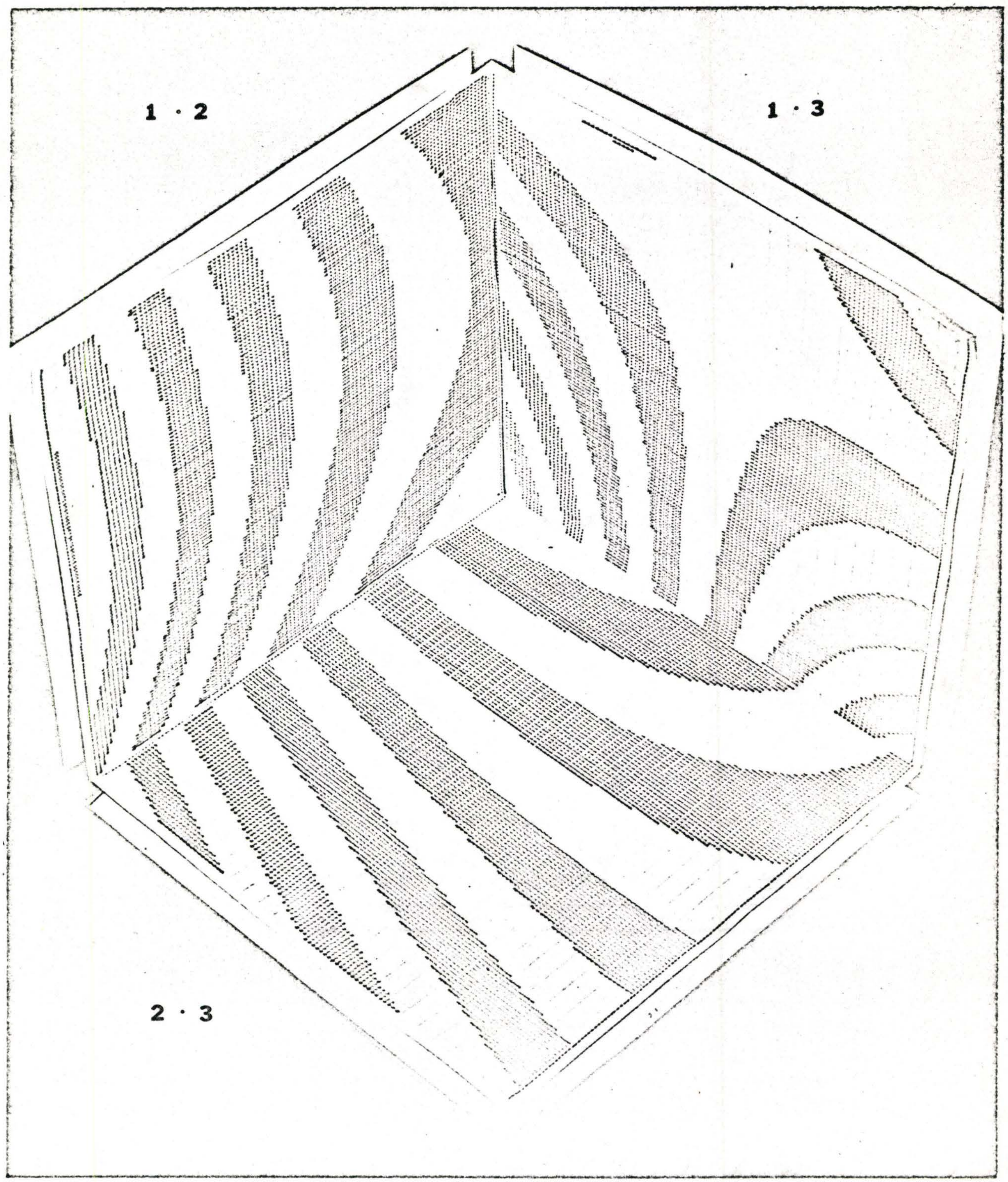


Figure 33. Combined trend surface for Dryas integrifolia.

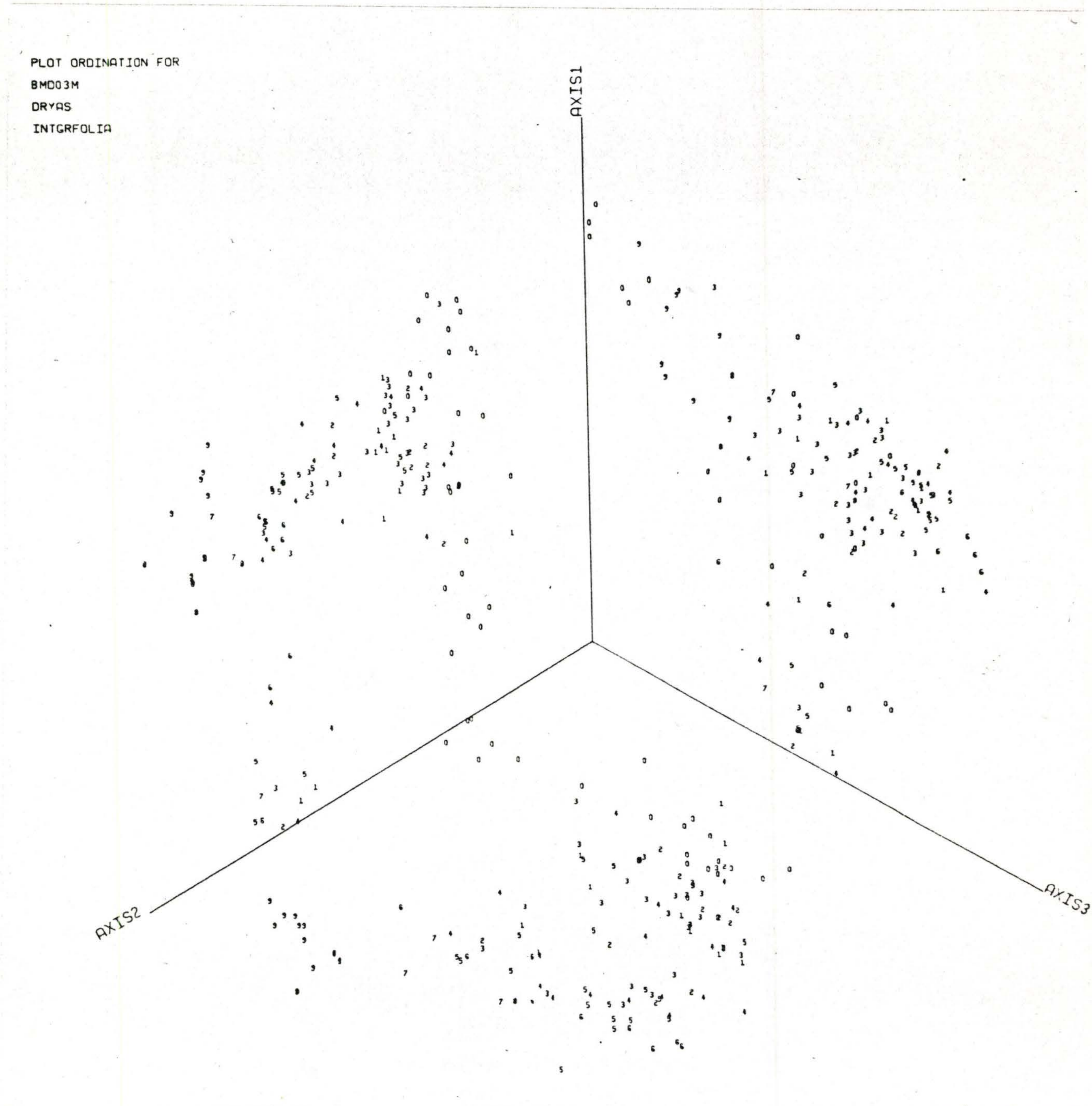


Figure 34. Overlay diagram for <u>Dryas</u> <u>integrifolia</u> based on ORDIN1.

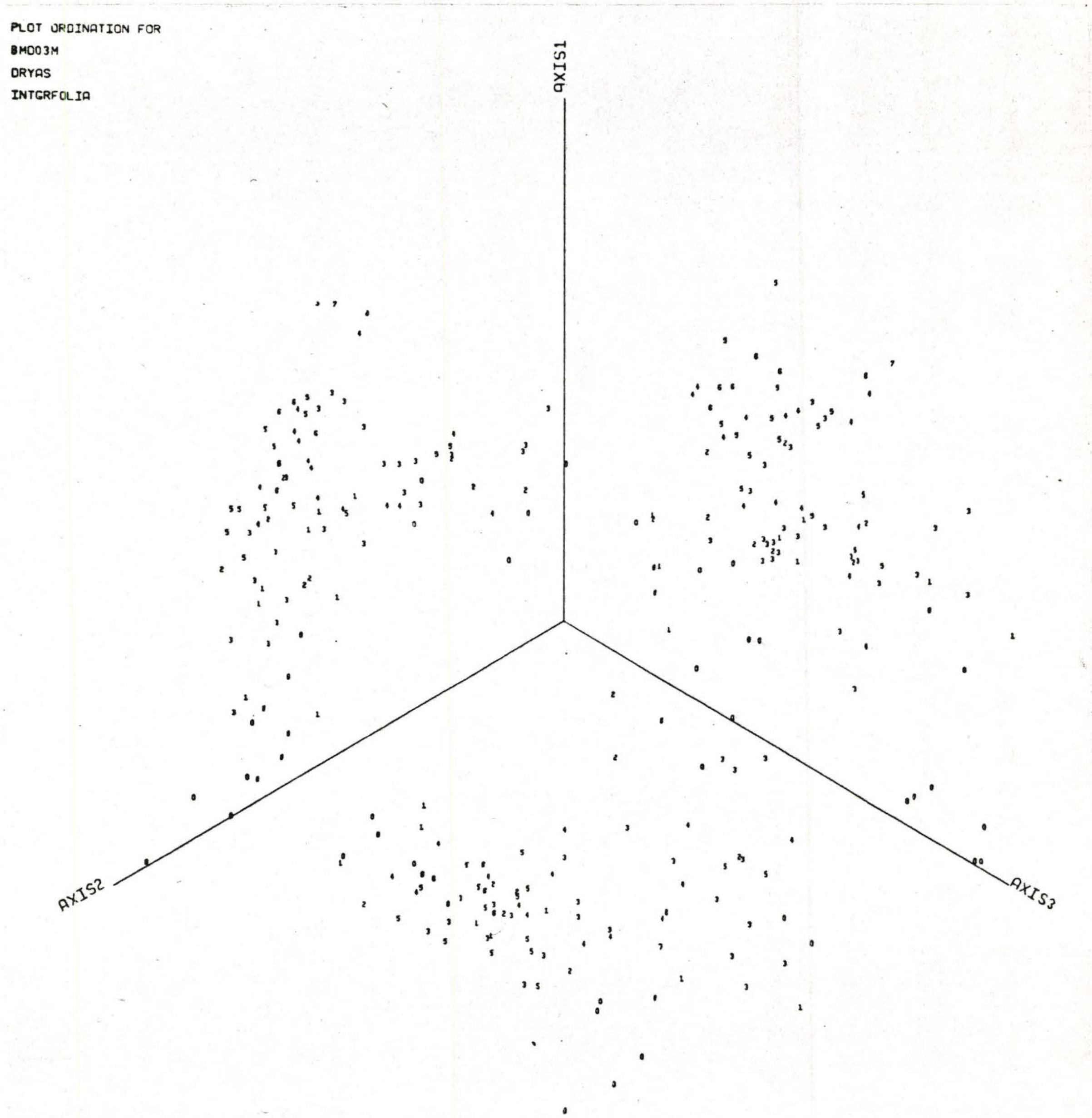


Figure 35. Overlay diagram for Dryas integrifolia based on ORDIN2.

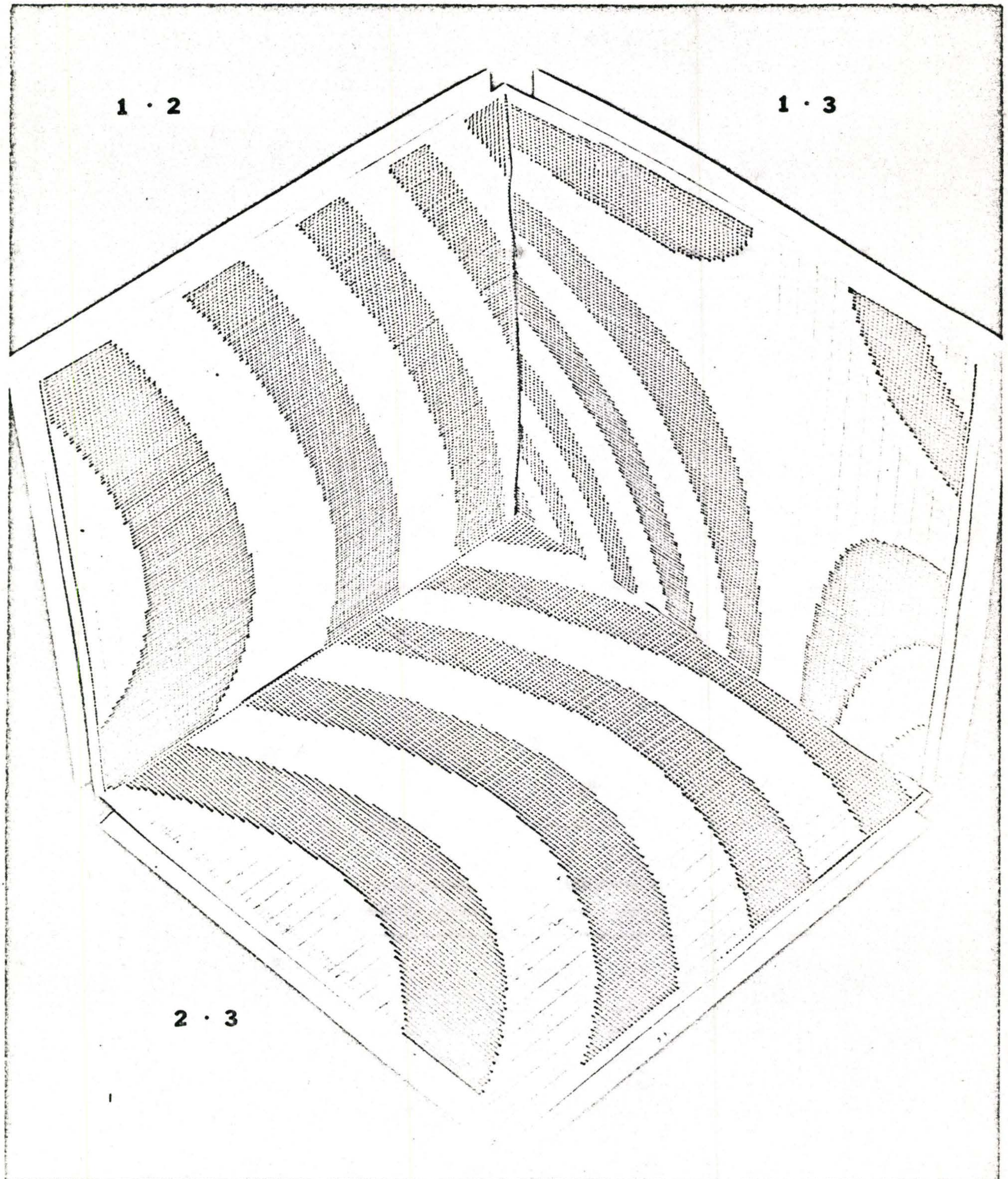


Figure 36. Combined trend surface for Empetrum nigrum.

