VEGETATION SUCCESSION ON GLACIER FORELANDS IN THE JOSTEDALSBREEN REGION AND JOTUNHEIMEN, SOUTH-CENTRAL NORWAY

VOLUME 1

by

GÜNTER ALBIN GRIMM

ST. JOHN'S COLLEGE
AND
SCHOOL OF GEOGRAPHY

UNIVERSITY OF OXFORD

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THESIS

THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
UNIVERSITY OF OXFORD

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To Clare

Declaration

The work embodied in this thesis has not already been accepted in substance for any degree and is not currently being submitted for any other degree.

Candidate: .....

Date: .....

I hereby declare that the work presented in this thesis is the result of my own investigations except where stated in the text.

Candidate: .....

Supervisor: .....

Date: .....

GLACIER FORELAND VEGETATION SUCCESSION IN THE JOSTEDALSBREEN REGION AND JOTUNHEIMEN, SOUTH-CENTRAL NORWAY

Thesis submitted to the University of Oxford for the degree of Doctor of Philosophy, Hilary Term 2000
Günter Albin Grimm, St. John's College

Abstract

In this study four different aspects of primary successions on glacier forelands in South-Central Norway are investigated. First, general vegetation and environment trends, which have been observed by other scientists, were studied on two forelands. It is shown that the two selected forelands (one low- and one high-altitude foreland, Nigardsbreen and Storbreen, respectively) differ in the speed of vegetation cover change and in the overall species richness developed over the last 250 years since deglaciation. This is attributed to differences in the severity of the environment between the two forelands. Some support for an early peak in the number of species was found for the Nigardsbreen foreland, whereas the Storbreen foreland shows no significant trend in the development of species richness. Life-forms and soil-depth change on both forelands in the predicted manner. A novel approach for the use of Ellenberg indicator values for the estimation of pH-values from the existent vegetation shows highly significant correlations between predicted pH values and trends measured for similar terrain ages from a study by Messer (1988).

Investigation at two different scales indicated that small-scale disturbances (< 100 m) may influence the mosaic of the environment, which affects the results of the chronosequence approach. By using a strict geometrical sampling design more variable conditions entered the analyses than with the stratified random sampling schemes adopted by others, such as Matthews (1979b). Some loss in the power of analysing the data occurred, but the results are still consistent with hypotheses about primary succession on glacier forelands.

Second, new aspects of the temporal development and successional change of plant communities were investigated on the same two forelands. There is some evidence of succession from a pioneer community to the local climax community of the

surrounding area for both forelands. There is also support for the correlation of time-dependent environmental variables with the successional development of plant communities. A new application of Ellenberg indicator values in ordinations was assessed for its value in estimating average environmental conditions derived from the vegetation. As with the previous analyses, investigation of community development at two different scales supported the importance of sampling scale on the analysis of succession data.

Third, spatially explicit analyses of distribution patterns of dominant woody species was developed as a means to investigate processes and formulate hypotheses about primary succession on glacier forelands. The data for this part of the study was collected on five glacier forelands, three low-altitude (Nigardsbreen, Austerdalsbreen and Bødalsbreen) and two high-altitude (Storbreen and Høgvaglbreen). Pattern descriptors including perimeter/area index, autocorrelation measures and fractal dimensions, support the hypothesis of differential colonisation of wind and animal-dispersed species. Even more convincing is the result that low- and high-altitude forelands show significant differences in the patterns exhibited by wind and animals dispersed species. This result is thought to be related to the differences in environmental severity affecting the establishment of colonising species.

Finally, logit modelling of the distributions of dominant woody species provides insights into the sampling effort needed to gather enough data for meaningful analyses. It also leads to the identification of important factors influencing the distribution of those species.

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Table of Contents

DECLARATION I

ABSTRACT II

ACKNOWLEDGEMENTS IV

TABLE OF CONTENTS V

LIST OF TABLES VIII

LIST OF FIGURES X

1. THESIS OUTLINE 1

2. INTRODUCTION AND LITERATURE REVIEW 3

SUCCESSION THEORY 3

FACTORS INFLUENCING SUCCESSION IN ARCTIC/ALPINE ENVIRONMENTS 12
Glacial Landforms and Processes 12
Periglacial Landforms and Processes 16
Other Physical Factors and Processes 20
Biotic Factors 23

VEGETATION AND ENVIRONMENTAL TRENDS IN SUCCESSION 27

CONTRASTING THEORETICAL FRAMEWORKS IN VEGETATION SCIENCE 28
Phytosociology and the Zürich-Montpellier (Braun-Blanquet) School 28
The North American School 30

MULTIVARIATE NUMERICAL TECHNIQUES 31
The Historical Context 31
Classification Techniques 32
Ordination Techniques 33

ELLENBERG'S INDICATOR VALUES 35

PATTERN ANALYSIS AND SPATIAL STATISTICS 38
Spatial Indices 38
Spatial Autocorrelation 39
Fractal Dimension 40

ENVIRONMENTAL MODELLING OF SUCCESSION 41

SPECIFIC OBJECTIVES AND RATIONALE 44

3. THE STUDY AREAS 48

LOW-ALTITUDE GLACIERS 50
Nigardsbreen (Figure 3-3) 50
Austerdalsbreen (Figure 3-5) 52

Bødalsbreen (Figure 3-7) 55

HIGH-ALTITUDE GLACIERS 58
Storbreen (Figure 3-9) 58
Høgvaglbreen (Figure 3-11) 60

4. TRENDS IN VEGETATION COVER, RICHNESS, LIFE-FORM , SOIL DEPTH AND SOIL-PH 65

PREFACE 65

INTRODUCTION 65

METHODS 69

RESULTS 71
Vegetation Cover 71
Species Richness 75
Life-form Changes 76
Soil Development 78
pH Trends 78

DISCUSSION 79

5. PLANT COMMUNITY ORDINATION AND VEGETATION AND ENVIRONMENT CORRELATIONS 84

PREFACE 84

INTRODUCTION 85

METHODS 85
Field Sampling 85
Ordinations 89
Two-Way INdicator SPecies ANalysis (TWINSPAN) 92
Data Selection, Data Transformation and Pre-Analysis Preparation of the Data 92

RESULTS 105
Nigardsbreen Large-Scale Data Set 105
Nigardsbreen Small-Scale Data Sets 112
Nigardsbreen Small-Scale Block I (N2-95, 192 and 245 years since deglaciation) 112
Nigardsbreen Small-Scale Block II (N7-95, 192 years since deglaciation) 113
Nigardsbreen Small-Scale Block III (-1N16-95, 122 and 999 years since deglaciation) 114
Storbreen Large-Scale Data Set 116
Storbreen Small-Scale Data Sets 118
Storbreen Small-Scale Block I (-1S2-95; 245 years since deglaciation) 118
Storbreen Small-Scale Block II (1S6-95; 143 years since deglaciation) 118
Storbreen Small-Scale Block III (1S12-95; 44 years since deglaciation) 118

DISCUSSION 120

6. SPATIAL ANALYSIS OF 1996 DATA SETS 122

PREFACE 122

INTRODUCTION 122

METHODS 123
Field Sampling 123
Two Dimensional Two-Term Local Quadrat Variance (TTLQV) 126
Geostatistics/Fractal Dimension 129

Spatial Indices 129
Spatial Autocorrelation 131
Analytical Methods 132

RESULTS 134

DISCUSSION AND CONCLUSION 147

7. SPATIALLY EXPLICIT MODELS OF SUCCESSION ON GLACIER FORELANDS 152

PREFACE 152

INTRODUCTION 152

METHODS 154

RESULTS 161

DISCUSSION 168
The initial three models 168
The stepwise selection model (model 4) 168
General considerations 169

8. SUMMARY AND CONCLUSIONS 171

9. REFERENCES 178

List of Tables

Table 2-1: Hierarchical system of successional causes (Pickett, Collins & Armesto, 1987a; 1987b) 10
Table 2-2: Growth forms of plants growing on moving substrate according to Schroeter (1926; after Reisigl & Keller, 1987, p 109) 20
Table 2-3: Life-forms according to the system of Raunkiaer (1934; descriptions translated from Ellenberg *et al.*, 1991: 70) 23
Table 2-4: The six indicator values used in this thesis with an abbreviated description of the ecological behaviour of the plants (after Ellenberg, 1986: 98) 36
Table 4-1: Regression equations for the estimation of soil depth and pH for the Storbreen and Nigardsbreen forelands (from Messer, 1988) 71
Table 4-2: Regression coefficients for measured soil depths (mean and extreme relate to the soil depth measurement method used in the regression; see Table 5-4 for explanation of the methodology) and predicted values from Messer (1988) 78
Table 4-3: Regression coefficients for estimated pH-values from qualitatively calculated Ellenberg values for reaction (Ellenberg et al. 1991) and predicted values from Messer (1988) 79
Table 5-1: Parameters of the physical environment and vegetation recorded in the 1995 field season 87
Table 5-2: Modified Braun-Blanquet scale for estimation of abundance and %-coverage of plant species within plots (after Braun-Blanquet, 1964) 88
Table 5-3: Two-way weighted averaging algorithm of CA (after ter Braak, 1995) 89
Table 5-4: Number and names of environmental variables and factors either recorded in the field (denoted by asterisk) or calculated from the original data, with short descriptions 93
Table 5-5: Clast sizes for the characterisation of substrate 94
Table 5-6: Spearman rank correlation between original Ellenberg indicator values (Ellenberg *et al.*, 1991) and Firbank *et al's* (2000) indicator values for the species present in the study sites. $p < 0.0001$ for all values 96
Table 5-7: Transformation table with symbols used in the field to record frequency and abundance of species and the corresponding values of the van der Maarel transformation used in the DCA 103
Table 5-8: Pearson's correlation coefficients for environmental and geographical variables with the first DCA Axis for individual transects. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level 106
Table 5-9: Kendall's tau correlation coefficients between the correlation coefficients of the environmental variables in Table 5-8. * and ** denotes significance at 95% and 99%, respectively 107
Table 5-10: Species variance explained by the first two DCA-axes (in % of total variance) 109
Table 5-11: Pearson's correlation coefficients for environmental and geographical variables with the second DCA Axis for individual transects. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level 110
Table 5-12: Eigenvalues of the first two DCA-axes for each transect 110
Table 5-13: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the whole large-scale data set. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level 111
Table 5-14: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the small-scale data sets. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level; NA = no age variation within Block II does not allow for correlation of agegrp and agemax with first DCA-axis 116
Table 5-15: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the whole large-scale data set. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level 117
Table 5-16: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the small-scale data sets. * and ** denotes significance