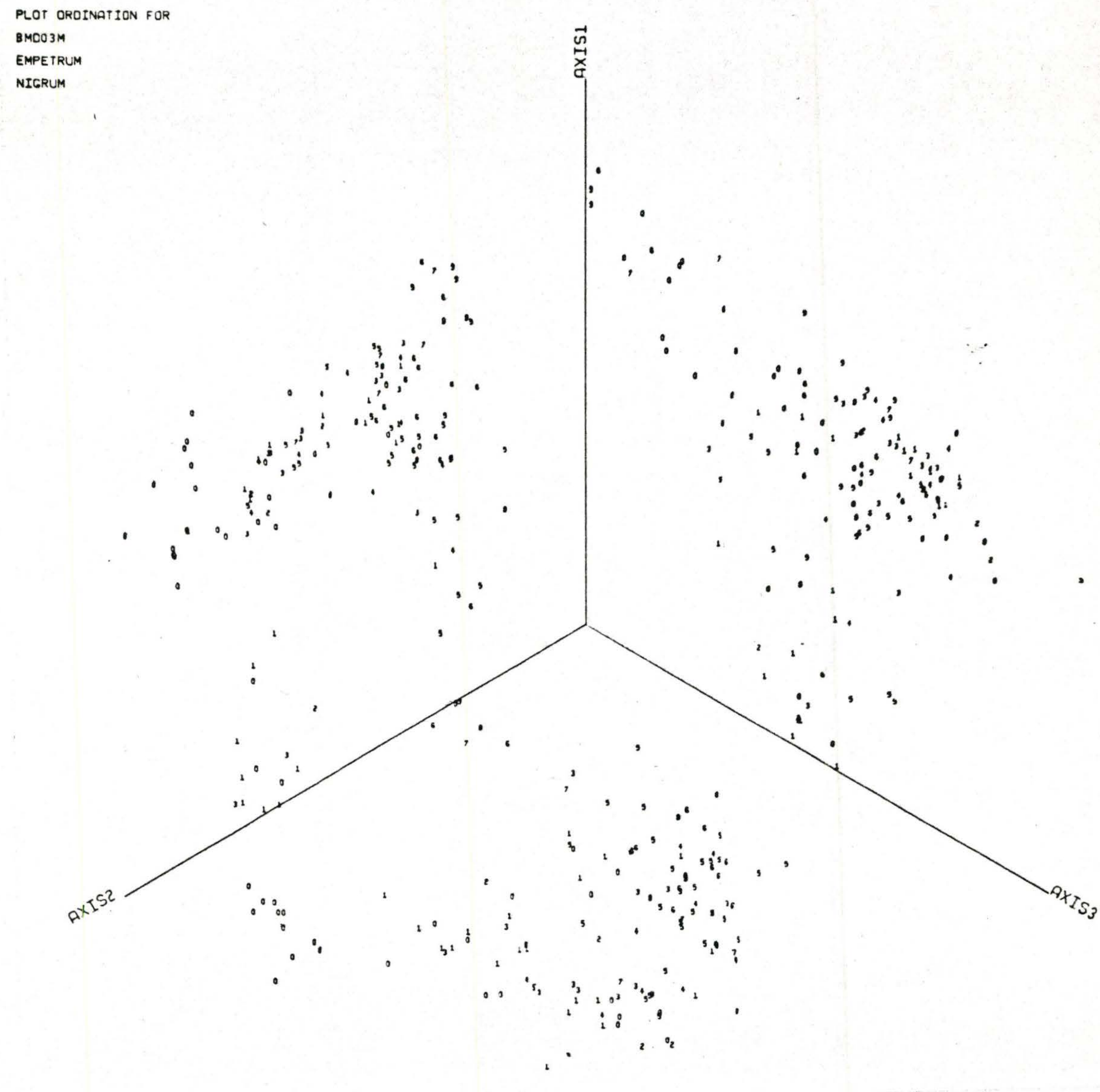


Figure 37. Overlay diagram for Empetrum nigrum based on ORDIN1.

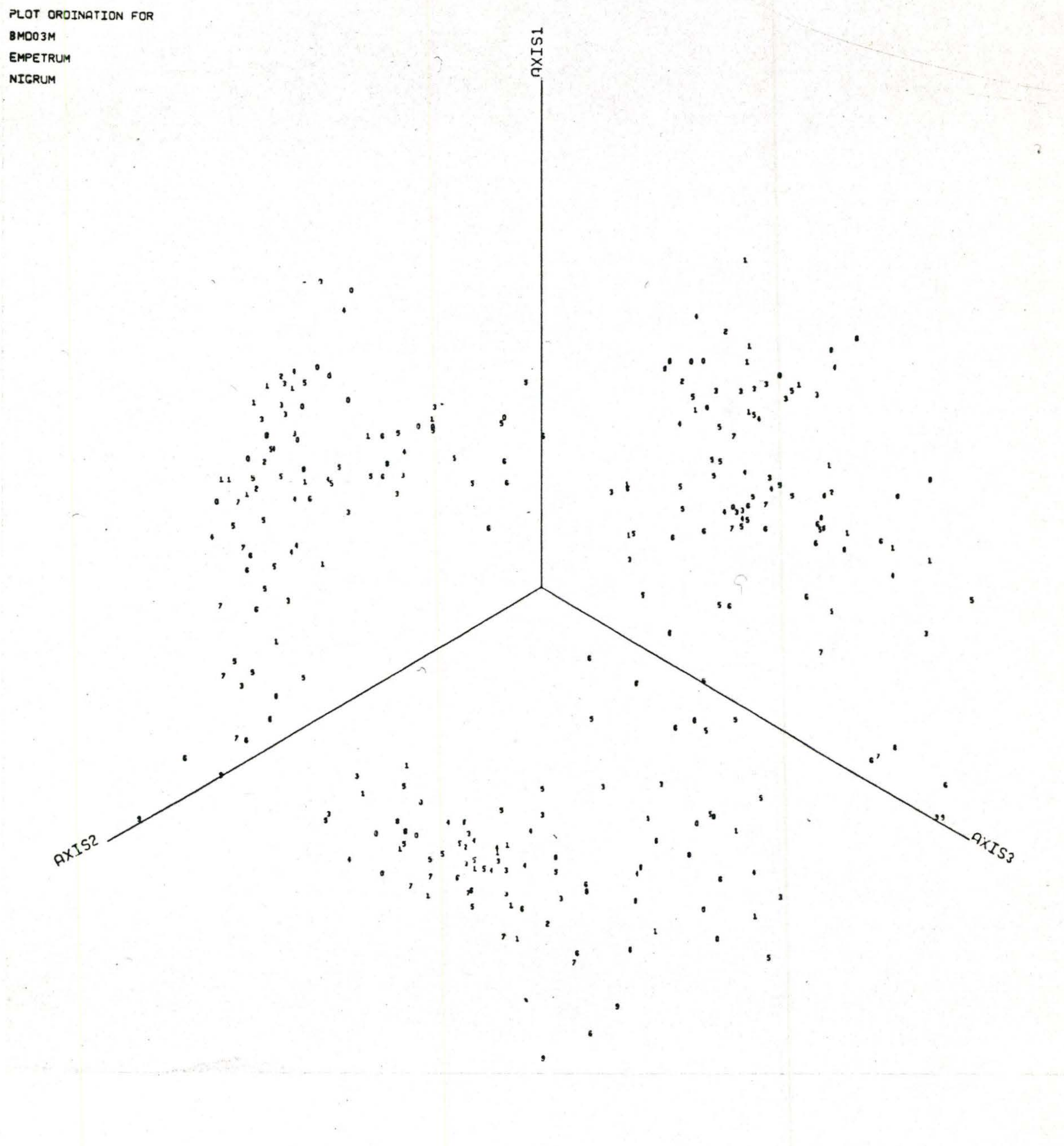


Figure 38. Overlay diagram for Empetrum nigrum based on ORDIN2.

The picture for *Cladonia alpestris* is somewhat confused. The overlay diagram appears to point to a correlation with axis 3 but this seems to be refuted by the statistics in Table 17, which indicate the highest values for 1 - 2 and 2 - 3. Upon closer examination of the trend map in Figure 39 it can be seen that the trend on 1 - 2 is closely associated with a cluster near the origin (see Fig.40). In addition, on the 1 - 3 plot, only the wide central contours are significant as these are the only ones which are positive and associated with the point cluster. With this in mind it appears that the trend is on axis 3 increasing from the origin.

Hedysarum Mackenzii is definitely associated with axis 2 showing an increasing trend towards the extreme end of the axis (Fig. 42 and 43).

The high frequency of *Vaccinium uliginosum* in the sample area shows up in the overlay diagram in Figure 46 which does not appear to show any clear trends. The trend map in Figure 45 however, shows a fairly clear trend on axis 1 increasing towards the origin but with some bias towards axis 3.

The last trend surface, *Cornicularia divergans*, (Fig.48) which was added as a result of its occurance in the species ordination results, seems to show a correlation with both axes 1 and 3 increasing toward the extreme.

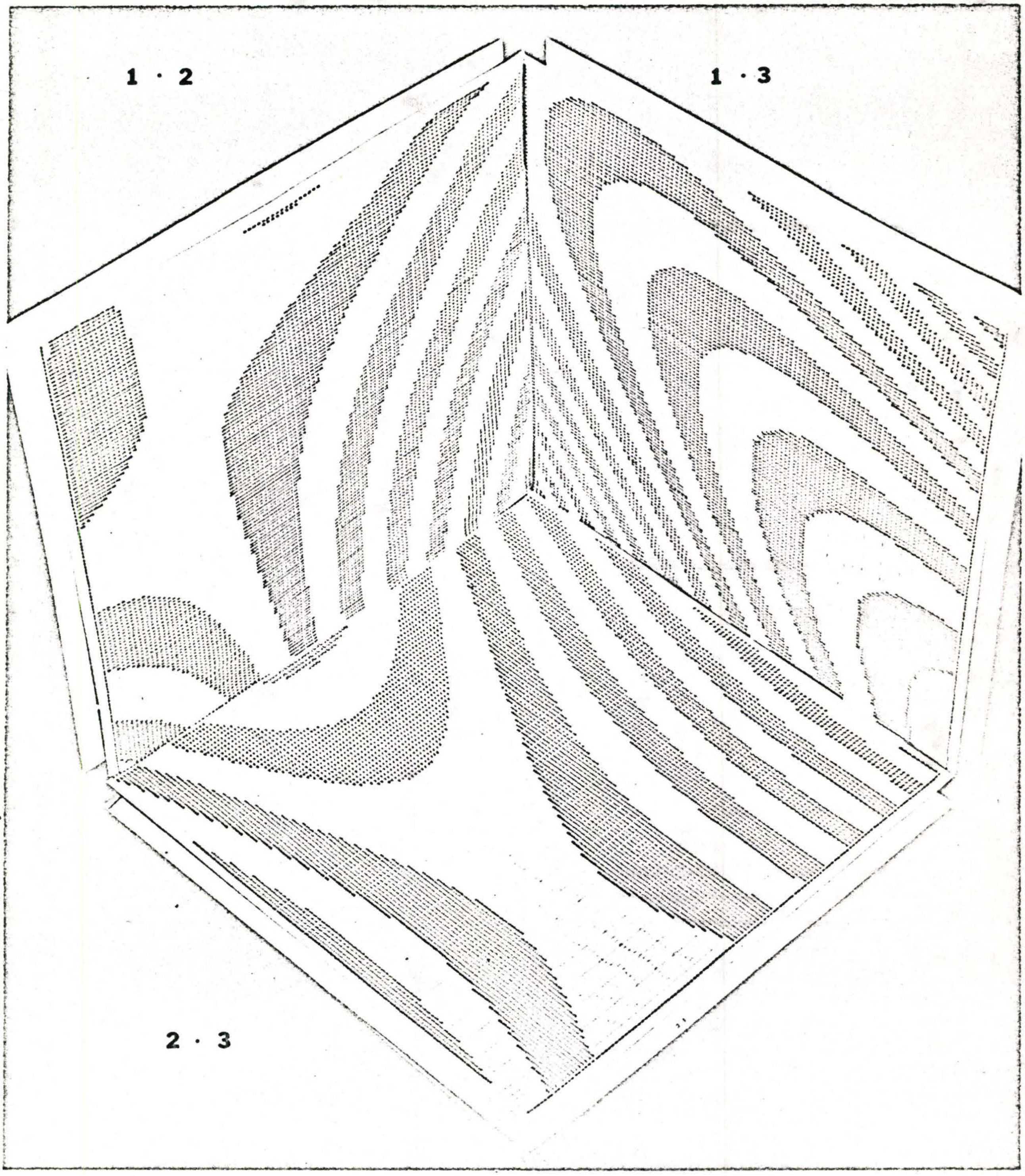


Figure 39. Combined trend surface for Cladonia alpestris.