at 95% and 99%, respectively; n.s. = not significant at either level; NA = no age variation within the Blocks does not allow for correlation of agegrp and agemax with first DCA-axis. Due to lack of data lich_rat could not be used for Block III 119
Table 6-1: List of all recorded species in the 1996 survey. P=Phanerophyte, tree or shrub with aerial dormant buds; C=Chamaephyte, perennial plant having buds at or just above ground level; H=Herb, seed plant with non-woody green stems 124
Table 6-2: Codes, names, dates visited, location and size of the 1996 blocks 125
Table 6-3: Local maxima of the total variance associated with block size ($V_2(b)$) for four animal-dispersed (a) species. Aus refers to Austerdalsbreen, Bod to Bødalsbreen and Nig to Nigardsbreen forelands. The age is estimated maximal time since deglaciation. nm stands for no maximum 134
Table 6-4: Mean perimeter/area index values for animal- and wind-dispersed species ordered chronologically. Aus refers to Austerdalsbreen, Bod to Bødalsbreen, Nig to Nigardsbreen, Hog to Høgvaglbreen and Sto to Storbreen forelands. Aus, Bod and Nig are low-altitude (l) and Hog and Sto are high-altitude (h) forelands 135
Table 6-5: Perimeter/area indices for four animal-dispersed (a) species. Aus refers to Austerdalsbreen, Bod to Bødalsbreen and Nig to Nigardsbreen forelands. The age is estimated maximal time since deglaciation 136
Table 6-6: Mean autocorrelation values (Moran's I; King's case) for animal- and wind-dispersed species ordered chronologically 137
Table 6-7: Autocorrelation values (King's case) for four animal-dispersed species. Aus refers to Austerdalsbreen and Bod to Bødalsbreen. The age is estimated maximal time since deglaciation 137
Table 6-8: Fractal dimension values ($D_{De\ Cola}$, after De Cola, 1989 and D_{Gau}, after Gautestad, 1994) for animal-dispersed and wind-dispersed species. Aus refers to Austerdalsbreen, Bod to Bødalsbreen and Nig to Nigardsbreen forelands 138
Table 6-9: Relation of mean descriptor values for animal (Animal) and wind (Wind) dispersed species on low- and high-altitude glacier forelands 149
Table 7-1: Environmental favourability index of geomorphological features in the 1996 blocks. Variables for d, w and s range from 1 to 5 (from least to most). The environmental favourability index is calculated as $(1/d + w + s) / 3$ 157
Table 7-2: Parameters entering the 3 basic models. Easting, northing and easting*northing are geographical location variables, rest is a measure of species richness and ac is an autocorrelation measure 157
Table 7-3: Naming convention for species calvul (*Calluna vulgaris*) using model 1 and the 9 possible subsets of calibration data. The first digit of the model name corresponds to the model number, the second to the layout and the third to the proportion 158
Table 7-4: Confusion matrix derived measures of classification accuracy 159
Table 7-5: Average of the AUC of ROC-plots for each species (mean over all model configurations and all blocks on all forelands where the species is present). * denotes mean AUC larger than total mean model performance 161
Table 7-6: Average AUC of ROC-plots for all species present in the relevant blocks. For the location of the blocks see Figure 3-13 162
Table 7-7: Average AUC values for different model configurations. Significant differences exist between the four models and between the three proportions ($p<<0.01$; Kruskal-Wallis) with no significant differences between the three layouts ($p=0.326$) 163
Table 7-8:Actual number of times variables have entered model 4 using the stepwise selection option 164

List of Figures

Figure 2-1: a) life-forms characterised by three primary strategies; b) successional pathways in relation to strategies under conditions of high (P1), intermediate (P2) and low (P3) potential productivity. In b) circle size represents biomass (adapted from Grime, 1977; Matthews, 1992: 302). 8
Figure 2-2: Individualistic process model of controls on species composition during succession: the influence of a) successional type and b) environmental severity on major successional processes are shown for colonisation (C), maturation (M) and senescence (S) stages of succession (from Walker & Chapin III, 1987). 9
Figure 2-3: Schematic representation of the relative importance of autogenic and allogenic processes during succession (from Matthews, 1992: 312). 11
Figure 2-4: Schematic illustration of moraine types; a) lateral moraine, b) ground moraine exposed by retreating glacier, c) end moraine, d) material transported on top of glacier. 14
Figure 2-5: Mean grain size curves for sediments of glaciers in the Alps (adapted from Boulton & Dent, 1974). 14
Figure 2-6: Accumulation of fines after heavy rains (Storbreen foreland, 1995; lens-cap for scale). 16
Figure 2-7: Example of solifluction on the Storbreen foreland (1995; see lens cap for scale). 17
Figure 2-8: Boulder-cored frost boil on Storbreen foreland (1995). 18
Figure 2-9: Sorted polygons on the Nigardsbreen foreland (1995). 19
Figure 2-10: Storbreen foreland on 16.7.95, showing large snow-fields due to late snowmelt. 22
Figure 2-11: Storbreen foreland on 23.6.96, with small snow patches. Pictures in Figure 2-10 and Figure 2-11 were taken from the same point opposite the glacier foreland. 22
Figure 2-12: Sheep grazing on the A-moraine (1750 AD), Nigardsbreen foreland, 1995. 25
Figure 2-13: Cattle grazing on the Bødalsbreen foreland, 1996. 26
Figure 3-1: Location of the five study sites in South-Central Norway. 49
Figure 3-2: Nigardsbreen foreland: a) the end moraine sequence (from Bickerton & Matthews, 1992); b) vertical aerial photograph (Fjellanger Widerøe AS, 27.8.1993). 51
Figure 3-3: The Nigardsbreen foreland from the southern valley side looking towards mouth of valley (1995). 52
Figure 3-4: Austerdalsbreen foreland: a) the end moraine sequence (from Bickerton & Matthews, 1993); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1981). 54
Figure 3-5: The Austerdalsbreen foreland in 1996 with view towards the glacier. 55
Figure 3-6: Bødalsbreen foreland: a) the end moraine sequence (from Bickerton & Matthews, 1993); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1981). 56
Figure 3-7: The Bødalsbreen foreland in 1996. 57
Figure 3-8: Storbreen foreland: a) the end moraine sequence (from Matthews, 1992: 23); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1968). 59
Figure 3-9: The Storbreen foreland from eastern Leira valley side (1996). 60
Figure 3-10: Høgvaglbreen foreland: a) the end moraine sequence (from Erikstad & Sollid, 1986); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1968). 61
Figure 3-11: Part of Høgvaglbreen foreland. View from 1750 moraine towards the glacier (1996). 62
Figure 3-12: Location of the 1995 sampling plots, superimposed on the relevant aerial photographs. 63
Figure 3-13: Location of the 1996 sampling blocks on the relevant forelands. 64
Figure 4-1: Vegetation cover chronofunctions for three successional pathways (A, B and C) characteristic of respectively more favourable habitats, Pasterzer Gletscher, Austrian Alps. Large filled circles represent all three pathways (from Zollitsch, 1969). 66
Figure 4-2: Species richness in three successional pathways (A, B and C) characteristic of respectively more favourable habitats, Pasterzer Gletscher, Austrian Alps. Large filled circles represent all three habitats (from Zollitsch, 1969). 67

Figure 4-3: Percentage cover of various life-forms on terrain of increasing age, Grosser Aletschgletscher, Swiss Alps (from Lüdi, 1945). 68
Figure 4-4: Location of plots recorded in 1995 with their respective numbers on the forelands. 70
Figure 4-5: Average amount of plant cover for *n* quadrats (quadrat size = 16m²) of the large-scale sampling design in relation to age groups since deglaciation on the Storbreen and Nigardsbreen forelands. 72
Figure 4-6: Histograms of the frequencies of recorded plant cover values on the Storbreen foreland, according to the time since deglaciation. Figures represent site age, 999 refers to quadrats from outside the foreland boundary. Quadrats from large-scale sampling design, quadrat size = 16m². 72
Figure 4-7: Average amount of plant cover of quadrats from three small-scale blocks on the Storbreen foreland. Age since deglaciation is a conservative estimate, using the youngest quadrat from each block. Error bars show 95% confidence intervals of mean. Individual quadrat size = 1m². 73
Figure 4-8: Histograms of the frequencies of recorded plant cover values on the Nigardsbreen foreland, according to the time since deglaciation. Figures represent site age, 999 refers to quadrats from outside the foreland boundary. Quadrats from large-scale sampling design, quadrat size = 16m². 74
Figure 4-9: Average amount of plant cover of quadrats from three small-scale blocks on the Nigardsbreen foreland. Age since deglaciation is a conservative estimate, using the youngest quadrat from each block. Error bars show 95% CI of mean. Individual quadrat size = 1m². 75
Figure 4-10: Average number of species in large-scale quadrats (quadrat size = 16m²) on terrains of increasing age. 76
Figure 4-11: Average number of life-forms represented in sampling quadrats in relation to terrain age groups on the Nigardsbreen foreland. 77
Figure 4-12: Average number of life-forms represented in sampling quadrats in relation to terrain age groups on the Storbreen foreland. 77
Figure 5-1: Grouping of different aspects into four classes. 94
Figure 5-2: Representation of varying proportions of clast sizes of substrate. 95
Figure 5-3: Regression plots of qualitatively and quantitatively calculated average Ellenberg indicator values calculated for the Nigardsbreen large-scale data. 97
Figure 5-4: Regression plot of relative distance and absolute distance of quadrats from glacier snout. Nigardsbreen large-scale data. 99
Figure 5-5: Regression plot of maximum estimated age using the dates provided by Bickerton & Matthews, 1992 and age group. Nigardsbreen large-scale data. 99
Figure 5-6: Kendall's tau correlation coefficients, significance levels and number of paired variables for the non-parametric correlation of various variables with time on the Nigardsbreen foreland (agemax). Italicised variables are referred to in the text as time-dependent 100
Figure 5-7: Location plots of time-dependent variables used in the DCA. Top of page is north, distance between quadrats is 100m (see Figure 3-12 for quadrat location). Size representation of the variables is relative for each figure. 101
Figure 5-8: Location plots of time-independent variables used in the DCA. Top of page is north, distance between quadrats is 100m (see Figure 3-12 for quadrat location). Size representation of the variables is relative for each figure. 102
Figure 5-9: DCA sample scores of the first DCA axis for Nigardsbreen large-scale data set. Sample scores derived from ordinations on individual transects. Top of page is north, distance between quadrats is 100m (see Figure 3-12 for quadrat location). Size representation of the variables is relative. 108
Figure 5-10: DCA sample scores of the first DCA axis for block I of the small-scale data set. Top of page is north, distance between quadrats is 10m. Size representation of the variables is relative. For location of block I on the Nigardsbreen foreland see Figure 3-12. 113
Figure 5-11: DCA sample scores of the first DCA axis for block II of the small-scale data set. Top of page is north, distance between quadrats is 10m. Size representation of the variables is relative. For location of block II on the Nigardsbreen foreland see Figure 3-12. 114

Figure 5-12: DCA sample scores of the first DCA axis for block III of the small-scale data set. Top of page is north, distance between quadrats is 10m. Size representation of the variables is relative. For location of block III on the Nigardsbreen foreland see Figure 3-12. 115
Figure 6-1: Schematic outline of sampling quadrats within one vegetation block. 126
Figure 6-2: The method used to calculate the two-dimensional variance. The data in the "+" square are added together and then the sums of the other squares, weighted as indicated, are subtracted. The variance is the average of the squares of such differences for all possible positions 127
Figure 6-3: 3 x 3 neighbourhood template with its values used for the calculation of contiguity values. 130
Figure 6-4: 5 x 5 neighbourhood template used for the calculation of clustering values. 131
Figure 7-1: Properties of the logistic response curve relating the probability p of an event to the value of a standardised explanatory variable $z=\alpha+\beta x$. 155
Figure 7-2: One example of a sub-sampling matrix for proportion 9.4% and square size 5*5. 156
Figure 7-3: A confusion matrix, b = false positives, c = false negatives, a and d = correctly predicted positives and negatives, respectively. 159
Figure 7-4: Average tolerance values of variables entering model 4 using stepwise selection (calculated from 1143 models). 163
Figure 7-5: Distribution maps, environmental sketch-maps, predicted probabilities from model1, layout 3*3 and 50 sub-sampling proportion, ROC curves and AUC values for *Empetrum hermaphroditum* in three Austerdalsbreen foreland blocks. 166
Figure 7-6: Distribution maps, environmental sketch-maps, predicted probabilities from model1, layout 3*3 and 50 sub-sampling proportion, ROC curves and AUC values for *Betula pubsecens* in three Austerdalsbreen foreland blocks. 167

1. Thesis Outline

The thesis consist of two volumes. The first contains the main body of the thesis and the second consists of a selection of distribution maps and the programming code. The thesis is also accompanied by a CD including all the information in digital format.