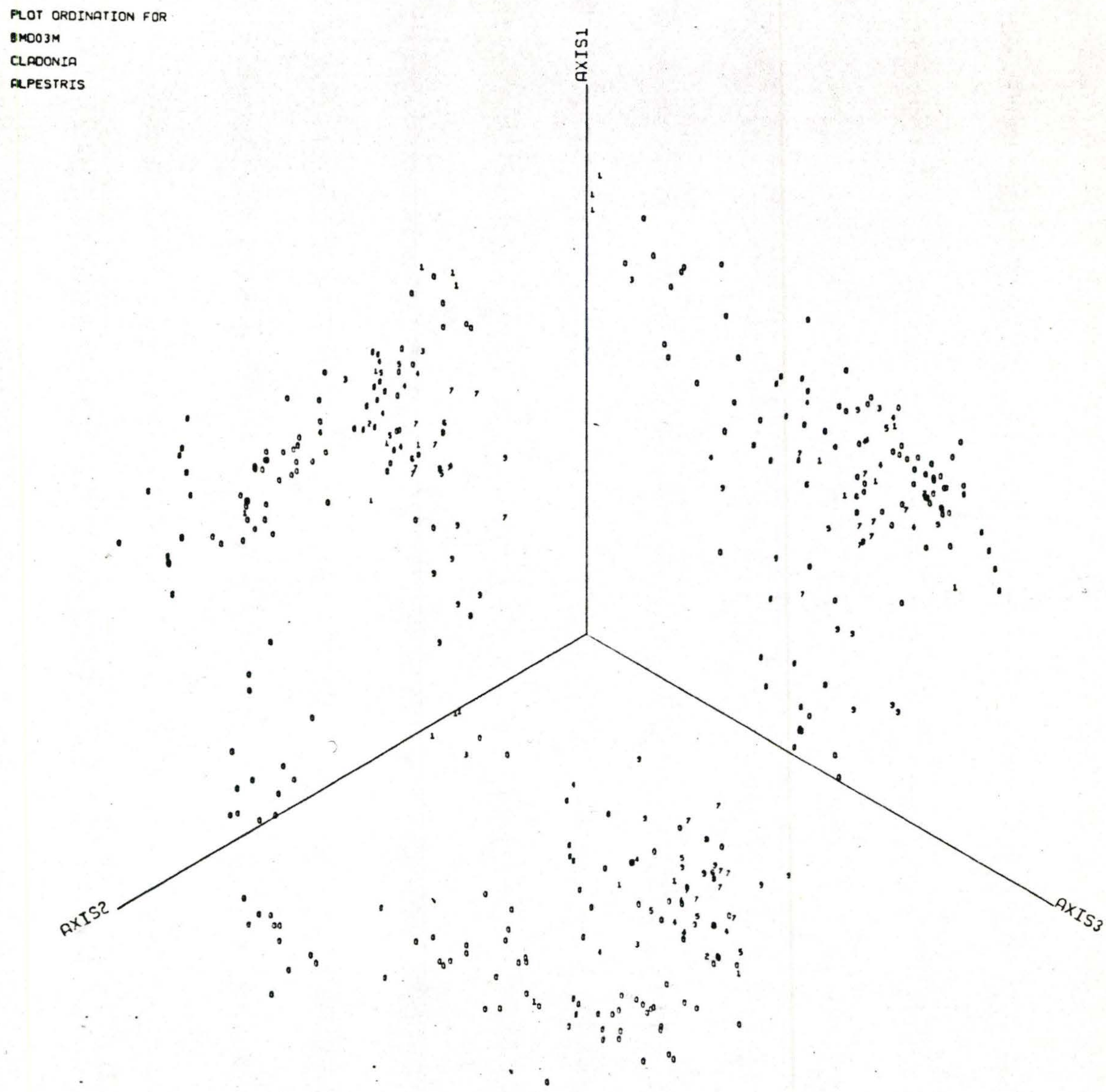


Figure 40. Overlay diagram for Cladonia alpestris based on ORDIN1.

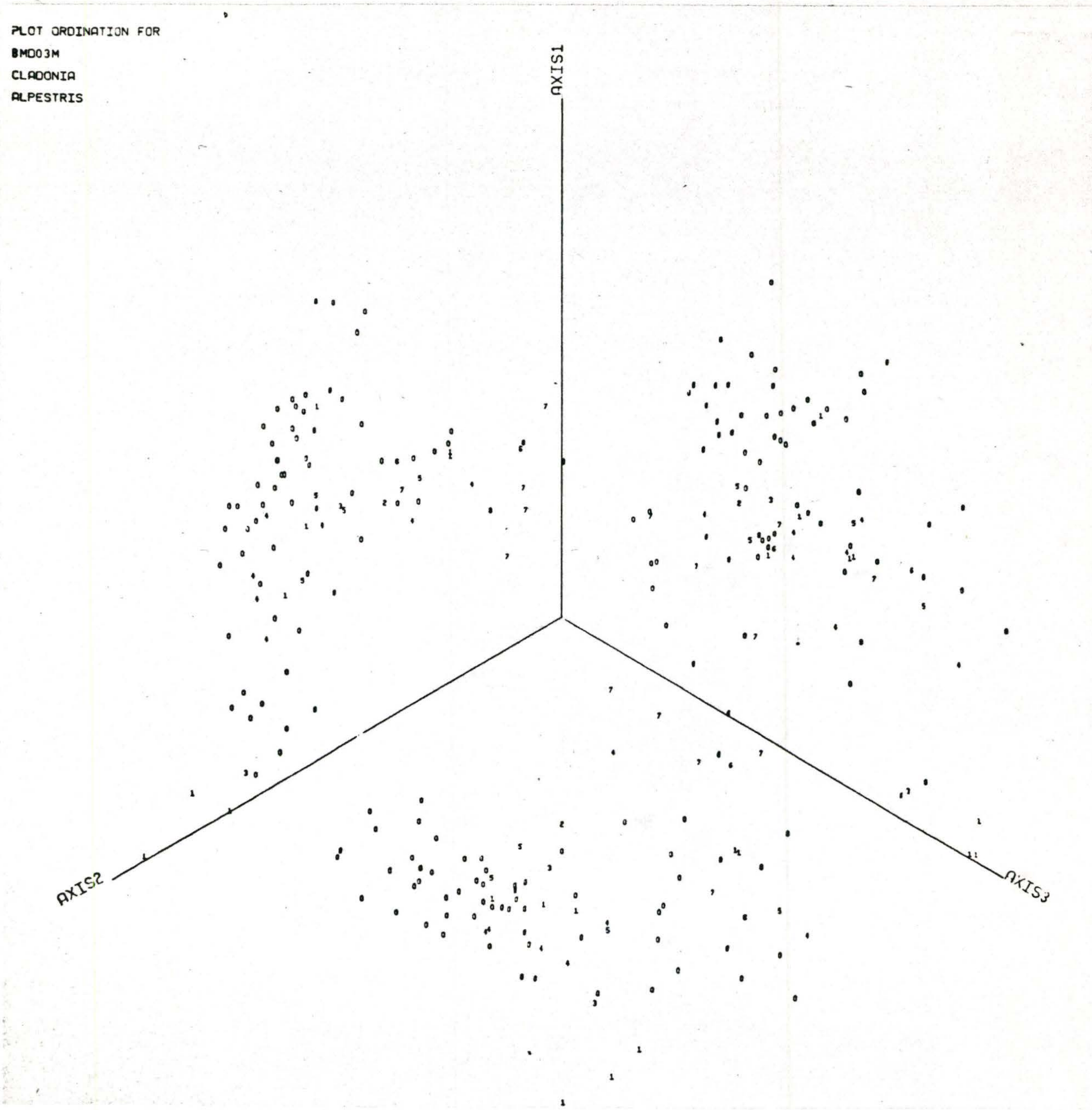


Figure 41. Overlay diagram for Cladonia alpestris based on ORDIN2.

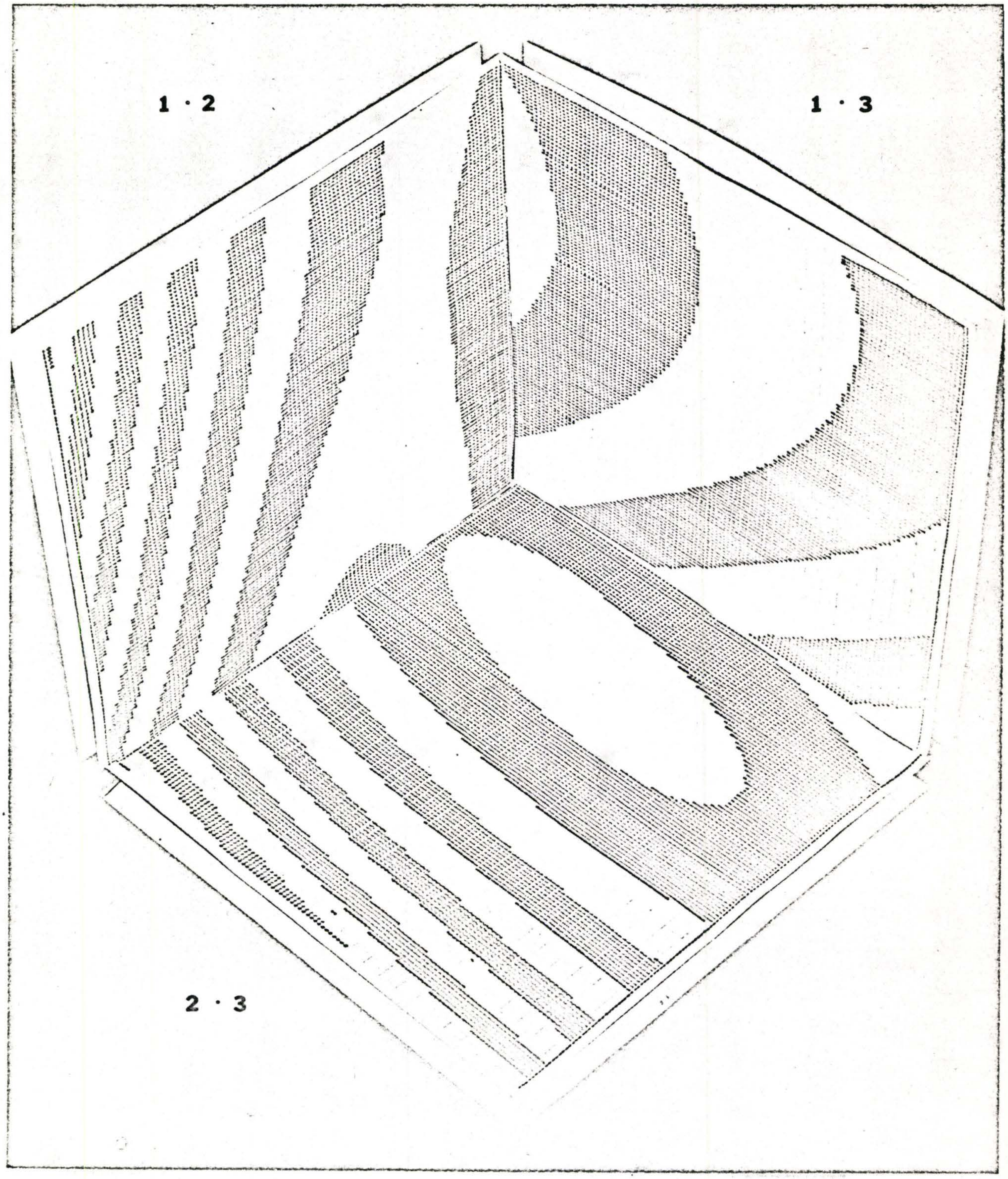


Figure 42. Combined trend surface for Hedysarum Mackenzii.

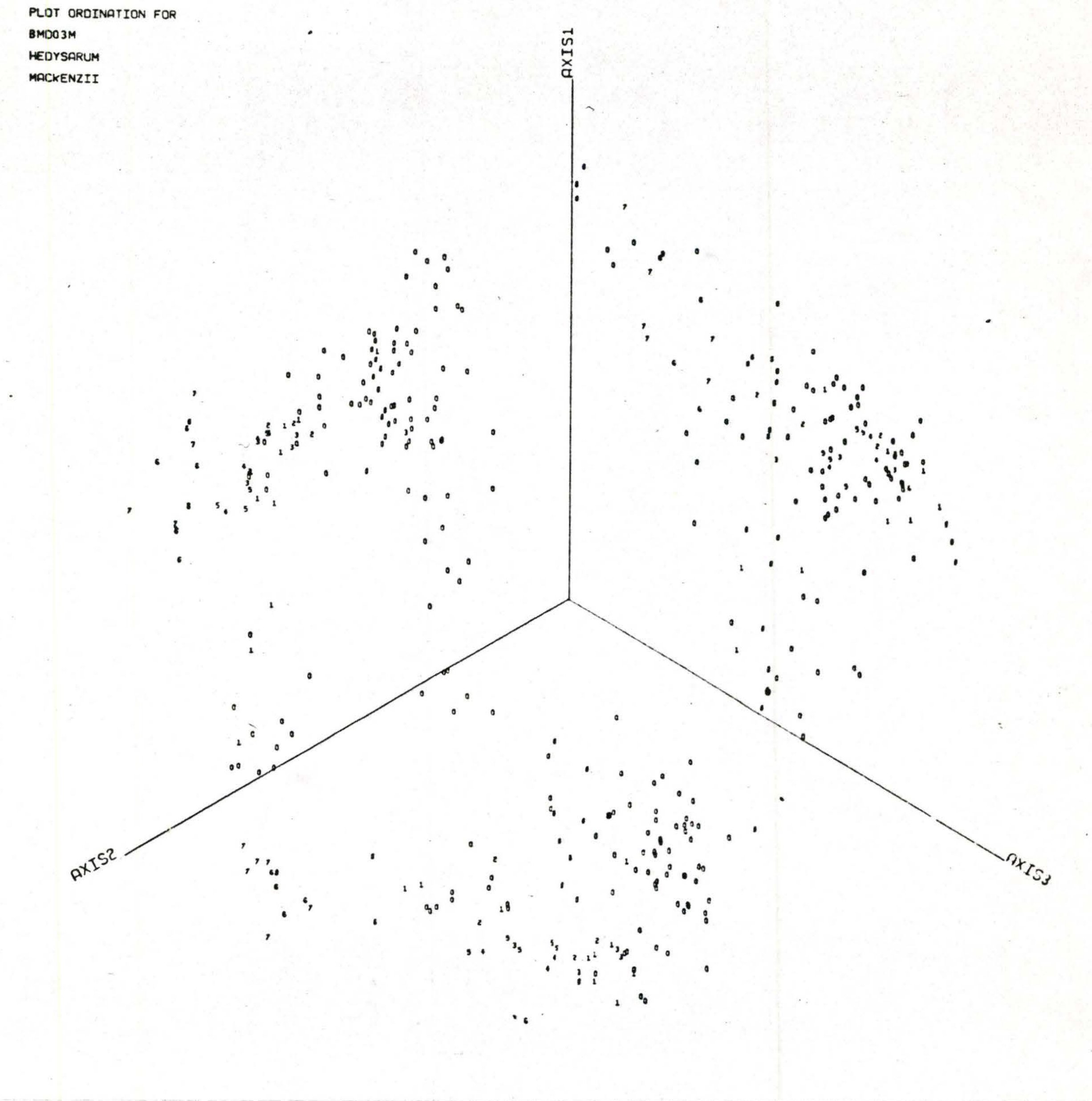


Figure 43. Overlay diagram for Hedysarum Mackenzii based on ORDIN1.

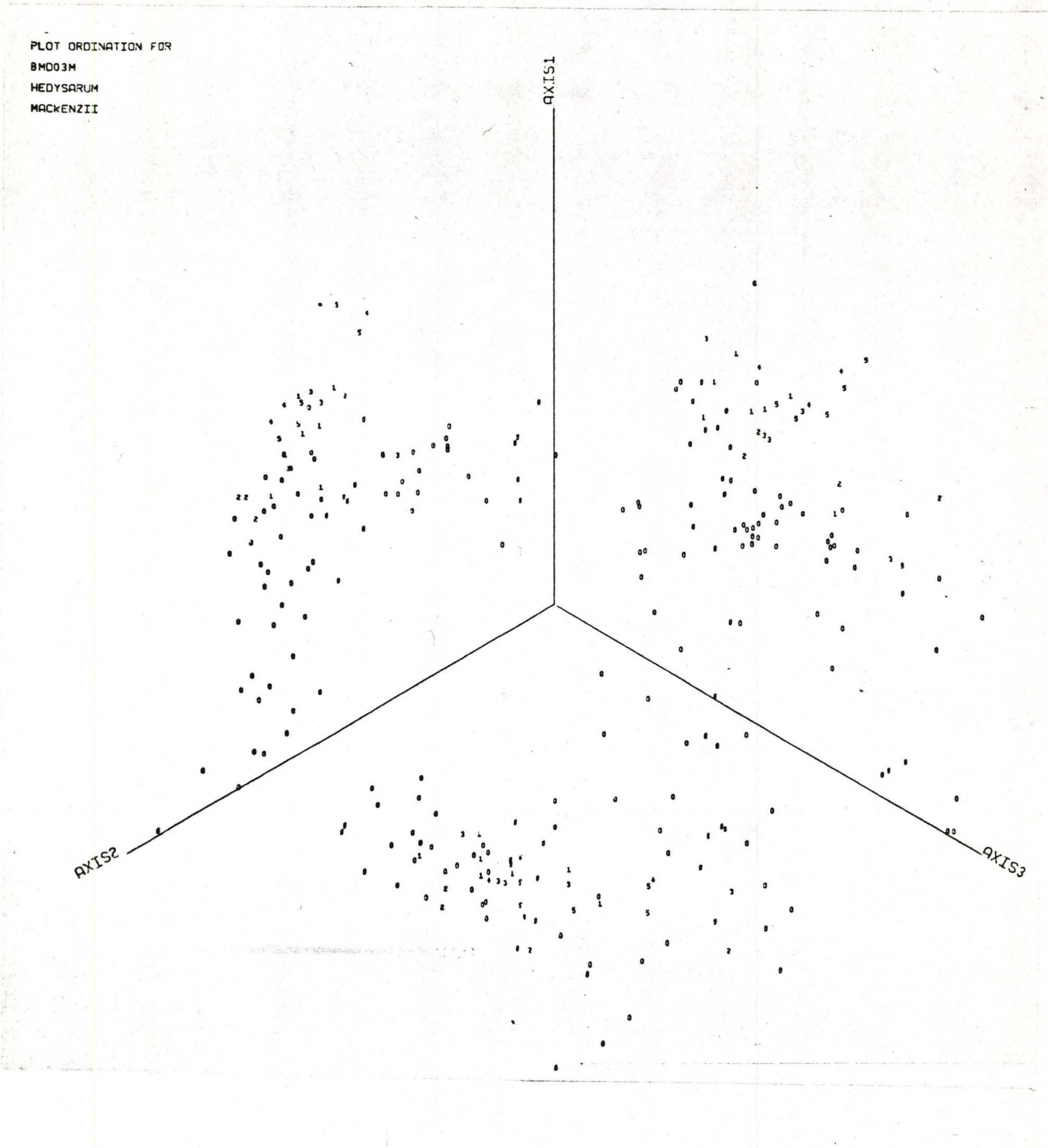


Figure 44. Overlay diagram for Hedysarum Mackenzii based on ORDIN2.

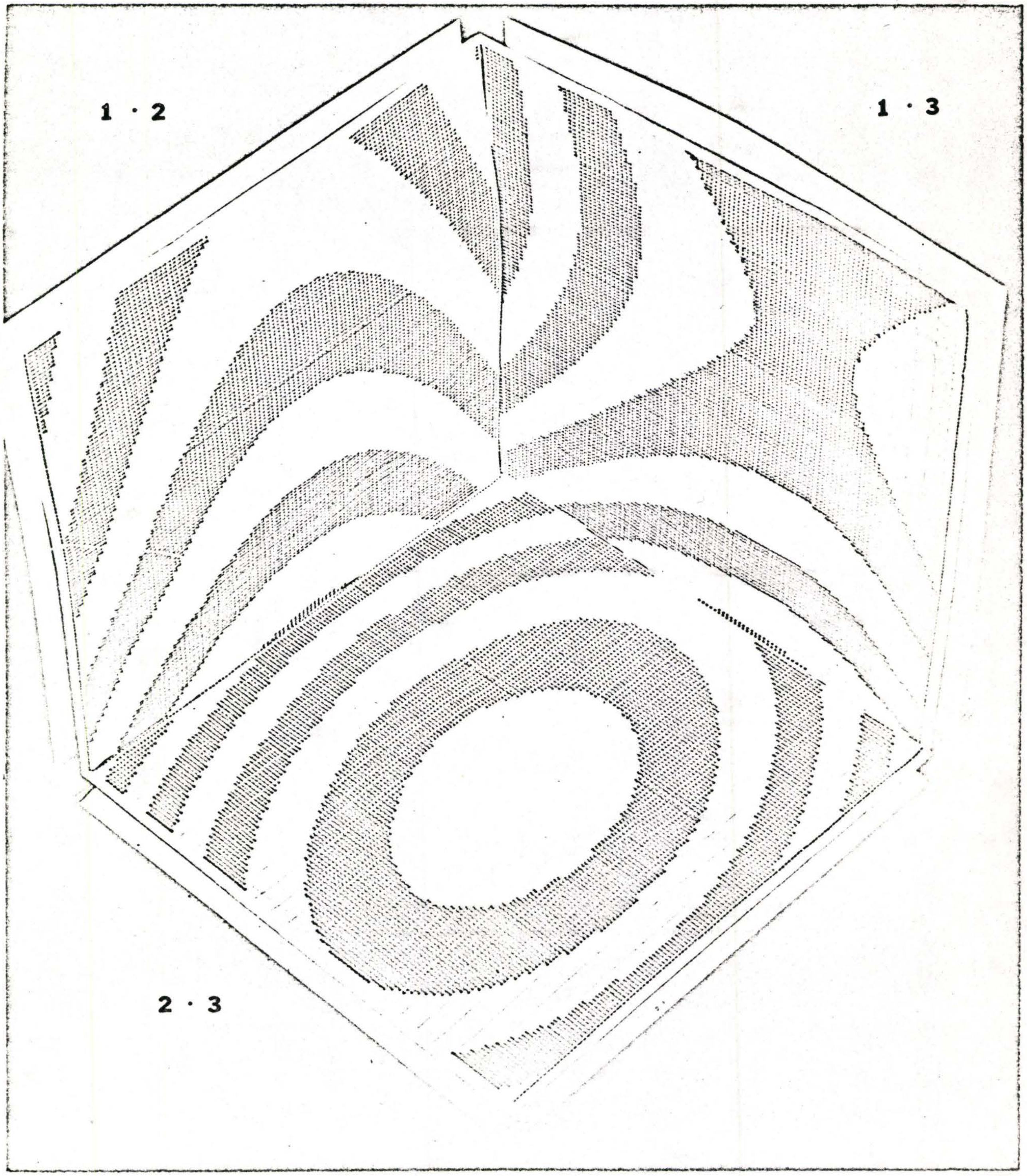


Figure 45. Combined trend surface for Vaccinium uliginosum.

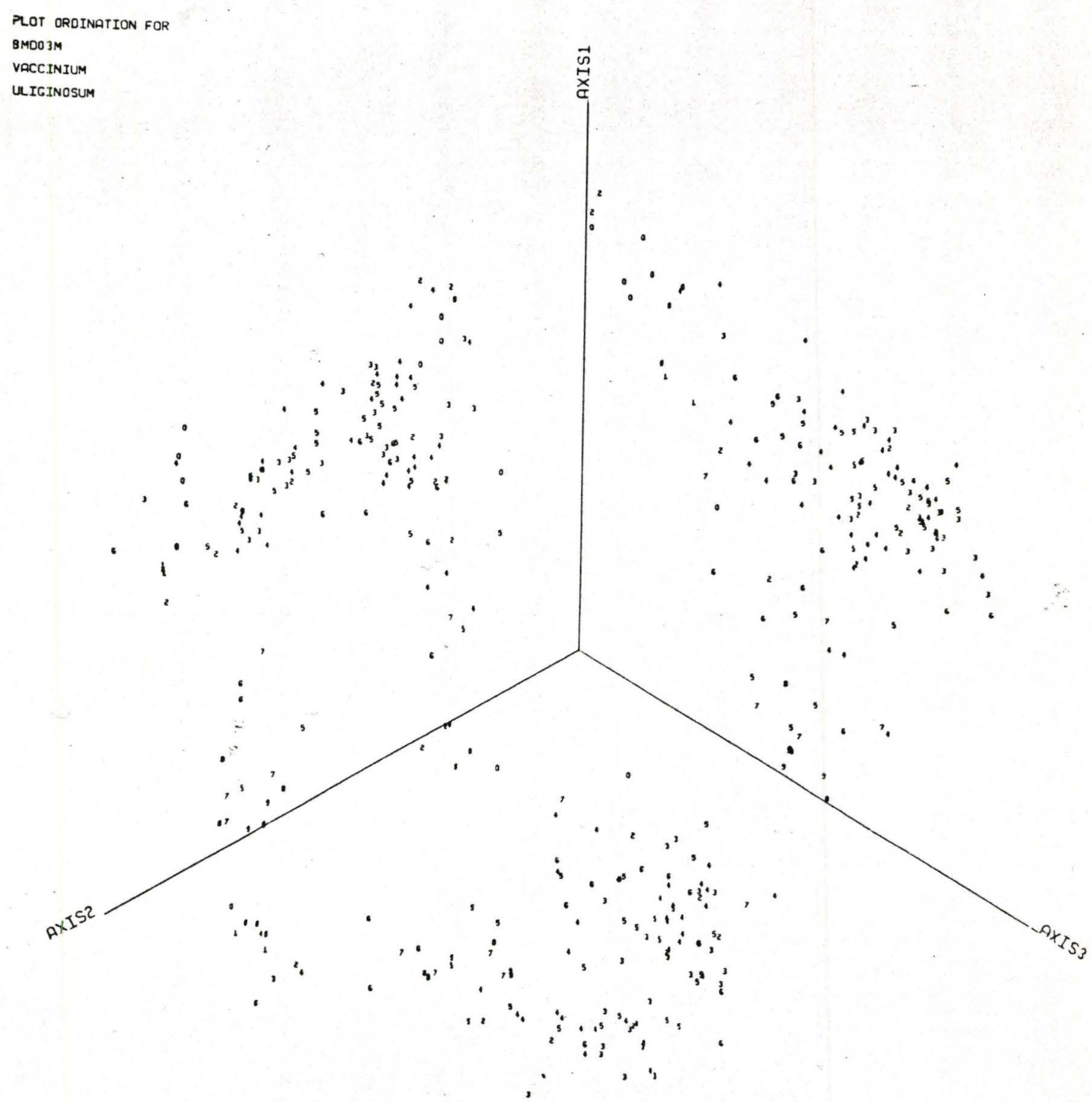


Figure 46. Overlay diagram for Vaccinium uliginosum based on ORDIN1.

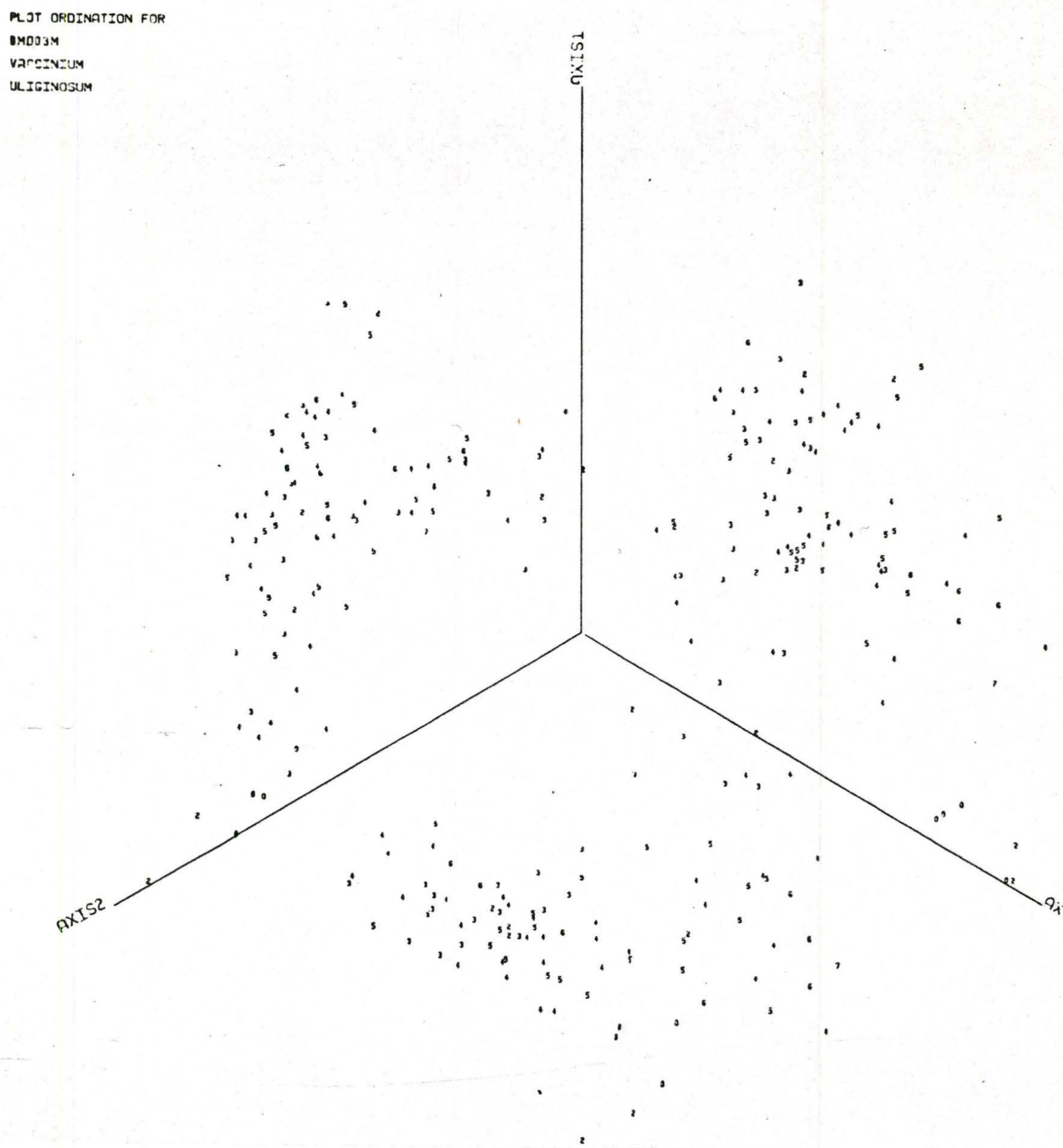


Figure 47. Overlay diagram for Vaccinium uliginosum based on ORDIN2.