Chapter 1 in Volume 1 gives this short outline of the thesis structure to guide the reader through the thesis. **Chapter 2** introduces the reader to the different aspects of this thesis. It explains the concept of succession and the historical development of the theoretical framework presently used by ecologists. It then goes on to highlight the processes and factors that form the environment of the study area and their influence on succession. Some of the perhaps most obvious successional trends for vegetation and environment, dependent on the processes described in the previous part of the chapter, are then outlined and evaluated. They have been the focus of many studies. The analyses in this thesis differ from most of the other studies in that they directly compare these trends for a low- and a high-altitude foreland. Along with the conceptual development of succession theory, the evolution of different methodological approaches is portrayed next. Within two main schools of thought, distinct analytical methods were developed and these are described in the next section of the chapter. A new approach of uniting both traditions is tried in this study, using Ellenberg indicator values (which are derived from the Braun-Blanquet school) in ordinations (from the North American school). The methods of direct spatial analysis of distribution patterns (mostly from the geophysical sciences) are presented. The next section of the chapter summarises modelling approaches that have been used in ecology. It is with those methodologies that a spatially explicit logit-model of species distributions was formulated. The chapter finishes with the presentation of the specific objectives and rationale of the thesis. **Chapter 3** describes the physical environment of the five selected study sites. It also contains the description of the sampling layout and the arrangement of sampling areas (blocks) on the forelands.

Each of the four analytical chapters (**Chapters 4** to **7**) investigates a different aspect of succession on glacier forelands in South-Central Norway. In "pseudo-paper" style: meaning that each has a short introduction to the specific aspect of succession research dealt with in the chapter, a methods section in which the relevant methodology

is described in detail, a results and a discussion section. Each of the chapters also contains a short preface which defines the chapter's position in the general framework of the thesis.

Chapter 4 deals with successional changes of vegetation characteristics not based on community structure. It concentrates on plant diversity and life-form changes. It also investigates the development of the physical environment, emphasising pH and soil depth development. **Chapter 5** is concerned with the change of plant communities during primary succession identified by ordination analysis. It also presents and discusses the results of a novel use of Ellenberg indicator values. **Chapter 6** analyses the development of spatial pattern on five glacier forelands using new methods to describe and quantify the state and temporal change of the patterns on those forelands. **Chapter 7** describes the possibilities of modelling the development of woody species on glacier forelands in South-Central Norway with a limited number of predictor variables. It goes on to discuss the use of this approach in succession studies in general and proposes new and more sophisticated means of analysis for further studies (e.g. the use of bootstrapping). The analytical procedure adopted in this study also allows an estimate of the sampling effort necessary to gather sufficient data to describe species distributions accurately.

Chapter 8 draws the conclusions of the thesis. The wide variety of methods used in this thesis calls for a comprehensive discussion of the results in context of the different aspects of the study. This chapter also incorporates suggestions for further research, which, in part, has been started already, but could not be incorporated into the body of the thesis.

2. Introduction and Literature Review

"God could cause us considerable embarrassment by revealing all the secrets of nature to us: we should not know what to do for sheer apathy and boredom."

- GOETHE, *Memoires*

Succession Theory

The study of succession in plant ecology is dealing with the change of plant community patterns in time (Begon, Harper & Townsend, 1990: 628) and the recovery processes of vegetation following any disturbance (Bazzaz, 1996: 1). This concept of succession has long been an influential idea in the natural sciences. At least as early as the beginning of the 19th century scientists recognised the presence of successional processes in nature (von Humboldt, 1800; and references in Straass & Trommer, 1992: 349) and until recently it was still considered to be one of the most important ecological concepts (Cherrett, 1989). To understand the present position of succession theory one has to look at its historical evolution. The formal development of succession research started in the early 20th century with Clements' model based on facilitation and reaction, sometimes also referred to as the "organismic concept" (Clements, 1916; Kent *et al.*, 1997). Similar to Davis' perception of an orderly development of landforms (Davis, 1909), Clements viewed vegetation forms as "superorganisms" with defined periods of birth, maturation and death. Like an organism, the vegetation units were thought to be distinct and easily definable, with certain sets of species occurring together in similar environments and behaving as organised wholes (Matthews, 1996a: 194). According to this view, the succession of the different phases shows a directionality towards a single climax community (monoclimax), which was thought to be characteristic of a regional climate. Retrogression, the development of vegetation units towards previous successional stages, is not allowed for in this deterministic and progressive view of succession.

The criticism the monoclimax model has received includes disagreement by many scientists with the following three main postulations. First, that all successions in an

area have to end up in the same, stable climax community, second, that this climax is mainly controlled by climate and third, that the climate itself is regarded as stable. It is also thought that the model cannot incorporate other stable communities in a satisfactory way, that transitional areas between community types cannot be fitted into the model and that it grossly overestimates the importance of changes brought about by the action of the plants themselves (autogenic changes; e.g. Colinvaux, 1973; Drury & Nisbet, 1973; Matthews, 1992; Kent *et al.*, 1997).

Doubt also exists in parts of the scientific community that plant *associations*, defined as the abstract, theoretical idea of species assemblages in space, exist at all. One of the first to challenge Clements' theory in this respect was Gleason with his "individualistic concept". In his theory he stressed the individualistic nature of vegetation dynamics (Gleason, 1917; 1926; 1927; 1937). Contra Clements' "superorganism" he rejected the notion that species were bound together in rigid communities (the concrete, observable assemblage of plant species in the environment) or other clearly defined units. He emphasised the variation which can be found within plant communities, resulting from the individualistic behaviour of plant species. He proposed that there was no co-evolution at the level of the plant association and no interactions of plant species of different communities (lack of genetic and dynamic connection between communities). This led him to question the logic of classifying series of communities into definite associations (Matthews, 1996a). Independently from Gleason, similar ideas developed in Russia, France and Australia (see Whittaker, 1953: 45).

Tansley's polyclimax model (Tansley, 1920; 1929) is another step in the development of succession theory. It differs from Clements' monoclimax model in that it recognises a number of different climax communities for a given region. Together these communities form a mosaic of vegetation covers, determined by the availability of favourable habitats. The controlling factors can be the parent material (edaphic climax), topography (topoclimax) or other environmental parameters.

Other models continued to be formulated, for example Egler's relay floristics and initial floristic composition models (Egler, 1954). The relay floristics model views the succession of different plant communities as a process where one set of species replaces the previous by invasion of the site at a certain stage of site development. It implies alterations of the site by the previous communities making it suitable for invasion by the

next set of species. In this respect it is compatible with Clements' organismic model. In contrast, the initial floristic composition model assumes the presence of all species at or near the beginning. The successional sequence arises from the differential growth rates and life histories of various groups of species, successively reaching dominant status.

Later, in the 1960s, other models were put forward stressing energetics, and being concerned with the structural changes in ecological systems due to successional changes. Margalef (1968) proposed a theory in which linkages between trophic levels and populations are conceptualised as representing information. According to this theory, succession follows the trend of accumulating more information within an ecosystem. Similarly, Odum (1969) put forward a theory in which ecosystems develop towards greater homeostasis, which in his view would be reflected by a development towards greater biomass and diversity.

Most of these theories have in common the directionality towards an end point (climax) and the more or less explicitly expressed recognition of the existence of defined plant communities and the plant associations derived from them. By the 1970s it became clear that the above concepts failed to explain adequately the processes in "the real world". Therefore researchers started to look for other explanations and theories and several trends evolved which need not be seen as replacements or exclusive, competing hypotheses for the above but as additional ways of explaining the complexity of succession.

R. H. Whittaker (1953) prepared the way for a new development by the introduction of a new climax concept (climax pattern hypothesis) which replaced the monoclimax sensu Clements (1916) and the polyclimax of the "British School" (Tansley, 1935). The new hypothesis recognises the diversity of climax stands,

> "...but these are regarded, not as two or more discrete climax associations, but as parts of a single, often continuously gradating climax pattern."
>
> **(Whittaker, 1953: 59)**

Whittaker follows, with this hypothesis, the direction started by Gleason (1926), not assuming the validity of the existence of a particular number of climax associations. Later on it was advocated that the paradigm of equilibrium (climax) should be replaced by a non-equilibrium paradigm to account for many phenomena encountered during succession studies (e.g. reversal, sticky states or multiple pathways; for early examples

see Whittaker, 1953: 43; Connell & Slatyer, 1977; Matthews, 1979b; Boerner, 1985; Fastie, 1995). With this development there was a shift away from models mainly focused on the structural manifestation of succession towards models predominantly concerned with the processes and mechanisms involved in successional series.

The three models proposed by Connell & Slatyer (1977) appear to be elaborations of Egler's concepts. The first one, the facilitation model, closely resembles the traditional view of primary succession, with the alteration of the environment by early successional species, thereby facilitating the invasion of late successional species (compare Egler's relay floristics model). The other two models, the tolerance and inhibition models, build on Egler's initial floristic composition model, in that all species of the different successional stages can invade the site at an early stage. The tolerance model postulates little or no effect of the early successional species on the recruitment of later successional species, whereas the inhibition model proposes alterations of the environment which have the overall effect of making it less suitable for invasion by later successional species. The success of later invading species depends on disturbances, which free space by killing early successional species and/or mobilising resources. Several authors argue that distinction between the three models is not always possible and that each may operate within a single succession (Finegan, 1984; Pickett, Collins & Armesto, 1987b; Burrows, 1990).

The term "patch-dynamics" appeared in the literature in the late 1970s (Pickett & Thompson, 1978). However, as pointed out by Jax (1994), it is not a narrowly defined concept, but a number of closely related approaches. They all stress the importance of the spatial heterogeneity and patchiness of ecological systems and their temporal dynamics. As compared to the closed system approach of some of the above models, they are dealing with open systems that consist of a large number of similar units (patches), each of which interacts with some of its neighbours. The driving forces for the changes in patchiness is the disturbance, defined by Pickett & White as:

> "... a relatively discrete event in time, which ruptures the structure of ecosystems, communities of organisms or populations and changes the availability of resources and substrates or the physical environment."
>
> **(Pickett & White, 1985: 7)**

A very closely related concept in the German literature is the "Mosaik-Zyklus-Theorie", which stems from investigations into the heterogeneity and temporal dynamics of forests and other plant assemblages (see Jax, 1994: 108 for references). It can be viewed as a special case of the patch-dynamics concept, however it still clings to the overall equilibrium of the supersystem (Remmert, 1991b) and therefore differs from the more general patch-dynamics concept, which does not include any prerequisites for a directional development of the system towards an equilibrium.

Wu & Loucks (1995) synthesise different aspects of the development in patch-dynamics and propose a new theoretical framework, hierarchical patch dynamics, which in their view is superior to the previous paradigm of the "balance of nature", by explicitly incorporating heterogeneity and scale and by integrating equilibrium, multiple equilibrium and non-equilibrium perspectives.

There have also been many mathematical and statistical attempts to model successional processes. These also encountered many difficulties and problems. For example, van Hulst (1980) pointed out that the application of Markov chain models or coupled differential equations "bear a severe danger". They are probabilistic matrix models where the transition of the system between states is modelled by a vector that describes the state of the system at time t and a matrix which contains the probabilities of different transitions in the system (Facelli & Pickett, 1990). Multiplication of the vector with the matrix results in a new vector describing the system at time $t+1$. The crucial assumption of the Markov model is, that it is irrelevant how the system reached its present state (known as the Markovity assumption). This assumption seems, on ecological grounds, unlikely to be satisfied in the majority of cases (van Hulst, 1980). There are several indications of the importance of a memory effect (hysteresis) first remarked upon for successions in forest communities. A "memory" of previous developments seems to exist in these systems, which influences the path of succession for these communities. This memory can take different forms, for example soil conditions, seed banks and the structure of pathogen or herbivore populations. It can also be found in the age structure and spatial density of communities (Facelli & Pickett, 1990).

Yet another way to model succession is to look at the so-called evolutionary strategies of the plants involved. One approach is to divide the plant species by their physiological characteristics into r-strategists (opportunistic, ruderal species), which

tend to be found in early successional stages and *K*-strategists (equilibrium, competitive species) which dominate later stages and mature patches (see MacArthur & Wilson, 1967; Bazzaz, 1979; Finegan, 1984; Fitter & Hay, 1987: 342). Grime's C-S-R model (competition, stress, disturbance) adds "stress" as another strategy to the two above mentioned (Grime, 1977). In Figure 2-1, different life-forms are represented in terms of their strategies and successional pathways are represented in relation to the three primary strategies. However, as Matthews points out the C-S-R and related models must nevertheless be regarded as a gross simplification of a very wide range of possible strategies (Matthews, 1992: 302).

Figure 2-1: a) life-forms characterised by three primary strategies; b) successional pathways in relation to strategies under conditions of high (P1), intermediate (P2) and low (P3) potential productivity. In b) circle size represents biomass (adapted from Grime, 1977; Matthews, 1992: 302).

Probably the three most comprehensive frameworks for understanding succession are provided by Noble and Slatyer's model of "vital attributes" (Noble & Slatyer, 1980), Walker and Chapin's "individualistic process" model (Walker & Chapin III, 1987) and Pickett *et al.*'s model based on a hierarchy of successional causes (Pickett, Collins & Armesto, 1987a; 1987b). All three models are based on process interactions as the driving force for succession.

In Noble and Slatyer's model vital attributes represent: 1) methods of recovery from disturbance; 2) the ability to establish in the face of competition and 3) the time taken to reach critical life history stages. The mechanisms that lead to those vital attributes are at the heart of the model as it seeks to identify the main processes of vegetation changes.

Walker & Chapin (1987) identified a series of processes which all have their influence on the successional pathway by acting simultaneously and in a complex way as directing forces. They stress the point that vegetational change is the result of the varying importance and strength of these processes along temporal and spatial gradients. Figure 2-2 gives the graphical representation of the relative importance of those processes for different successional stages.

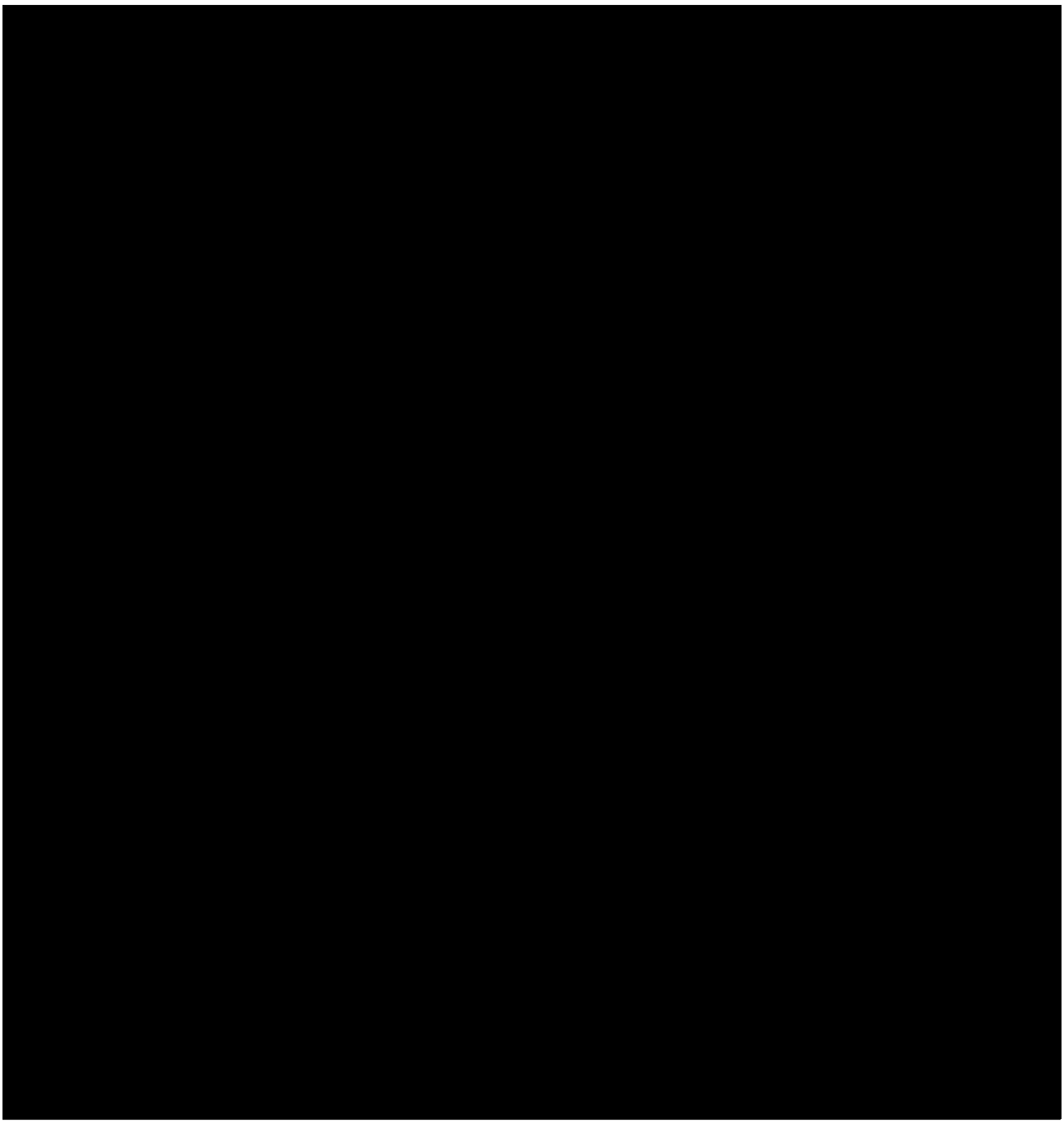


Figure 2-2: Individualistic process model of controls on species composition during succession: the influence of a) successional type and b) environmental severity on major successional processes are shown for colonisation (C), maturation (M) and senescence (S) stages of succession (from Walker & Chapin III, 1987).

The third of these process-oriented models represents a hierarchical system with three levels. The first level contains the general causes of succession, the second explains the corresponding contributing processes or conditions and the third defines the factors or behaviours which influence these processes (Pickett, Collins & Armesto, 1987a; 1987b; see).

Table 2-1: Hierarchical system of successional causes (Pickett, Collins & Armesto, 1987a; 1987b)

General causes of succession	Contributing processes or conditions	Defining or modifying factors or behaviours
Site availability	Coarse-scale disturbance	Size, Severity, Time, Dispersion
Differential species availability	Dispersal	Landscape configuration
		Dispersal agents
	Propagule pool	Time since disturbance
		Land use
Differential species performance	Resource availability	Soil conditions
		Topography
		Microclimate
		Site history
	Ecophysiology	Germination requirements
		Assimilation rates
		Growth rates
		Population differentiation
	Life history strategy	Allocation pattern
		Reproductive timing
		Reproductive mode
	Environmental stress	Climate cycles
		Site history
		Prior occupants
	Competition	Presence of competitors
		Identity of competitors
		Fine-scale disturbance
		Predators and herbivores
		Resource base
	Allelopathy	Soil characteristics
		Microbes
		Neighbouring plants
	Herbivory, disease and predation	Climate cycles
		Consumer cycles
		Plant vigour
		Plant defences
		Community composition
		Patchiness

Matthews (1992) introduced a further model for succession with special emphasis on succession on recently deglaciated terrain. He calls it a geoecological model and

stresses two distinctive features. First, that physical *and* biological processes both contribute to successions on recently deglaciated terrain and therefore both have to be included in the model ("coupling of physical and biological processes", Matthews, 1992: 307; the lack of inclusion of physical processes is also his major criticism of the above three models). Second, the consideration of spatial variation at different scales. This second point stresses the importance of site location and environmental characteristics of the habitat on succession ("spatio-temporal dynamics", Matthews, 1992: 307). The inclusion of physical and biological processes is seen to be important because both are present at any site and therefore are likely to influence succession. The way Matthews sees the change of relative importance of internal and external (autogenic and allogenic) processes during successions is summarised in Figure 2-3.

Figure 2-3: Schematic representation of the relative importance of autogenic and allogenic processes during succession (from Matthews, 1992: 312).

This short overview of the development of succession theory highlights a point present in all disciplines of science. The accumulation of data and knowledge about a certain topic makes it necessary to review continuously existing models and hypotheses of "how things work". In accordance with Popper's view that hypotheses cannot be verified ("critical realism", Störig, 1981: 686), progress in the sciences depends on falsification of existing hypotheses, which leads to a need to modify or replace them by

better and more accurate hypotheses. In this process, the level of detail included in a hypothesis has an important influence on the longevity of a hypothesis.