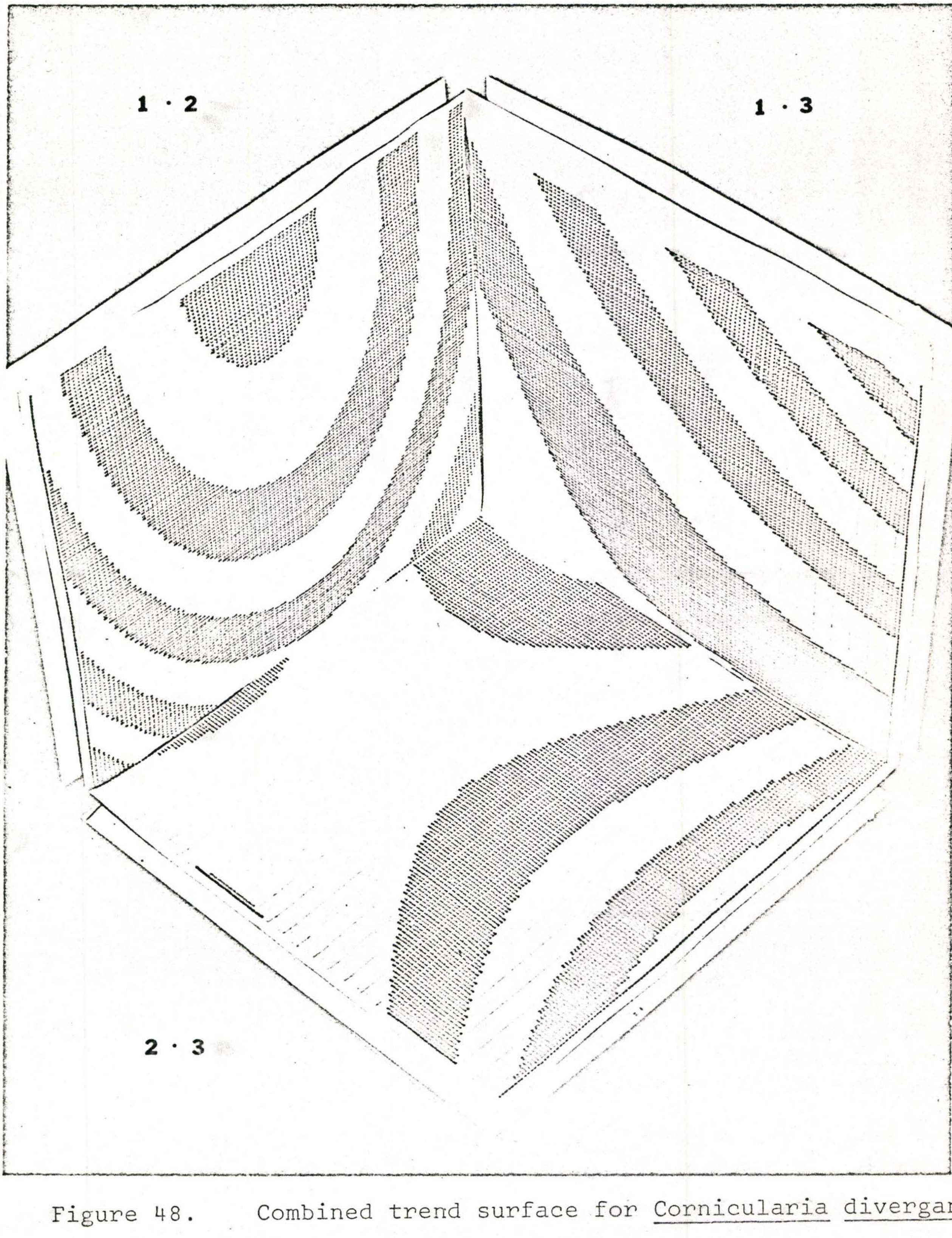


Figure 48. Combined trend surface for *Cornicularia divergans*

Unfortunately the amount of computer time and space required to run the trend surface analysis program made its use on the rest of the overlay results impossible at this time. Hence for the remaining dependent variables (see Fig.49 to 58) the correlations with the various axes had to be determined subjectively from the overlay diagrams. These and the previous results are summarized in Table 18. It must be emphasized however, that less confidence can be put on these results.

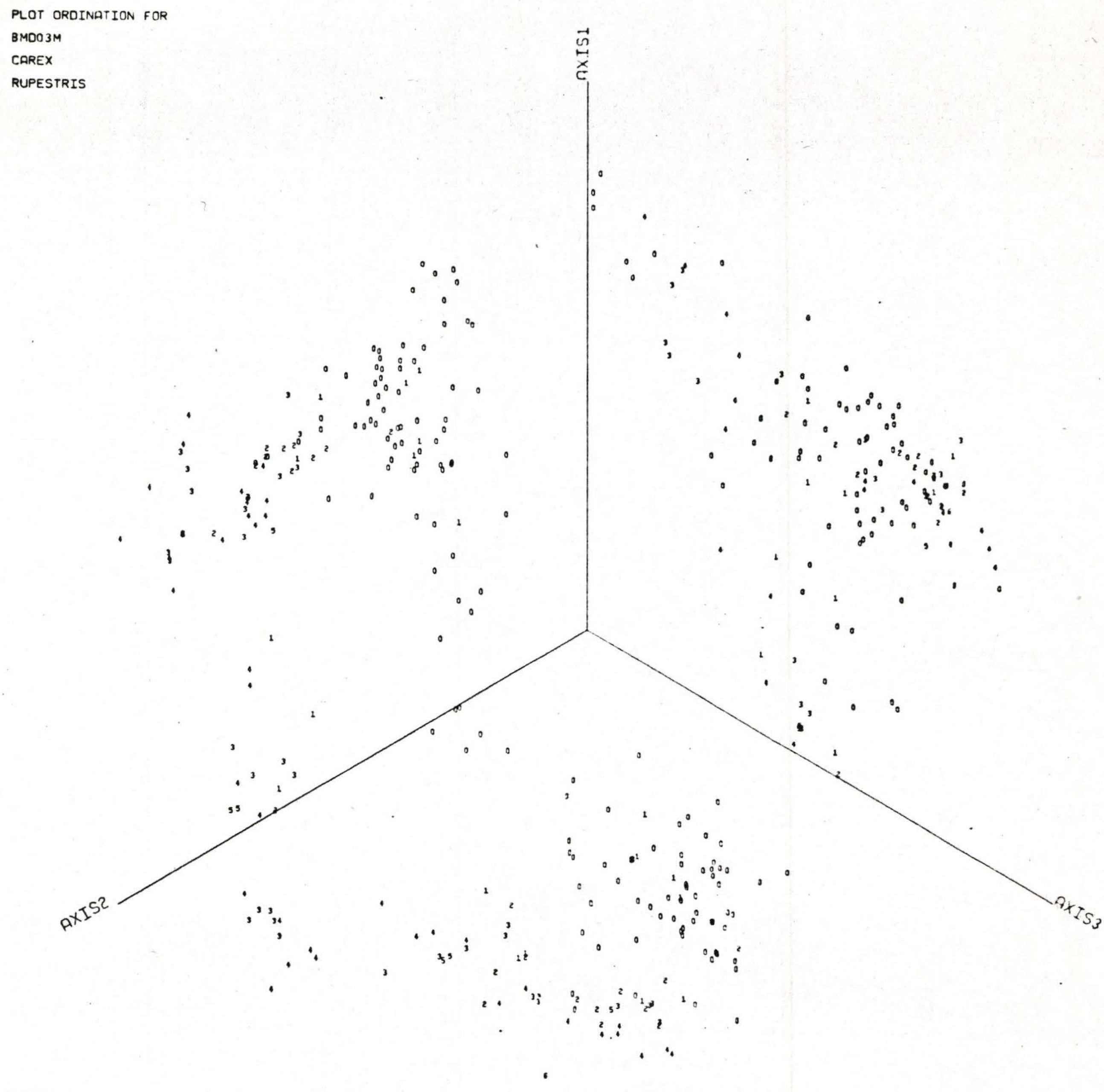


Figure 49. Overlay diagram for Carex rupestris based on ORDIN1.

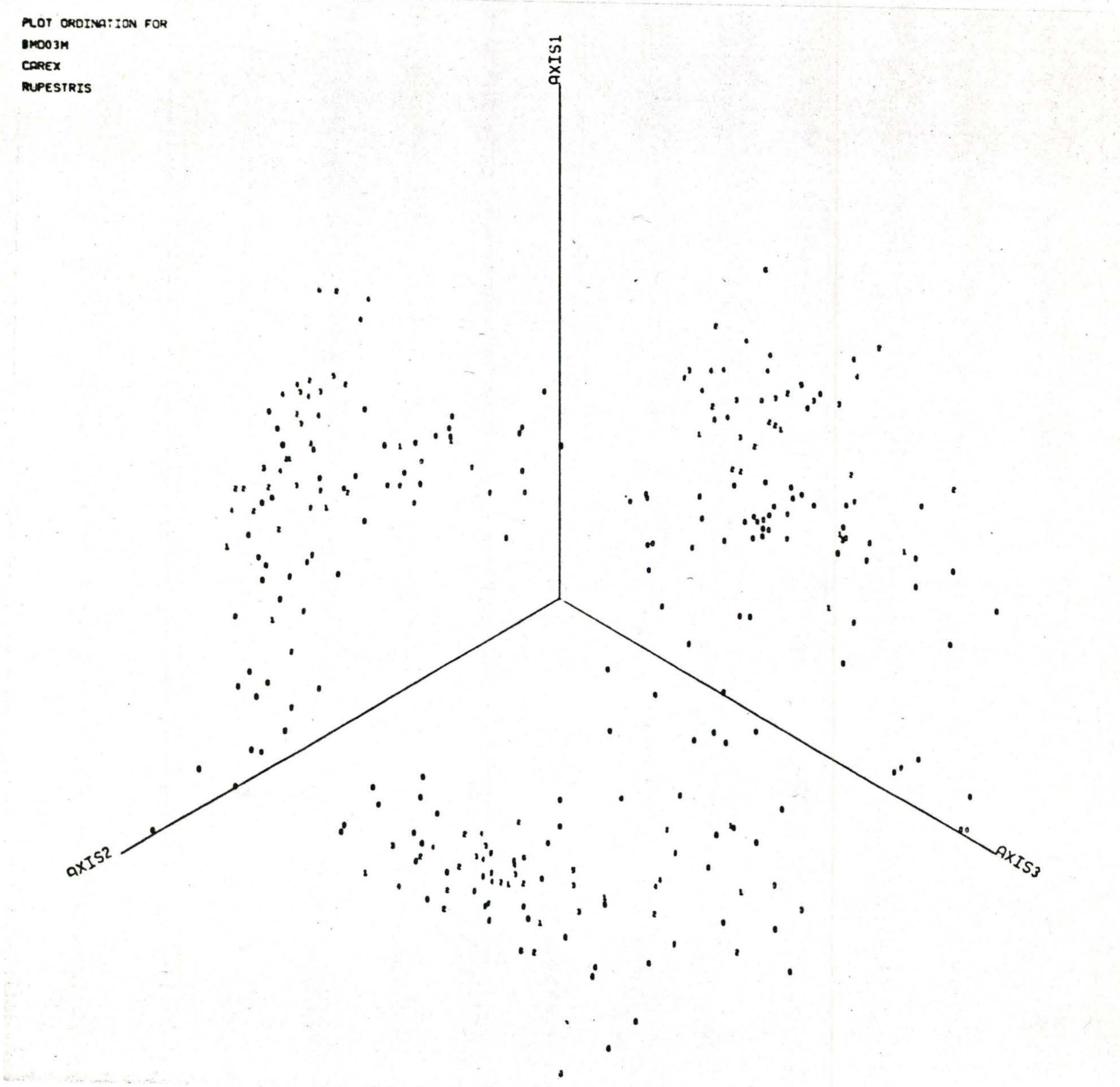


Figure 50. Overlay diagram for Carex rupestris based on ORDIN2.

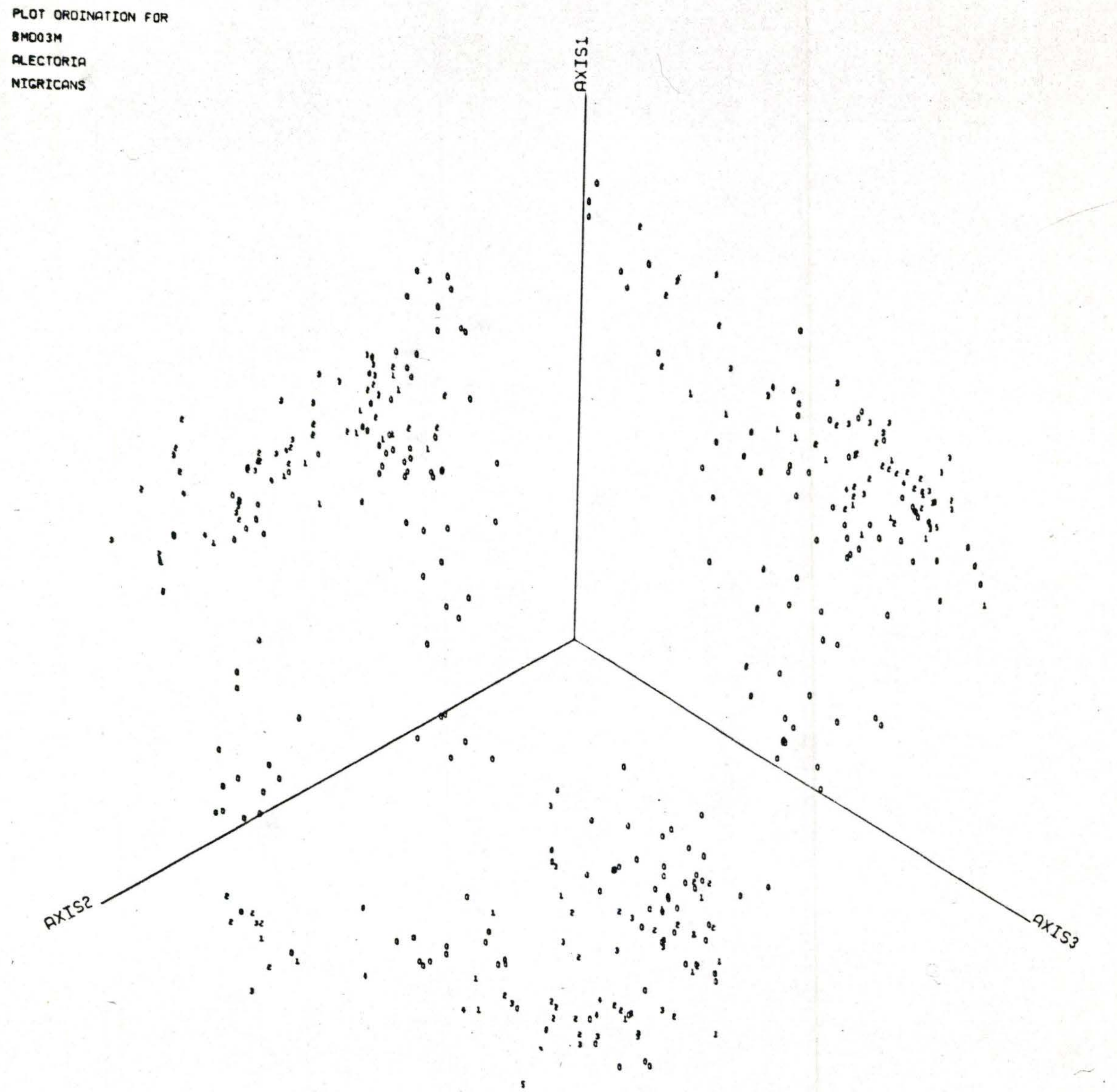


Figure 51. Overlay diagram for Alectoria nigricans based on ORDIN1.