Data for the development of the above mentioned hypotheses were collected from a variety of different environments. But due to a generally restricted species inventory and their location in arctic and alpine environments, glacier forelands are thought to be amongst the best places in which to study succession (Ellenberg, 1986: 581; Matthews, 1992). The study of primary succession on glacier forelands has therefore a long-standing tradition in the scientific community (e.g. Braun-Blanquet & Jenny, 1926; Faegri, 1933; Zollitsch, 1969; Archer, Simpson & Macmillan, 1973; Sommerville, Mark & Wilson, 1982; Matthews & Whittaker, 1987; Chapin III *et al.*, 1994; Vetaas, 1994) and covers many areas in the Alps, Scandinavia, North America and New Zealand. Another reason why glacier forelands are considered to be ideal field laboratories for the study of succession is the chronosequence approach introduced by early studies (Coaz, 1887), which is still being used extensively in succession studies (Bormann & Sidle, 1990; Helm & Allen, 1995; Frenot *et al.*, 1998) and also constitutes the basis for parts of this thesis.

Factors Influencing Succession in Arctic/Alpine Environments

It has recently been proposed that the availability of "safe sites" controls the distribution patterns of wind-dispersed plants, especially on very young ground (Houle, 1997; Jumpponen *et al.*, 1999). Therefore, the processes leading to the formation of these environments have to be considered. There are two sets of processes that are thought to explain the formation and change of arctic and alpine landforms. Glacial processes, which influence the landforms by direct action of a glacier, and periglacial, non-glacial cold climate processes, which comprise a range of climatic and regional conditions under which certain landforms are created.

Glacial Landforms and Processes

These landforms refer to those brought about primarily by immediate glacial action. The term is to be used purely descriptively and without any relation to specific periods of time (e.g. it can be used for recent as well as for Pleistocene glaciation and ice movements). Both erosional and depositional processes are involved.

Erosion landforms are created by four basic processes. **Detersion or abrasion** denotes the scouring of bedrock by material carried in the basal layers of a glaciers (Sugden & John, 1976). **Detraction** is the breaking and plucking of rock material, caused by rather complex processes, involving mechanisms like crushing, freezing-on, ice movement and variations in water-pressure (Röthlisberger & Iken, 1981; Drewry, 1986). **Exaration** is the pushing together of material at the end of the glacier. It is the main force for the formation of end-moraines. **Sub-glacial fluvial erosion**, the final process, involves removal of products of chemical and physical weathering and the mechanical action of high-velocity streams (Souchez & Lorrain, 1987).

The direct effect that glacial action has on the vegetation in these areas is very drastic. The weight of the ice and its crushing power destroy all higher plants and their propagules. Lichens are also deprived of their habitats when pieces of rocks are relocated and sometimes covered with other material. Considering the time spans during which the ice covers certain areas (sometimes thousands of years, e.g. Zackenberg area, Northeast Greenland, Christiansen & Humlum, 1993) the dimension of this impact is not surprising.

Glacial erosion landforms are one of the reasons that glacier forelands are interesting fields for succession studies, since when the glacier retreats a "virgin" surface is left behind without any established vegetation. The fact that processes like abrasion or detraction tend to remove any finer substrate and soil down to the bedrock level also influences the re-invasion of colonising species when they begin re-establishing after a glacier retreats. Deglaciation creates a pattern of more suitable environments for colonisation (where fines accumulate due to processes described below) intermingled with less suitable or even unsuitable rock surfaces. The lack of a seed bank requires the colonisers to arrive with new propagules. These can be, as in the case of phanerogams, windblown or animal-dispersed seeds or parts or whole plants falling onto the glacier foreland from the valley sides or mountain slopes bordering the forelands (later referred to as pseudo-viviparous) or spores, as in the case of cryptogams.

Depositional landforms, which are created by accumulation processes, contain several distinct landform types, one group of which is moraines. Several forms of moraines can be distinguished and they typically consist of unlayered, angular to roughly rounded, grooved blocks of rocks of varying size (Figure 2-4).

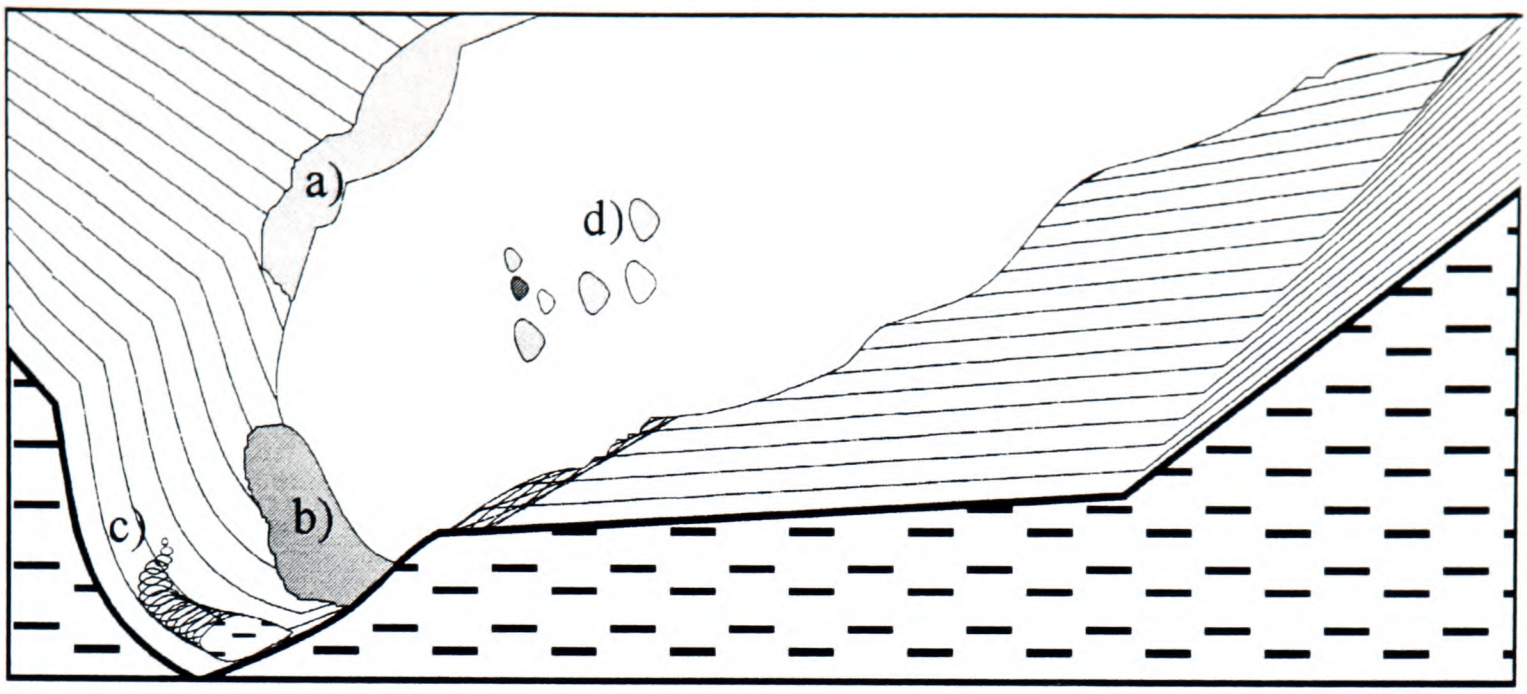


Figure 2-4: Schematic illustration of moraine types; a) lateral moraine, b) ground moraine exposed by retreating glacier, c) end moraine, d) material transported on top of glacier.

Since material transported on top of or within glaciers is not exposed to such great pressure and grinding action, the overall appearance is coarser, with angular clasts dominating (Reheis, 1975). To illustrate differences in grain size for supraglacial and subglacial till, Boulton & Dent (1974) produced mean grain size curves (Figure 2-5). It can be seen that sub-glacial samples render finer material due to the higher physical stresses they have been subject to.

Figure 2-5: Mean grain size curves for sediments of glaciers in the Alps (adapted from Boulton & Dent, 1974).

The influence moraines have on the vegetation is varied. First, at their creation, terminal moraines cover the area where they form with heaps of till, thereby extinguishing all the vegetation previously present. Second, once in place all moraines create a variety of micro-climates. Their slopes can have a variety of effects, for example they can provide shelter from prevailing winds and alter the temperature regime by influencing exposure to direct sunlight. On the ridge tops, however, increased wind action and drought can cause additional stresses for the plants growing there (Lutz, 1930; Vetaas, 1995). Soil development, a factor which is known to influence plant performance, has also been shown to vary in different locations on moraines (Messer, 1988).

Other depositional landforms are created by the action of the drainage network on glacier forelands. Glacio-fluvial sediments (particularly cobbles, gravels and sands) consist of material usually derived from the glacier and further transported by meltwater streams. Due to the movement in water, it is more rounded and more sorted than the primary material of the glaciers. The combination of glacio-fluvial erosion and deposition is crucial to the reorganisation and creation of existing landforms on glacier forelands and is regarded as the fastest form of landform change on recently deglaciated landscapes (Price, 1980). Figure 2-6 gives a small-scale example of the redistribution of fines on the Storbreen foreland. In the Austerdalen study area, a sandur, one of the most striking glacio-fluvial landforms, has developed (Petch & Whittaker, 1997). With its expanse of glacio-fluvial sediments, interlaced with a series of braided meltwater channels (both active and abandoned), it forms a highly dynamic environment.

Figure 2-6: Accumulation of fines after heavy rains (Storbreen foreland, 1995; lens-cap for scale).

Glacial landforms set the stage for the chronosequence approach used on glacier forelands. The retreat of the glacier and intermittent advances create morainic landscapes that allow scientists to estimate time since deglaciation for defined areas on the foreland. Dating techniques include historical sources of moraine positions, biological dating with lichenometry and dendrochronology, and physico-chemical dating, which includes techniques such as the assessment of weathering rates and radiocarbon (^{14}C) dating (Matthews, 1992: 12pp). The large-scale timeframe provided by the glacial process is, however, modified at a smaller scale by a set of processes described in the next section. These change what may actually appear as fairly simple landscapes into mosaics, consisting of areas with different disturbance histories, thereby providing differing potential for successional development (e.g. Petch & Whittaker, 1997).

Periglacial Landforms and Processes

Arctic and alpine areas are characterised not only by glacial landforms and processes but also by periglacial forms and processes. Periglacial conditions are a set of environmental factors related to the non-glacial, cold climate. There are three major

types of periglacial processes and landforms: solifluction, cryoturbation and free rockfaces.

Solifluction is the term given to the slow mass movement of soil (translation: "soil flowing"). A slope of as little as 1-2° is sufficient to cause the topsoil layer (top meter or so, Matthews, 1992: 56) to flow off tilted surfaces (Figure 2-7). The uppermost layer is often supersaturated with water due to thawing of interstitial ice and surface ice and snow (Christiansen & Humlum, 1993). The resulting pattern ("Rasengirlanden" in the German literature = "grass garlands") shows a consistent zonation of plants, generally without vegetation on the flatter upper regions and some plants at the front of the lobes (Zuber, 1968; Archer, Simpson & Macmillan, 1973).

Figure 2-7: Example of solifluction on the Storbreen foreland (1995; see lens cap for scale).

Cryoturbation comprises some of the most widespread frost disturbance processes in arctic/alpine environments. With the formation of ice lenses parallel to the surface, ground is displaced upwards (Harris, 1981). The susceptibility to this **frost heave** is dependent on the grain size of the ground. It increases from near zero in coarse sand (0.6-2.0 mm) to a maximum in fine silt (0.006-0.02 mm), reducing once again to values near zero for heavy clay (< 0.006 mm, Matthews, 1992: 50). A feature which can be found on the Storbreen and Høgvaglbreen forelands is the formation of boulder-cored frost boils, which owe their creation to a particular form of frost heave process

described by Harris & Matthews (1984; Figure 2-8). **Particle-size sorting** produces another class of feature where the substrate is being sorted vertically and horizontally (Washburn, 1979). This sorting takes place due to processes like gravity sorting, frost-heave, preferential removal of fines by thaw water and the migration of fines ahead of a freezing front.

Figure 2-8: Boulder-cored frost boil on Storbreen foreland (1995).

The formation of **patterned ground** is another example of the effect of cryoturbation processes. Polygons are thought to form after frost cracking or desiccation (Price, 1981), whereas circles seem to form in the absence of cracking (Washburn, 1979). Many forms of sorted, patterned ground have been described and studied by different scientists (e.g. Ballantyne & Matthews, 1982; 1983; Harris & Matthews, 1984; Kling, 1998).

Figure 2-9: Sorted polygons on the Nigardsbreen foreland (1995).

The third group of periglacial landforms described here are **free rock faces** and **accumulations of talus**. These landforms exist in areas with extreme potential energy. The weathering of the free rock faces leads to a constant fall of debris that in due course forms a talus at the foot of the rock wall. The boulders making up the bulk of the talus are mostly large (0.2-2 m) and angular, which makes them distinguishable from the more rounded and smaller substrates derived from glacial and fluvial action.

As with glacial processes, the effect of periglacial processes on plants is manifold. In areas subject to cryoturbation, the physical stress exerted on plant roots is most important. This can lead to damage to the roots, which requires the plants to have high rates of regeneration (French, 1988). Whenever plants colonise moving substrates, similar situations exist. Areas with a moving talus or with ground subject to solifluction are two examples for these locations. It has been shown that different adaptations to cope with this kind of stress exist and Schroeter (1926) therefore divided groups of plants into different "strategists" (see Table 2-2).

Table 2-2: Growth forms of plants growing on moving substrate according to Schroeter (1926; after Reisigl & Keller, 1987, p 109)

Strategy	Species example
Plants that produce fine networks of long runners	*Thlaspi rotundifolia*, *Campanula cochlearifolia*, *Geum reptans*
Plants that crawl over the surface	*Arabis alpina*, *Linaria alpina*, *Arenaria biflora*
Plants that work their way through the rubble by producing elongated and thickening shoots	*Oxyria digyna*, *Cryptogramma crispa*
Plants that form a rooting mat on the talus	*Dryas octopetala*, *Saxifraga oppositifolia*, *Gypsophila repens*
Plants that first form steady islands by producing massive cushions with tap roots and an additional network of fine roots	*Ranunculus glacialis*, *Leontodon montanus*, *Saxifraga moschata*

These adaptations allow the plants to persist on moving substrates and by doing so these plants contribute to the stabilisation of this substrate, making it more favourable for plants which cannot cope with the extreme physical stress to their root systems.

Free rock faces represent extreme environments for plants to live. On cloudless days the locations can become very warm (+14.3°C rock temperature at -9.4°C air temperature in 2667 m height; Jaag, 1945). In combination with the exposure to wind and frost the plants must show some adaptations to the reduction of transpiration. Therefore, many succulent species like *Primula auricula* or plants in the genus *Sedum* can be found in these locations.

Other Physical Factors and Processes

The effect **wind** has on the terrain is very well demonstrated by examining the smooth surface of a wind-polished boulder. Additionally to the sand blasting effect, wind also plays a major role in removing and re-depositing silt and fine sand of the top surface layers (Boulton & Dent, 1974). In the winter, wind shifts snow and accumulates it in topographic lee positions. Christiansen & Humlum (1993) showed in the Zackenberg area, Northeast Greenland, that wind rather than insolation controls the position of snow patches. Aeolian deposition is yet another aspect of how wind influences the environment. Baranowski & Pekala (1982) found that the mean annual deposition of both organic and mineral material on a glacier foreland in SW Spitzbergen was 29 g m^{-2}. Plants exhibit some adaptations to strong winds, such as cushion growth-forms, which serve to reduce the frequency of parts being broken off by strong winds. The growth of hairs on the surface of the leaves helps to deal with another influence

wind has on the physiology of plants. These hairs create a calm boundary layer reducing transpiration (Reisigl & Keller, 1987). They are also often silvery thereby increasing the reflection of the sunlight, creating the added benefit of protecting the leaf cells from excessive insolation, which is common in those environments.

As mentioned in the preceding sections the distribution of **snow patches** seems to be controlled by wind action rather than insolation (Christiansen & Humlum, 1993). It seems clear that in areas bordering snow patches, particular geomorphological processes may be enhanced. For example, Thorn (1976) showed that slope wash and solifluction were increased by additional moisture availability. Certain rapid mass movements, such as avalanches and slush-flows, are also commonly associated with melting snow (Washburn, 1979). Snow fields in certain areas tend to last well into the growing season. These locations thus have shorter vegetation periods than open areas. Such areas will only support plant species that complete their life cycle in a very short time (e.g. members of the *Salix herbacea – Polygonum vivparum* snowbed communities, Matthews & Whittaker, 1987; *Soldanella alpina*, Reisigl & Keller, 1987: 72).

During the field seasons of 1995 and 1996, the inter-annual variation of the times by which the snow melted on the Storbreen foreland could be observed directly. Figure 2-10 and Figure 2-11 illustrate this variation and show the differing extent of snow-fields early in the growing seasons.

Figure 2-10: Storbreen foreland on 16.7.95, showing large snow-fields due to late snowmelt.

Figure 2-11: Storbreen foreland on 23.6.96, with small snow patches. Pictures in Figure 2-10 and Figure 2-11 were taken from the same point opposite the glacier foreland.

Once the glacier foreland has been "created" by glacial processes and the speed of the glacier retreat has set the time-frame within which succession can operate, periglacial processes in combination with glacio-fluvial processes, tend to modify the environment, altering the distribution of plants by resetting successional seres or arresting succession in certain states.

Biotic Factors

Life histories and life-forms of plants are thought to have big influences on how well plants do in primary successions on glacier forelands. Raunkiaer (1934) was one of the first to come up with a system to classify a variety of life-forms. The main factor to distinguish between life-forms in his system is the location of the perennating organ. Table 2-3 gives an overview of the recognised life-forms. They can be viewed as adjustments of the plants to their life in certain, sometimes extremely stressful, environments. There is a long standing tradition to view the succession on glacier forelands as progressively advancing from lower plants (bacteria, mosses and lichens) over annuals and shrubs towards mature forests (see also previous section on succession theory, e.g. Chapin III *et al.*, 1994). The data collected in 1995 was used to evaluate this hypothesis for the Nigardsbreen and Storbreen forelands.

Table 2-3: Life-forms according to the system of Raunkiaer (1934; descriptions translated from Ellenberg *et al.*, 1991: 70)

Abbreviation	Description
P	Phanerophytes (trees, potentially higher than 5 m)
N	Nanophanerophytes (shrubs or small trees, between 0.5 m and 5 m)
Z	Woody chamaephytes (German "Zwergstrauch", buds above the soil, rarely more than 0.5 m)
C	Chamaephytes (herbaceous with buds above the soil, buds survive winter in snow cover)
H	Hemicryptophytes (buds on top of or near soil)
G	Geophytes (surviving below ground, often with some sort of storage organs)
T	Therophytes (short lived, surviving unfavourable times as seeds)

Dispersal modes are also important in determining how species will reach the foreland and the way they colonise it. The two main modes found on the glacier forelands in South-Central Norway are wind-dispersed and animal-dispersed species. Wind-dispersed species tend to have small, light-weight seeds with appendages (e.g. *Salix* spp. and *Betula* spp.). Animal-dispersed species on the other hand tend to have heavier seeds, encased in fleshy fruits (e.g. *Vaccinium* spp., *Empetrum hermaphroditum*)

which are eaten by animals. After passage through their digestive system the seeds are deposited, sometimes a long way from the parent plant. Alternatively the seeds of some other species possess structures that provide means for the seed to become attached to the animal vector (hooks, resins, etc.; e.g. *Gallium aparine*, *Carduus* spp.). It is envisaged that the different dispersal modes manifest themselves in distinct distribution patterns and it is one aim of this thesis to test this hypothesis.

Competition is ubiquitous in nature. It occurs at different levels and some of the resources identified as being most highly competed for by plants are light, nutrients and space. If not investigated in controlled experiments the influence of competition is very hard to establish and to unravel from other factors influencing the distribution of plants. The design of this thesis was not suitable to provide other than circumstantial evidence for the occurrence of competition.

The possession of **Mycorrhizal** symbionts is one of the factors that can influence the competitive ability of plant species. It has been shown that the fungal network enables plants to exploit patchily distributed nutrients in soils more efficiently than can their own root system (Hayman & Mosse, 1972; Allen & Allen, 1990). In an environment where patchiness is developed to such a high degree as it is on glacier forelands, this ability is expected to be of great benefit to the plants living there. It is also known that plants actually redistribute assimilates through the mycorrhizal network (Read, Francis & Finlay, 1985). This might enable individuals of pioneer species in sub-optimal sites to keep a supportive "life line" to other individuals that grow in more favourable conditions (patches).

Another effect that has been attributed to mycorrhizal infection is the greater drought resistance of infected plants (Duddridge, Malibari & Read, 1980; Nelson, 1987). It is conceivable that this effect could contribute to a competitive advantage of some species on glacier forelands enabling them to withstand the sometimes drastic changes in water availability (Reisigl & Keller, 1987). As with competition, distinguishing the effects of mycorrhiza on the plants within the glacier forelands studied herein was not part of the investigation, although their possible influence on the patterning of plants has to be kept in mind at the time of the interpretation of the results.

Grazing of sheep and cattle was observed on many of the forelands during the two field seasons (e.g. Figure 2-12 and Figure 2-13). The influence of grazing pressure is manifold. The selective nature of grazing due to preference of the animals for some

plant species or due to the accessibility of certain areas will eventually lead to a change in community composition. Plants not adapted to the continued "clipping" will, over a period of time vanish, whereas plants which can deal with this sort of physical stress will be able to survive. Plants that are avoided by the grazers due to their metabolic contents (alkaloids, etc.) or physical properties (tough, spiky, woody, etc.), may also have a competitive advantage in the community. Grazers have yet another impact on the vegetation. The foraging animals will injure and dislocate plants, causing small-scale disturbances that pose a certain demand on the regeneration potential of the plants.