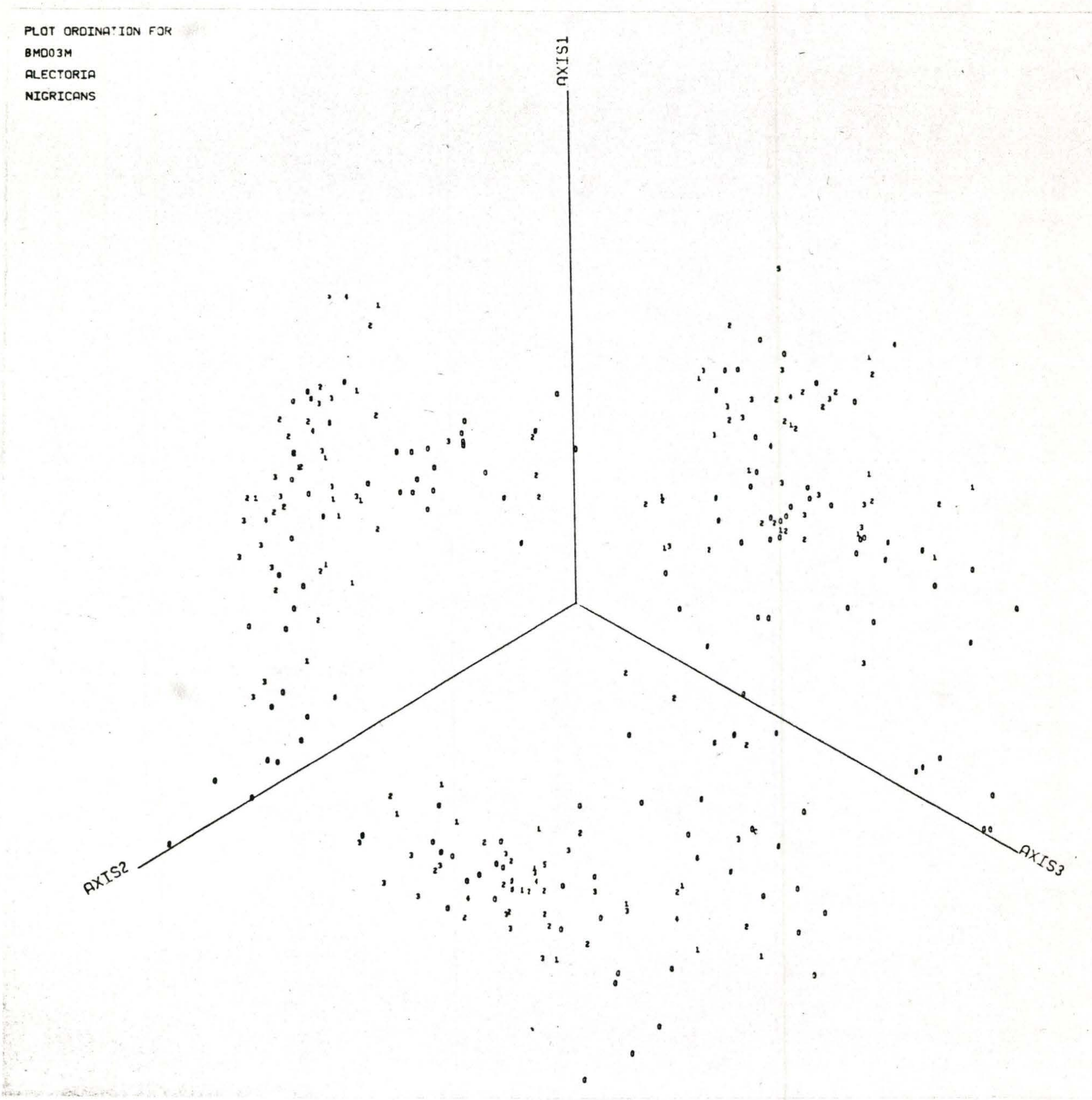


Figure 52. Overlay diagram for Alectoria nigricans based on ORDIN2.

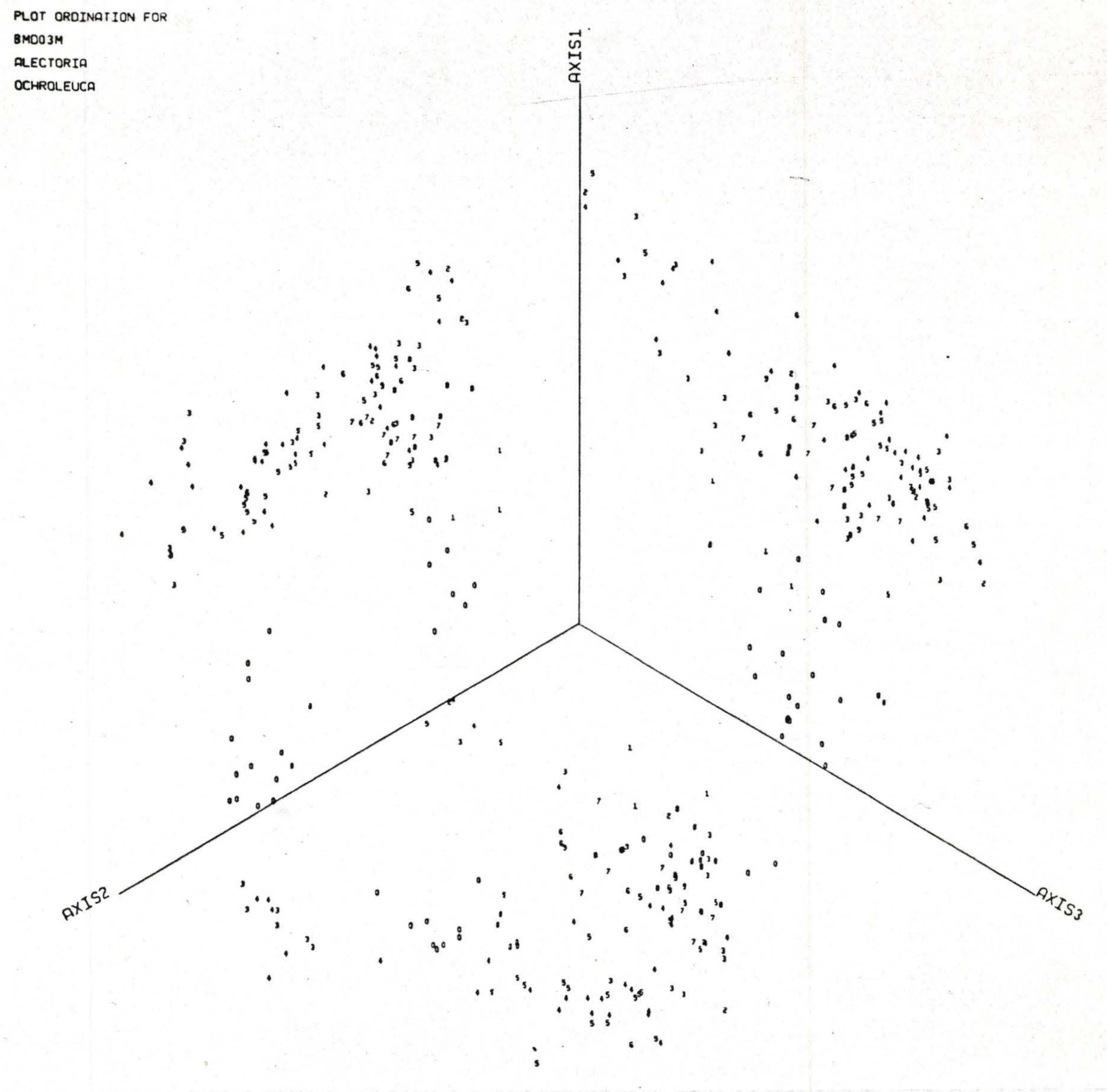


Figure 53. Overlay diagram for <u>Alectoria</u> <u>ochroleuca</u> based on ORDIN1.

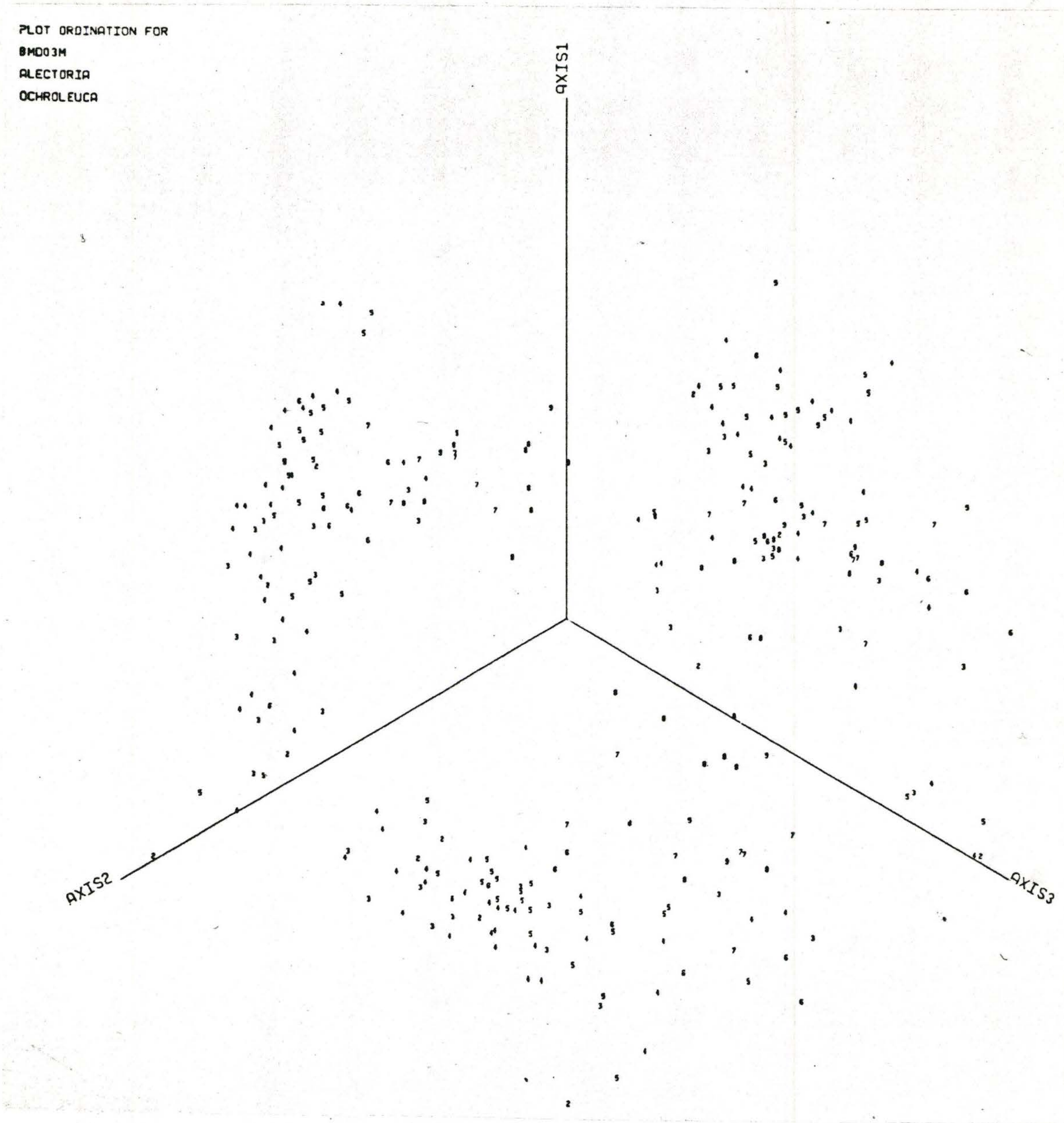


Figure 54. Overlay diagram for Alectoria ochroleuca based on ORDIN2.

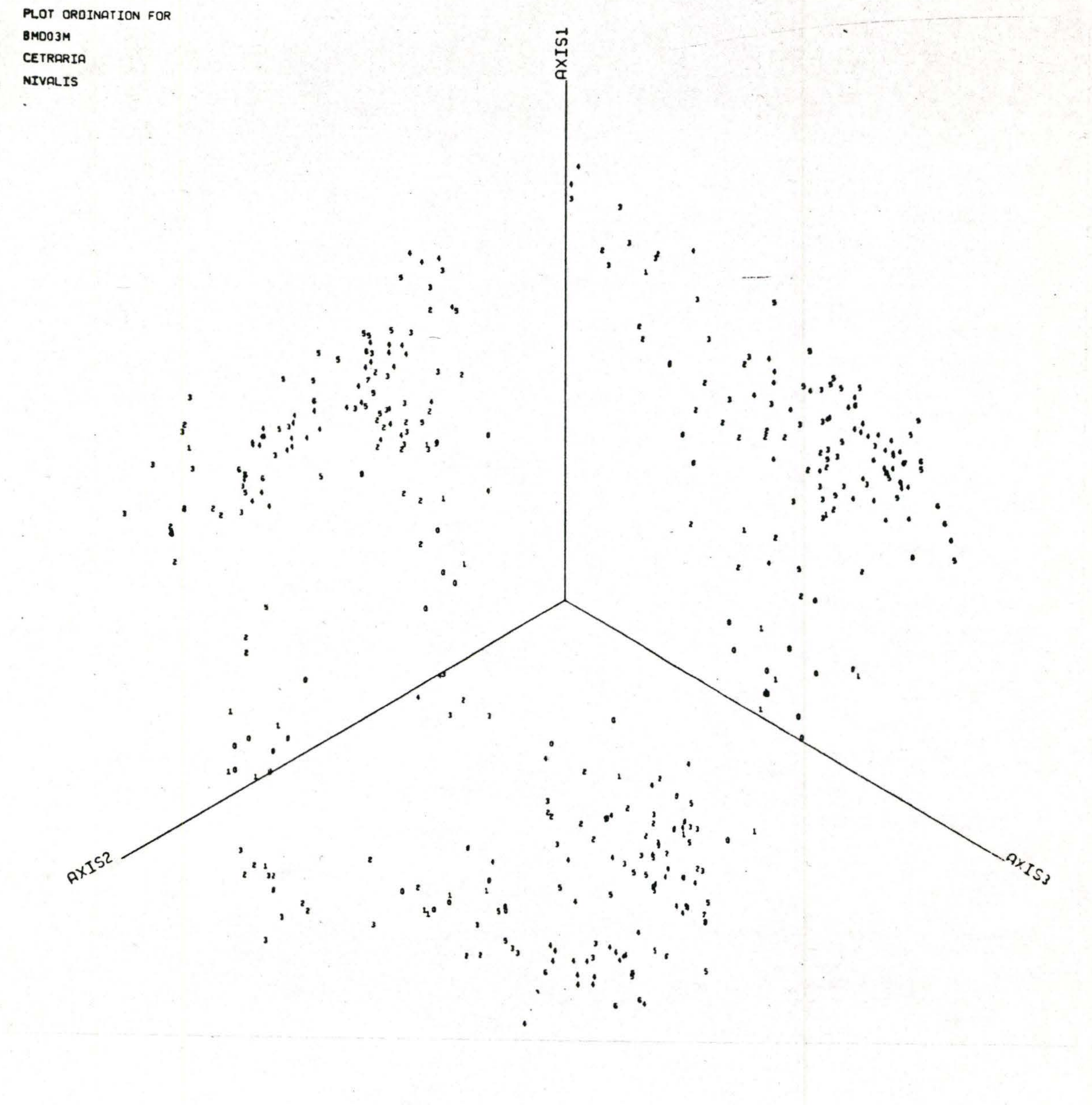


Figure 55. Overlay diagram for Cetraria nivalis based on ORDIN1.

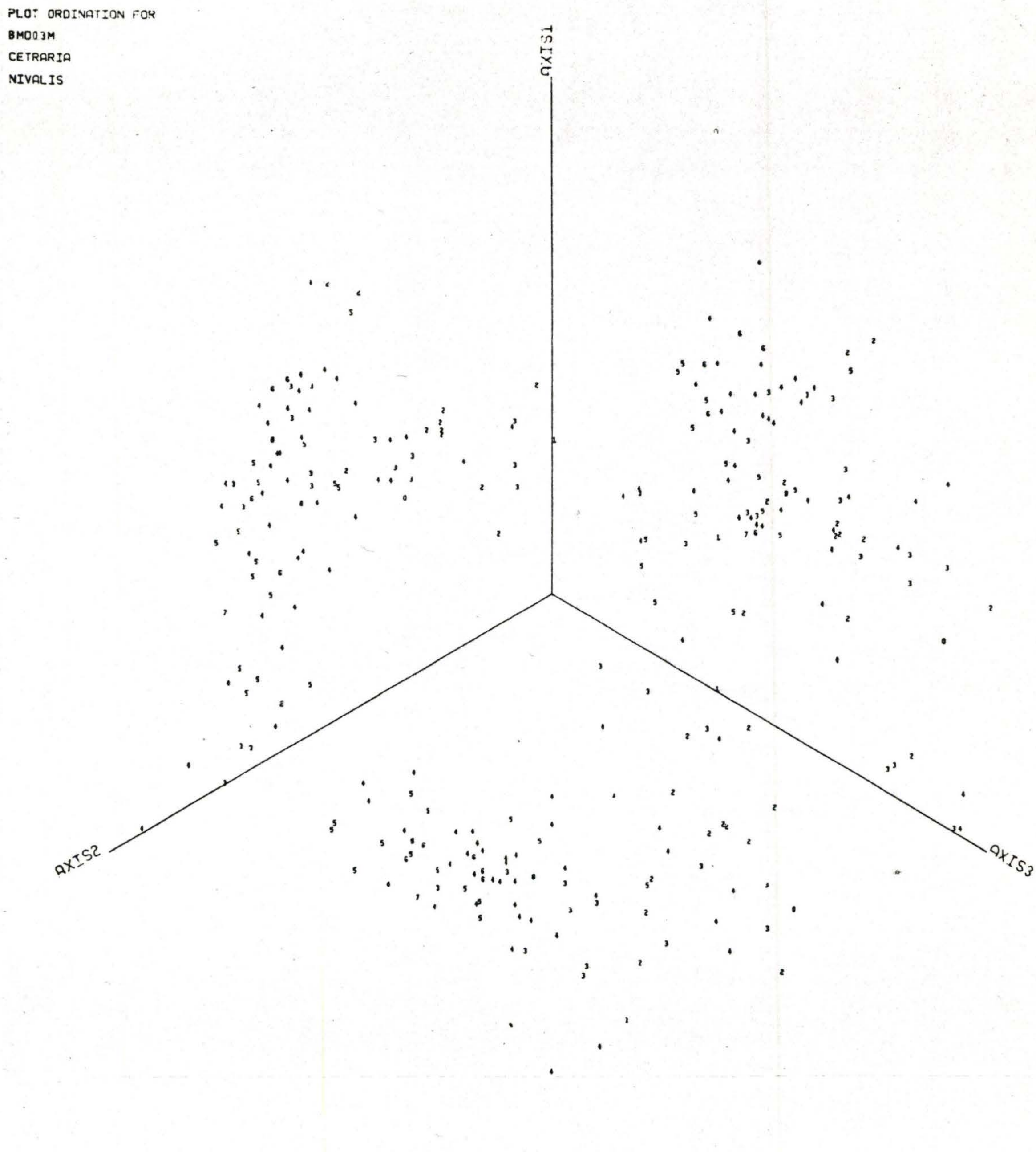


Figure 56. Overlay diagram for Cetraria nivalis based on ORDIN2.

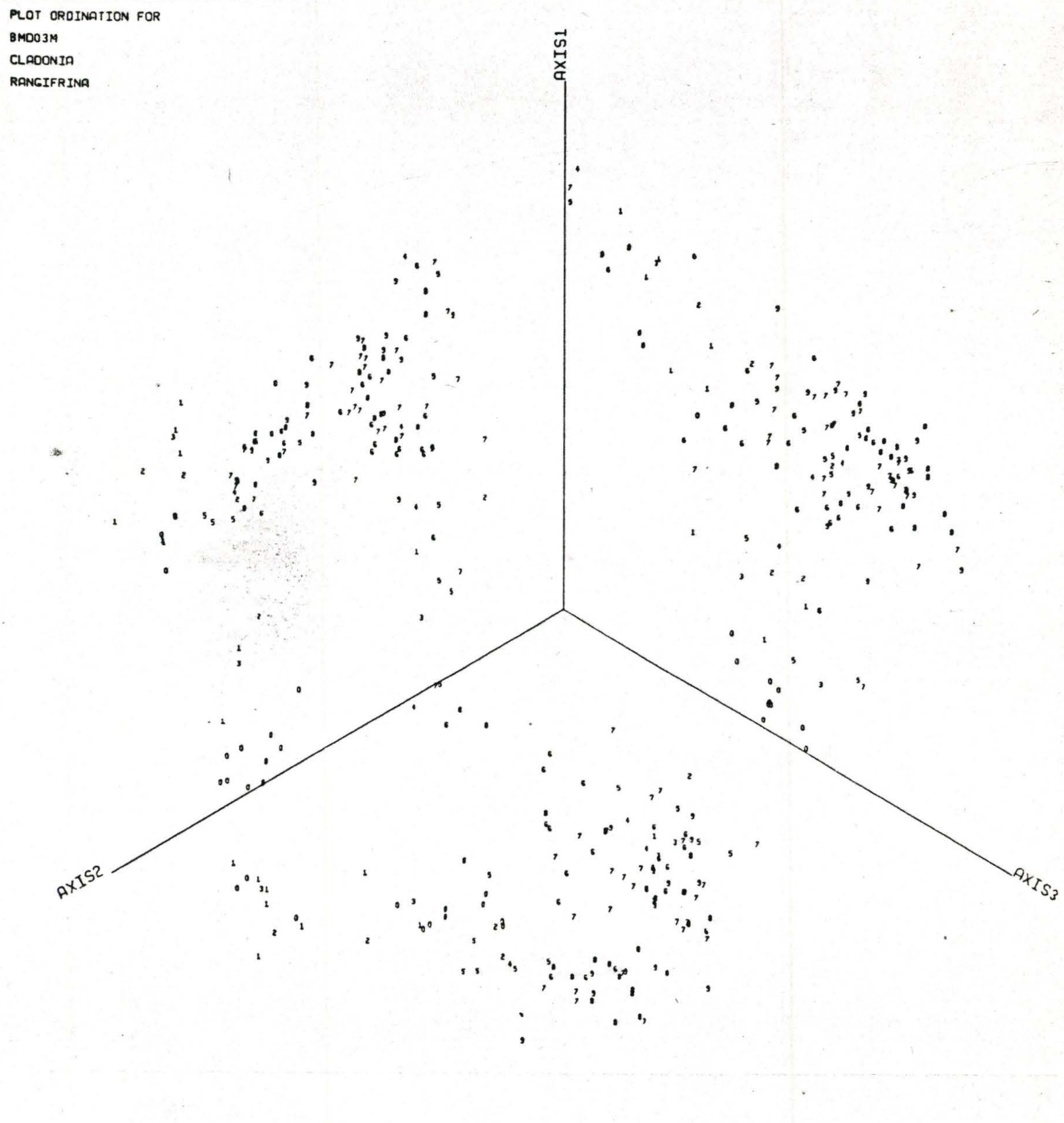


Figure 57. Overlay diagram for Cladonia rangiferina based on ORDIN1.

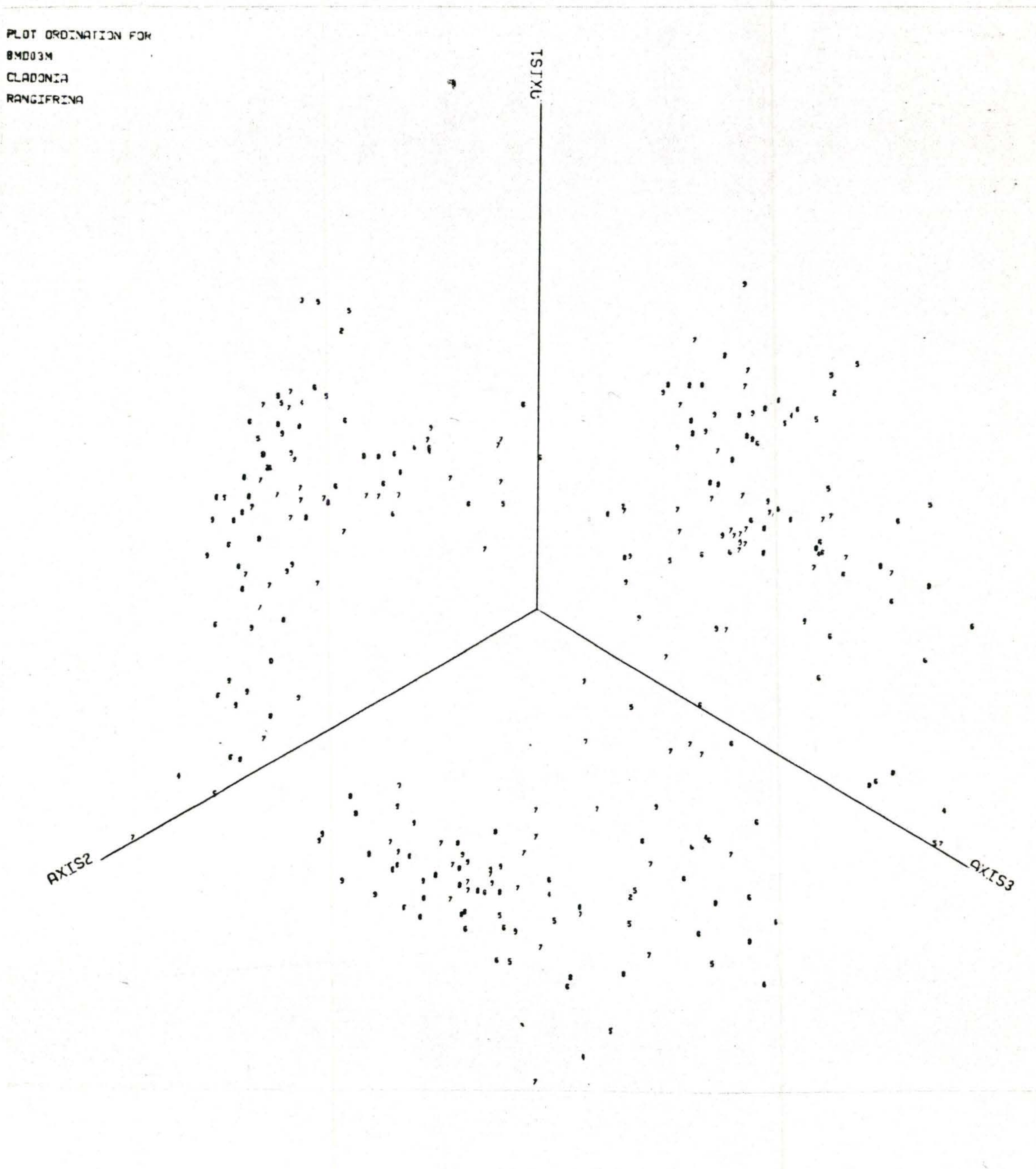


Figure 58. Overlay diagram for <u>Cladonia</u> <u>rangiferina</u> based on ORDIN2.

Table 18

Summary of Ordination Trend Results

Ordination	Dependent Variable	Correlated Axis	Trend Direction
Long	pH	2	Extreme
	Soil Moisture	1, 2	Origin
	Dryas integrifolia	2	Extreme
	Empetrum nigrum	2	Origin
	Cladonia alpestris	3	Extreme
	Hedysarum Mackenzii	2	Extreme
	Vaccinium uliginesum	1	Origin
	Cornicularia divergans	1, 3	Extreme
	The remainder of these correlations are determined subjectively.		
	Cladonia rangiferina	2	Origin
	Cetraria nivalis	1	Extreme
	Alectoria ochroleuca	1	Extreme
	Alectoria nigricans	1	Extreme
	Carex rupestris	2	Extreme
Short	pH	1	Extreme
	Soil Moisture	1	Origin
	Dryas integrifolia	1	Extreme
	Empetrum nigrum	2	Extreme
	Cladonia alpestris	2	Origin
	Hedysarum Mackenzii	1	Extreme
	Vaccinium uliginesum	1	Extreme
	Cladonia rangiferina	2	Extreme
	Cetraria nivalis	2	Extreme
	Alectoria ochroleuca	2	Origin
	Alectoria nigricans	3	Origin
	Carex rupestris	1	Extreme

Table 17

TREND SURFACE ANALYSIS STATISTICS FOR ORDIN1

Fig. Ref.	Identification	Order	Total Variance	Variance Extracted	% Variance Extracted	Mean	Standard Deviation	F-Ratio	Degrees of Freedom
9, 27	pH /1-2	1	15234.7	7229.9	47.5	63.38	7.84	37.93	3 & 126
10	pH/1-2 Res.	2	8004.7	992.1	12.4	0.00	7.34	2.90	6 & 123
-	pH /1-3	1	15234.7	956.3	6.3	63.38	10.48	2.81	3 & 126
-	pH/1-3 Res.	2	14278.3	438.1	3.1	0.00	10.31	0.64	6 & 123
-	pH /2-3	1	15234.7	6989.2	45.9	63.38	7.96	35.6	3 & 126
-	pH/2-3 Res.	2	8245.5	336.1	4.1	0.00	7.80	0.87	6 & 123
11	pH /1-2	2	15234.7	8222.1	54.0	63.38	7.34	24.03	6 & 123
12	pH/1-2 Res.	3	7012.5	400.5	5.7	0.00	7.13	0.72	10 & 119
-	pH /1-3	2	15234.7	1394.4	9.2	63.38	10.31	2.06	6 & 123
-	pH/1-3 Res.	3	13840.2	1886.0	13.6	0.00	9.58	1.87	10 & 119
-	pH /2-3	2	15234.7	7325.3	48.3	63.38	7.80	18.98	6 & 123
-	pH/2-3 Res.	3	7909.3	444.7	5.6	0.00	7.57	0.70	10 & 119
13	pH /1-2	3	15234.7	8622.7	56.6	63.38	7.13	15.51	10 & 119
14	pH/1-2 Res.	4	6612.0	133.4	2.0	0.00	7.05	0.15	15 & 114
-	pH /1-3	3	15234.7	3280.5	21.5	63.38	9.58	3.26	10 & 119
-	pH/1-3 Res.	4	11954.2	2525.0	21.1	0.00	8.51	2.03	15 & 114