Human impact in the study areas apart from pastoral activities consists mainly of trampling. On the Nigardsbreen foreland a well-frequented, black-top road leading from the visitor centre outside the foreland to a parking lot near the glacial lake gives easy access to tourists. Generally, there are a number of footpaths on all of the forelands and the compaction of the substrate in combination with enhanced erosion has a considerable influence on the environment. The fact that some of the glacier forelands are the place of ongoing scientific investigations also leads to a rather high level of disturbance by scientists.

Figure 2-12: Sheep grazing on the A-moraine (1750 AD), Nigardsbreen foreland, 1995.

Figure 2-13: Cattle grazing on the Bødalsbreen foreland, 1996.

It also has to be mentioned, that due to landuse changes over the last decades some of the influences and their past extents may not be immediately obvious. For example, it is known that in the Austerdalen area, trees and shrubs from the foreland as well as from its vicinity were used well into the 20th century as timber and firewood for the local production of cheese (R. J. Whittaker, personal communication). Recent changes in the landuse affect both surrounding land (dispersal distances, etc.) and grazing intensities on the foreland, although none of these changes have been quantified and very little is known even at a descriptive level (but see Petch & Whittaker, 1996).

The distinction between the above mentioned factors and their individual influence on the distribution and succession of plant species on glacier forelands is very hard to make. Often, one will deal with a complex of many factors acting together. Unfortunately, the investigation of many of these factors lay outside the scope of this thesis and could not be included other than through casual observations. It is nevertheless clear that these factors influence succession on glacier forelands in a substantial way and that further research to incorporate their role in succession models would be valuable.

Vegetation and Environmental Trends in Succession

The multitude of succession theories produced many hypotheses about the development of vegetation and environmental parameters during primary succession on glacier forelands. The trends for vegetation and environment observed or inferred from previous studies of primary successions on glacier forelands have been summarised by Matthews (1992: chapters 4.1 and 5.2). Most of these trends originate from observations using the chronosequence approach, in which the distance from the glacier snout is used as an estimate for the time the terrain has been deglaciated. Many studies report the successional trend of an increase in **plant cover**, especially during early stages of succession (Crocker & Major, 1955; Palmer & Miller, 1961; Zollitsch, 1969; Ellenberg, 1986). The hypothesis for the development of cover values is, that influenced by the severity of the environment shortly after deglaciation, cover starts to increase slowly. With the amelioration of the environmental conditions by both autogenic and exogenic processes the increase in cover quickens until complete cover is reached. Another generally recognised trend, which has been demonstrated in many studies is the increase in **species diversity** (e.g. Zollitsch, 1969; Elven & Ryvarden, 1975; Vetaas, 1986). This trend usually shows an early peak, which has been attributed to the presence of large numbers of available sites, which provide habitats for both pioneers and later colonisers. The subsequent decrease in diversity is thought to be caused by competition as more species invade the area. The third trend that has received considerable interest is the change of **life-forms** during successions. It could be shown that herbaceous plants are generally followed by shrubs and then trees (e.g. Lüdi, 1945). The description of those life-form changes has added to our understanding of the complexity of glacier foreland ecology. By realising that there is no general development that holds true for every foreland, interest was focused on the diversity of the environmental conditions and the various factors that influence the colonisation of recently deglaciated terrain (e.g. Matthews, 1992). This must be seen as an important development in succession research and this study tries to add to the recognition of the variability of these environments.

The successional development of the environment can be described by **soil depth** development and the change of **soil pH** with time. There have been a score of studies explicitly dealing with the investigation of soil development. They originated mainly from the work of Jenny (1941; 1958) and include studies in the study areas of this thesis

by Messer (1988) and Mellor (1985). In his functional, factorial approach Jenny identifies soil formation as being dependent on various factors, one of which is vegetation. Despite the soil-forming properties of vegetation, plants also require specific soil properties to be able to colonise and survive in an area. This ecological behaviour of plants towards soil pH has been quantified by Ellenberg in his indicator values (see later section) and it is this relationship that will be used to estimate changes in pH (according to the prevailing vegetation) and correlate the estimates with predictions derived from Messer's study.

Contrasting Theoretical Frameworks in Vegetation Science

After having established the concept of succession and the physical and biological factors that influence its development, a short history of two of the main contrasting methodologies applied to succession research is necessary. These frameworks originated in two different geographical regions and developed into separate schools of thought. For practical reasons, I represent the two traditional approaches as seemingly mutually exclusive ways to conduct vegetation research. Scientific research is, however, usually a combination of those traditions and it is thus a simplification to ascribe any research projects exactly to either of the two approaches.

Phytosociology and the Zürich-Montpellier (Braun-Blanquet) School

Phytosociology rests on the assumption that plant communities form recognisable entities with a certain, rather constant composition of plant species, which can be identified by means of classification. In large measures this is consistent with the Clementsian view of vegetation as a "superorganism" (Clements, 1936), a theory that influenced the Continental School of vegetation science for a long time. The development of this view in the light of a highly fragmented, cultured landscape in Central Europe at the beginning of this century is understandable. Vegetation units are defined by more or less discrete boundaries, which can be caused either by abrupt natural changes in geology, pedology or hydrology, or by human influences and management.

The main aim of phytosociology, as it was developed by Braun-Blanquet (e.g. 1928) at the beginning of the 20th century, is the identification of plant communities and

the construction of a global classification system, using theoretical associations (in phytosociology *associations* are the basic units). To this end, the phytosociologist compiles floristic tables of the vegetation under investigation. These floristic tables are derived from field work, which requires that the scientist selects a homogeneous area of what s/he recognises as an existing community in which s/he records the abundance and/or cover of the plant species present in quadrats (sampling areas of rectangular shape, differing in size). This need for *a priori* recognition of the communities that are under investigation has been one major point of criticism of this technique. It means that it can only be used effectively, if the scientist already has both a very sound understanding and a good general knowledge of the vegetation of a certain region.

The second prerequisite, the selection of a homogeneous area within the vegetation unit, poses another problem to the researcher. Scale is very important in this problem, since it is well established that environments as well as the vegetation growing in them are usually heterogeneous mosaics at different levels of scale (Archer, 1990; Remmert, 1991a; Jax, 1994). There is however a method the scientist can use to determine what is called the "minimal area" of a quadrat within which the vegetation will be described adequately. This method consists of a number of vegetation samples in quadrats of ever increasing size (quadrat size is usually doubled at each step) and the determination of species numbers within those samples. When the species numbers are plotted against the quadrat size (species/area curve) the graph usually levels off at some point, indicating the minimal size of the quadrat which can be used to describe this particular sort of vegetation. This minimal area is dependent on the physiognomy and diversity of the vegetation (e.g. Dierßen, 1990: 22).

After collection of the field data, the early methods involved subjective sorting of the floristic tables, by hand. The sorting procedure usually follows different steps of rearranging species and relevés (vegetation samples or stands) in the table (see Kent & Coker, 1996: 245 for a discussion). The result of this rearrangement is a tabular representation of associations of plants, with relevés which are similar in their plant inventory appearing close together in the table.

With the advent of increasing computing power, several more objective sorting procedures were developed, based on matching coefficients or numerical classification (e.g. the computer program TABORD, van der Maarel, Janssen & Louppen, 1978; and see later chapters). But even with these more objective ways of sorting the floristic

tables, it has to be kept in mind that the overall approach and the sampling and the selection of so-called representative areas is highly subjective in nature.

The North American School

It is not surprising that the most vehement critique of the previously described Braun-Blanquet School methodology came from North American scientists, who stand in the tradition of the Gleasonian individualistic view of plant communities (e.g. Egler, 1954). Their theory mainly evolved on a continent with huge expanses of gradually changing environments, where the change between adjacent areas might not be apparent, but where the endpoints of those gradients differ substantially in their floristic composition.

This leads to the approach of ordering vegetation samples. Ordinations (from the German word *Ordnung*) do not require the data to be put into classes, but rather produce an ordered list of samples or species by observing the floristic similarity of vegetation samples according to their species composition. Ordinations form a part of a number of multivariate techniques (see next section) which are used in gradient analysis.

With numerical classification, a field developed where the Zürich-Montpellier (Braun-Blanquet) school and the North American school converge. Numerical classification involves the grouping of quadrats or vegetation samples into classes on the basis of their floristic composition. The main difference between the subjective sorting of the floristic tables and the numerical classification could be seen in the objectivity and reproducibility of the processes involved in the latter. But since there is a whole range of methods used for the exploration and classification of vegetation data (Correspondence Analysis, Principal Component Analysis, classification, etc.) the objectivity only relates to the repeatability of the analyses. The selection of the method of analysis is still a subjective decision made by the scientist and the choice will usually fall on the methodology that results in the best ecological interpretation of the vegetation data (which again is subjective) or the one which is available to the researcher at the time of analysis.

Numerical classification and ordination techniques are most often used as means of data exploration and data reduction. By simplifying the structure of the data and highlighting special relationships and patterns, they are very often the start of further

investigations and research. When using those numerical classifications on vegetation data an important point has to be kept in mind. There is a distinction between natural classes of vegetation, which are mirrored in the data (and which it is desirable to detect by the analysis) and artificial classes which can be forced on data by the nature of the classification method. Because of the danger of imposing artificial classes on non-structured, patternless data, followers of the Gleasonian individualistic view of vegetation will therefore argue against or plead for caution with the use of numerical classification.

Multivariate Numerical Techniques

The methodology developed in connection with gradient analysis is based on multivariate numerical techniques. They have been widely used (e.g. Birks & Austin, 1992) and provide valuable insights into the change and development of plant assemblages. In this thesis they are used in the traditional way of reducing the multivariate space to a manageable number of ecologically relevant variables.

The Historical Context

With the growth of the two schools of thought described in the previous section, two approaches to the analysis of vegetation data have been developed. Classification, the first of them, is closely related to the disciplines of taxonomy and systematics and has its roots in the very first attempts of naturalists to put nature into defined categories (Linnaeus, 1758). It's main aim is to create more or less "natural" entities which are used to define different types of plant or animal communities. In central Europe, the concept of plant sociology was developed as a classification technique mainly by the work of Braun-Blanquet (1926; 1964). It has been adapted by many followers all over the world (Du Rietz, 1930; Tüxen & Ellenberg, 1937; Oberdorfer, 1957; Hill, Bunce & Shaw, 1975; Matuszkiewicz, Matuszkiewicz & Matuszkiewicz, 1995) and is still being used in its modern equivalent, numerical classification performed with the help of computer programmes like TWINSPAN (Hill, 1979). The use of computerised analytical methods was seen to be of paramount importance in the context of objective sampling, which is being used increasingly as a modification of the subjective sampling strategies of the early plant sociologists.