Fig. Ref.	Identification	Order	Total Variance	Variance Extracted	% Variance Extracted	Mean	Standard Deviation	F-Ratio	Degrees of Freedom
-	pH / 2-3	3	15234.7	7770.0	51.1	63.38	7.57	12.38	10 & 119
-	pH / 2-3 Res.	4	7464.6	778.7	10.4	0.00	7.17	0.88	15 & 114
33	D. integrifolia / 1-2	2	857.5	633.7	73.9	3.41	1.31	58.03	6 & 123
	D. integrifolia / 1-2 Res.	3	223.8	17.7	7.9	0.00	1.25	1.02	10 & 119
	D. integrifolia / 1-3	2	857.5	55.8	6.5	3.41	2.48	1.42	6 & 123
	D. integrifolia / 1-3 Res.	3	801.7	192.3	24.0	0.00	2.16	3.75	10 & 119
	D. integrifolia / 2-3	2	857.5	629.6	73.4	3.41	1.32	56.64	6 & 123
	D. integrifolia / 2-3 Res.	3	227.8	21.1	9.3	0.00	1.26	1.21	10 & 119
36	E. nigrum/1-2	2	852.6	468.9	55.0	3.25	1.71	25.05	6 & 123
	E. nigrum/1-2 Res.	3	383.7	12.1	3.2	0.00	1.69	0.39	10 & 119
	E. nigrum/1-3	2	852.6	61.7	7.2	3.25	2.46	1.60	6 & 123
	E. nigrum.1-3 Res.	3	790.8	177.4	22.4	0.00	2.17	3.44	10 & 119
	E. nigrum/2-3	2	852.6	452.8	53.1	3.25	1.75	23.21	6 & 123
	E. nigrum/2-3 Res.	3	399.8	50.9	12.7	0.00	1.63	1.73	10 & 119
39	C. alpestris /1-2	2	1132.6	746.7	65.9	1.74	1.72	39.67	6 & 123
	C. alpestris /1-2 Res.	3	385.8	17.5	4.5	0.00	1.68	0.56	10 & 119

Fig. Ref.	Identification	Order	Total Variance	Variance Extracted	% Variance Extracted	Mean	Standard Deviation	F-Ratio	Degrees of Freedom
	C. alpestris /1-3	2	1132.6	329.0	29.0	1.74	2.48	8.39	6 & 123
	C. alpestris /1-3 Res.	3	803.6	148.2	18.4	0.00	2.24	2.69	10 & 119
	C. alpestris /2-3	2	1132.6	643.4	56.8	1.74	1.93	26.96	6 & 123
	C. alpestris /2-3 Res.	3	489.1	27.3	5.6	0.00	1.88	0.70	10 & 119
42	H. Mackenzii /1-2	2	630.8	514.3	81.5	1.20	0.94	90.50	6 & 123
	H. Mackenzii /1-2 Res.	3	116.4	4.3	3.7	0.00	0.92	0.46	10 & 119
	H. Mackenzii /1-3	2	630.8	92.0	14.6	1.20	2.03	3.50	6 & 123
	H. Mackenzii /1-3 Res.	3	538.7	68.5	12.7	0.00	1.90	1.73	10 & 119
	H. Mackenzii /2-3	2	630.8	460.5	73.0	1.20	1.14	55.43	6 & 123
	H. Mackenzii /2-3 Res.	3	170.2	36.3	21.3	0.00	1.01	3.22	10 & 119
45	V. uliginosum /1-2	2	467.2	218.7	46.8	4.07	1.38	18.04	6 & 123
	V. uliginosum /1-2 Res.	3	248.4	15.9	6.4	0.00	1.33	0.81	10 & 119
	V. uliginosum /1-3	2	467.2	251.5	53.8	4.07	1.28	23.91	6 & 123
	V. uliginosum /1-3 Res.	3	215.6	7.5	3.5	0.00	1.26	0.43	10 & 119
	V. uliginosum /2-3	2	467.2	173.5	37.1	4.07	1.50	12.11	6 & 123
	V. uliginosum /2-3 Res.	3	293.6	63.0	21.5	0.00	1.33	3.25	10 & 119

Fig.	Identification	Order	Total Variance	Variance Extracted	% Variance Extracted	Mean	Standard Deviation	F-Ratio	Degrees of Freedo
48	C. divergans / 1 - 2	2	456.1	233.8	51.3	2.55	1.30	21.56	6 & 123
	C. divergans / 1 - 2 Res.	3	222.2	20.4	9.2	0.00	1.24	1.20	10 & 119
	C. divergans / 1 - 3	2	456.1	300.4	65.9	2.55	1.09	39.55	6 & 123
	C. divergans / 1 - 3 Res.	3	155.7	6.3	4.0	0.00	1.07	0.50	10 & 119
	C. divergans / 2 - 3	2	456.1	170.0	37.3	2.55	1.48	12.18	6 & 123
	C. divergans / 2 - 3 Res.	3	286.0	46.4	16.2	0.00	1.35	2.30	10 & 119
30	Soil Moisture / 1 - 2	2	17177.5	6958.3	40.5	39.06	8.86	13.95	6 & 123
	Soil Moisture / 1 - 2 Res.	3	10219.1	541.0	5.3	0.00	8.62	0.66	10 & 119
	Soil Moisture / 1 - 3	2	17177.5	3371.8	19.6	39.06	10.30	5.00	6 & 123
	Soil Moisture / 1 - 3 Res.	3	13805.6	1251.8	9.1	0.00	9.82	1.18	10 & 119
	Soil Moisture / 2 - 3	2	17177.5	3771.3	22.0	39.06	10.15	5.76	6 & 123

Section V.

DISCUSSION AND CONCLUSIONS

The following statement was made by Ahti (1961) concerning the low arctic, lichen tundra near Cape Henrietta Maria, on the south coast of Hudson Bay: "In the ground layer Alectoria ochroleuca, Cetraria nivalis, and Cetraria islandica are dominant. Only 10 percent is covered by reindeer lichens (Cladonia mitis and Cladonia rangiferina)." This study has indicated that most of the area is in fact dominated by reindeer lichens, namely, Cladonia rangiferina. In five out of the nine final associations arrived at Cladonia rangiferina is the leading dominant. This domination by the Cladinas could have important connotations with regards to the management of Caribou herds in the Canadian sub-arctic.

The use of the Braun-Blanquet type of analysis, although somewhat clarified by Poore (1955,56) and by Moore (1962), still represents a rather confused area of ecology. This is due mostly to its subjective approach and the nebulus definition of its terminology. The Braun-Blanquet approach is meant to be applied to 'homogeneous' areas of vegetation, which once having been chosen, supposedly predetermine the association. This circular argument has been discussed in Poore (1955-56) where it is defended on the basis of the time saved in using this method of vegetation analysis. In a paper by Moore et al (1970) it is pointed out that in a comparison of strictly random sampling methods with the Braun-Blanquet technique that "the pattern which emerged on the salt marsh differed in no appreciable way from the result of previous work in the same area using traditional (Braun-Blanquet) methods." Moreover, random sampling tended to lead to the omission of obvious vegetation types and samples containing conspicuous or common species.

Moore has even gone so far as to compare the formation of the association tables with a "polythetic subdivisive classification of rélevés followed by their linear ordination." That this may be true probably depends a great deal on the author of the tables and it is felt that this criticism is sufficient to recommend the use of more objective multivariate techniques. The use of semi-random sampling methods combined with both subjective and objective techniques of analysis in this project was considered to have eliminated most of the criticisms inherent in vegetation surveys of this nature and to provide a solid basis for a preliminary study. This was emphasized in the decision on the basis of the ordination results to regroup the three upper slope associations as indicated in the final block diagram on page 93.

The section of the project concerned with generating hypotheses concerning the factors controlling the distribution of the plant communities appears to owe much of its success to the use of the trend surface analysis method for determining the major direction of large scale variations. Although the use of this technique has been mentioned in the literature (Orlocci, 1972), no instance of this particular use of the method was encountered. Closest was a paper by Gittens (1968) in which he described the use of trend analysis on topographic variation in Goodall's Australian Mallee data.

The results as shown in Table 18 were related back to the original ordination diagrams of plot numbers (Fig.19 and 20). It was found that the component represented by axis 2 showed a fairly clear correlation with soil pH. This conclusion was supported by the trend surface on pH and by the fact that the calcicolous species such as Dryas integrifolia and Hedysarum Mackenzii show trends toward the extreme of axis 2 while Empetrum nigrum, a calcifuge shows a trend towards the origin of this axis.

Axis 3 appears to be related to the presence/absence of a peaty substratum, this conclusion supported by the fact that Cladonia alpestris, which is always found in zones with a thick underlayer of peat in this region, shows an increasing trend toward the extreme of axis 3. Ahti (1961) points out that Cladonia alpestris "may often be abundant in some highly calcarious areas if the surface soil is composed of a more acid humus or peat. Thus in the Hudson Bay lowlands in northern Ontario, where extensive highly calcareous peatlands form the dominant vegetation, C. alpestris is one of the most abundant plant species (except on the coastal strip). This is because Sphagnum fuscum, an ombrotrophic moss forming acid peat, is also extremely abundant building solid mats or hummocks." More recent work in the Penn Island area in Northwestern Ontario indicates that a time sequence of this type is in effect in the establishment of beach ridge vegetation but the trends are not clear.

Axis 1, however, does not allow such a clear interpretation at first glance. It shows a trend surface partially correlated with soil moisture and correlated with the abundance of Vaccinium uliginosum, which prefers wet areas. On the other hand the presence of the peat polygon area plots, which are certainly not the dryest, at the extreme end of this axis appears to refute these interpretations. It was only by examination of the short ordination, with the outliers removed, that the correlation on this axis was resolved. In this case the peat polygon plots show very high loadings towards the origin of axis 1. At the extreme of axis 1 are plots 11, 12, and 15 which are the highest topographically with the exception of the ridge area which has been removed. Supporting evidence comes from the fact that soil moisture shows a trend towards the origin of this axis, while Dryas integrifolia and Hedysarum Mackenzii show trends toward the extreme. Although this later evidence appears to point toward a correlation with soil moisture it is considered that a trend of late snow lie fits the total data better, due to the original presence of the peat polygon plots. It is quite likely, however, that these factors are related in some way as a result of the mathematics of the ordination. Since the principal component axes are uncorrelated and orthogonal, but derived from a reference space in which the attribute axes may be correlated, some factors are bound to be linked to more than one axis. The use of trend surface analysis tends to point out this non-linearity in the results. In fact, it has been shown by Krumbein and Graybill (1965) that trend surface analysis provides a method for examining in a linear framework, data that are related in non-linear ways. Had the interpretation of the data been made using the overlay diagrams only, for instance in the case of soil moisture, the tendency would be to try to relate this variable with one particular axis.

The effect of outliers appears not to have affected the ordination but this is difficult to determine without resorting to the use of simulated data. A possible solution to this problem might be to run the data through a computer routine to identify the outliers. Such a program is available (Dixon, 1970) which calculates the Mahalanobis distance of each case from the center of the distribution of the remaining cases. This analysis was in fact attempted, however the amount of time required to adapt the program to run on large data sets necessitated this project being dropped. It must suffice in this case to accept the fact that the results of the analysis fitted a reasonable ecological interpretation and are themselves acceptable.

The advantages and disadvantages of the use of subjective measures of vegetation have been discussed previously in this study (page 66) and by Bannister (1966). Mention was also made of the reasons for choosing Domin data over measures of Frequency and Cover for this project. Bannister's scaling coefficient was not applied since it was felt that the results obtained from the preliminary analysis of frequency data were not good enough to warrant biasing the Domin measures in this direction. Additionally, running all the analyses on these sections of the data would have effectively tripled the time and expense necessary to carry out the project.

The use of principal components techniques for detection of plant associations gave reasonably good results. If however, it was necessary to take the classification process to a more statistical conclusion, the use of one of the many clustering programs available presently would be strongly recommended. The subjective choice of clusters is avoided in this type of analysis. Successive removal of outlying plots and re-analysis of the remaining central cluster, as done in this study, serves only as an approximation to the clustering procedure, and although fairly effective can only be used to a limited extent.

The importance of the method of graphical output or representation involved on this type of procedure has been underemphasized in the past. As seen from the comparison of the three-dimensional and plane graphics used here, what the eye sees and what it interprets from this is largely a function of how the input is presented. The three-dimensional representation, although this involves enormous increases in computer time and cost, more clearly represents the actual cluster of points represented in a space defined by a set of new reference axes. Of course the use of trend analysis in the interpretation process goes a long way toward eliminating the need for a large number of overlay diagrams so that the use of three-dimensional graphics could provide a useful tool.

Two ordination programs were used in this analysis, their respective differences having been mentioned previously (page 69). The two programs give results which although basically similar, differ sufficiently for one to be preferred over the other. This opens up an important question: "how do the various so-called standard component analysis programs work?"

A partial answer can be obtained from this study. It is accepted that the type of similarity/dissimilarity coefficient used will determine to a large extent the outcome of the analysis, (Orlocci, 1966a, 1966b, 1972). This effect might account in part for the disparity in the results although Greig-Smith (1968) did find that in data from temperate regions, various standardization procedures did not show important differences in their results. However, a point that is rarely mentioned in the literature, is the type of calculation procedure used and the foundations of the mathematical model employed. Of the routines used here, BIGMAT is documented as a routine for "extracting eigenvalues and eigenvectors from a large symetrical matrix" (Elson and Funderlic, 1965) which when put together with a routine for calculating this matrix would be expected to yield a principal component analysis program. The Biomed program on the other hand (Dixon, 1965) is documented as a factor analysis routine, which if the communalities are set to unity, should also carry out the extraction of principal components. An interesting difference between the models used in the two programs is that while BIGMAT supposedly rotates the reference system based on the original cluster of data, the Biomed program constructs a new cluster of points from the model which fits a hypothesized reference system and then rotates this to fit some simplicity criterion. Since so often the program used for component analysis is an unknown quantity, and this over and above the type of similarity coefficient will introduce a number of sources of variability into the results, it is impossible to make an exact statement as to how any given set of data should be analysed. Extensive use of these methods, commonly referred to as information analysis, in a great many different fields would appear to warrant further research into the mathematics behind them. Equally perhaps more communication is needed between disciplines such as ecology and psychology, both extensive users of the techniques.

In conclusion, the associations of the beach ridge system appear to be controlled in their distribution by three major factors, or at least show correlations with three of the principal components. These components or factors are; (1) the presence/absence of late snow lie zones; (2) the presence/absence of a peaty substratum; and (3) pH of the soil/peat substratum. The distribution over the beach system of the nine associations seems to correspond to these gradients although other factors are certainly in operation. Nevertheless, this information at least provides a strong basis upon which further research could be built, that is it accomplishes the aims of a preliminary survey by defining the problem under study and suggests a number of possible hypotheses for future testing.

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