The use of ordination in ecology, the second approach, was mainly developed by North American ecologists (Whittaker & Niering, 1975). As compared to classification, ordination does not presuppose discrete boundaries around plant or animal communities, but rather views their assemblages as more or less fortuitous juxtapositions influenced by the arrangement of individual species along environmental gradients. This method also has modern analogues in computer programs based on the principles of ordination, designed to handle large amounts of data (ter Braak, 1987-1992; McCune & Mefford, 1997).

The historical background and further development of these techniques in their specific ideological environments have led to the preference for one or the other analytical method by certain groups of researchers. This, however, masks the conceptual differences between both modern approaches. Classification programs like TWINSPAN (Hill, 1979) are written to produce classes and they will do so, even if there are no natural classes present in the data. The question remaining is how meaningful the resulting classes are. The use of classifications is nevertheless of great value when they accompany ordinations, which allow for classes but don't impose them. In the end there is still the need for the scientist's experience of the ecology of his research area which will enable him to judge the results obtained by the different techniques in terms of their validity and ecological interpretability.

Classification Techniques

Computer programs such as TWINSPAN (Hill, 1979), MVSP (Kovach, 1993) or PC-ORD (McCune & Mefford, 1997) allow different forms of classifications. One purpose of using a classification program is to create classes, which represent groups of samples or sites with similar vegetation. Conceptually, classification is considerably easier to understand than ordination. It forms part of our every day life and we are usually aware that classifications can be arbitrary though helpful. Most geographical applications employ hierarchical forms of classification. A hierarchical classification is one which branches like a tree so that at one end of the classification all samples are joined in one all-inclusive cluster, whereas at the other end they are split into single samples. There are two different way to arrive at this tree-like structure of ordered sites.

An agglomerative classification is one that starts with all the sites considered as separate clusters. The analysis begins by joining the two most similar clusters together to form a new composite cluster of two sites. The similarities of each cluster pair are again considered, and the two most similar are joined together and so on, until all are joined together. Hill (1975) points out that the outcome of agglomerative methods can be strongly dependant on the way in which the sites are combined at the beginning of the analysis. He therefore favours the second approach, which comprises divisive methods (see also Gauch Jr., 1982; Greig-Smith, 1983; Kent & Coker, 1996). In a divisive classification, all sites are considered as forming a single cluster and then split into two groups - not necessarily of equal size - which are the two most dissimilar groups that can be identified. This process continues step by step, group by group, until ultimately, all sites are separated out. Noy-Meir (1973) established that divisive methods use the overall structure of the data at the beginning of the analysis, which leads to a relative insensitivity of the higher levels of the hierarchy to the details of the clustering at the lower levels.

Hill (1975: 598) identifies 4 points that should be satisfied by a successful classification method. They are ecological interpretability, open-endedness (which is to say that new stands should be capable of being assigned to their correct place in the resulting classification without necessitating further calculations), computational efficiency and avoidance of serious misclassification errors. At the time he proposed that TWINSPAN satisfied all of the four points and was therefore the best classification method available for use in vegetation studies. This remains the consensus today (e.g. see Jongman, ter Braak & van Tongeren, 1995; Kent & Coker, 1996).

Ordination Techniques

Since many questions in ecology are very complex and multidimensional in nature (there are usually a whole array of factors influencing the patterns and processes of plant distributions) a reduction in the dimensionality of the problems under investigation almost always leads to a better understanding of the observed phenomena. Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) are all members of a group of ordination techniques performing such a reduction of the dimensionality of ecological data. This

reduction facilitates the interpretation of species arrangements and the analysis of the relationship between environmental factors and community patterns. Ordination techniques order the sites along theoretical axes depending on their species composition and vice versa. The main result of an ordination is an ordination diagram in which species and sites are represented as points in a two dimensional space. By the properties of the ordination, sites with similar species composition are placed close together in the diagram. Likewise species with similar environmental behaviour will be closer together than species with differing environmental behaviour. The interpretation of the ordination diagram is therefore usually the first step in trying to understand the influence of environmental factors on the composition of plant or animal communities.

There are two different classes of ordination techniques. The first class, indirect gradient analysis (including ordination techniques such as CA and DCA), is in essence an exploratory tool to analyse and try to detect underlying structures of the species data under investigation without the explicit use of environmental data during the procedure of the ordination analysis (Whittaker, 1967). Any available environmental data can later be used in interpreting the resulting ordination diagram, although such data do not influence the arrangement of the sites and species on the ordination axes.

The second class, direct gradient analysis (including ordination techniques such as CCA and DCCA), is from the outset concerned with the influence that specific environmental factors might have on the species and their distribution. It therefore is closely related to techniques such as regression analysis or calibration (Jongman, ter Braak & van Tongeren, 1995).

There are practical reasons why indirect gradient analyses have been widely used by many scientists (Whittaker, 1987; Eilertsen *et al.*, 1990; van Groenewoud, 1992; Zhang & Oxley, 1994; Kindscher & Wells, 1995; Porembski, Brown & Barthlott, 1995; Johnson, 1996). In contrast to the multitude of environmental variables which might (or might not) influence the distribution of plant species and the difficulties of measuring them in a standardised way, presence, absence or abundance of species of plants is easily recorded (e.g. Kent & Coker, 1996). Since direct gradient analyses depend on the use of environmental data collected in the field, they work best when the scientist already has a good understanding of the ecology of the area s/he researches. It is also helped by strong gradients, like the ones present in the original works of Whittaker (1967) and Whittaker & Niering (1975), to enable the scientist to select and measure the

most important environmental factors. Direct gradient analysis is widely used in ecology, limnology, palaeolimnology and other areas of the sciences (Birks & Austin, 1992). Quite a few studies combine the two forms of gradient analysis thereby making the point that it is useful to use different techniques for slightly different aspects of research projects (e.g. Whittaker, 1989; Hill & Whittaker, 1992; Palmer, 1993; Charman & Pollard, 1995; Schaefer & Messier, 1995; ter Braak, 1995).

Ellenberg's Indicator Values

The next aspect of the thesis also originates from the continental phytosociological school. Time and money constraints often determine the amount of environmental data vegetation scientist can gather for a study site. Ellenberg indicator values may be a way of eliminating these constraints, by enabling the scientist to estimate the average values of some important environmental factors from the vegetation (see Table 2-4). These indicator values, which originate from the phytosociological work of Heinz Ellenberg (1974), are used in this thesis in ordinations to evaluate their usefulness for describing average environmental conditions of six environmental factors of a site with the help of its vegetation cover. By evaluating the strength of the correlation between the average Ellenberg indicator values for the site and the observed values of the environmental factors, their power for the use on glacier forelands in South-Central Norway is estimated. In 1974 Ellenberg published the first edition of his indicator values of vascular plants in Central Europe (Ellenberg, 1974). They have since been in use mainly by continental phytosociologists to characterise ecological parameters of specific plant communities or individual vegetation stands. In the introduction to the third edition of the "Indicator Values of Plants in Central Europe" Ellenberg *et al.* (1991: 5) defend the utility of the indicator values by stating that they were mainly conceived to get indications about the magnitudes of directly acting environmental factors or to get some ideas about rough scales of temporal changes. In this latest edition of indicator values, 2726 species (and varieties) of vascular plants are covered, for which Ellenberg and his co-authors compiled values for three climate factors (light, temperature and continentality), three soil factors (moisture, reaction and nitrogen), and some other indicator values, such as tolerance to salts in the soil, appearance in red lists, abundance, etc.

The creation of this extensive list of indicator values is mainly based on the great field experience of the authors involved. For the assignment of the values to the different species the main guideline is the definition of the values in terms of the ecological behaviour of the respective species towards the different factors (see Table 2-4). For the original, more comprehensive descriptions see Ellenberg *et al.* (1991: 67).

Table 2-4: The six indicator values used in this thesis with an abbreviated description of the ecological behaviour of the plants (after Ellenberg, 1986: 98)

Original letter	Anglicised letter	Description of the Ellenberg indicator value
L	L	Light value, i.e. the occurrence in the continuum of very little light (1) to unrestricted light in open land (9).
T	T	Temperature value, i.e. the occurrence in the continuum of changing temperatures from the arctic or the alpine zone (1) to the lowlands with mediterranean climate (9).
K	C	Continentality value, i.e. the occurrence in the continuum of continentality from the Atlantic coast (1) to the centre of Eurasia (9).
F	M	Moisture value, i.e. the occurrence from shallow-soiled, dry cliffs (1) to wet, boggy soils (9). Three additional values (10-12) correspond to occurrence in shallow to deep water.
R	R	Reaction value, i.e. occurrence in the continuum from extremely acidic (1) to alkaline, calcareous substrates (9).
N	N	Nitrogen value, i.e. mean occurrence in areas with very poor (1) to excessive (9) input of mineral nitrogen (NH_4 and NO_3)

Ellenberg *et al.* (1991) stress that the assignment of the indicator values has always been influenced by subjective decisions by Ellenberg or other ecologists/vegetation scientists involved in their creation, but that those scientists possess a lot of field experience and that, where possible, measurements and/or distribution data were used to compliment the personal experience of the researchers. For example, direct measurements of soil pH and their correlation to the mean reaction indicator value are quite common and render regression equations which allow direct measurements to be translated into the appropriate indicator values (e.g. Rodenkirchen, 1982; from Ellenberg *et al.*, 1991: 30).

The subjectivity of the method led to cautions or critical comments, e.g. Wiegleb (1986) refers to the set of indicator values as a "set of unproven hypothesis". Other authors, however, have offered critical acclaim, stressing the value of the Ellenberg indicator values in situations where measurements of environmental variables are not feasible due to time or money constraints, and where an evaluation of the site in terms of its environmental conditions nevertheless is required or wished for (Kowarik &

Seidling, 1989). Kowarik & Seidling (1989) therefore think that Ellenberg's indicator values can be very helpful in situations where their use is valid and useful.

A critical point Ellenberg *et al.* (1991) emphasise is that users should be careful not to mix up the "ecological behaviour" of plants, which the indicator values aim to characterise with the ecological "requirements" of those plants, which can only be investigated with physiological experiments in controlled conditions. Another limitation is the regional restriction of the indicator values to central Europe (Ellenberg *et al.*, 1991: 11). This is of some interest herein, as the study area lies at the north-western border of the original area for which the indicator values were produced. It was one aim of this research to assess their validity and usefulness in northern Europe, by using them in this study area and carefully interpreting the results, using the experience on the ecological behaviour of the plants which was gained during the two field seasons. There have been other attempts to widen the geographical range for which Ellenberg indicator values can be used. In the ECOFACT research series a list of Ellenberg indicator values for the whole British and Irish Flora was established (Firbank, 2000). The advantage of using numbers in qualifying ecological behaviour of plant species lies in the possibility of calculating averages, spectra and other descriptive statistics to describe such vegetation stands and classify their ecological behaviour. However, it has to be kept in mind that the calculation of average indicator values is mathematically problematic, because they are calculated from ordinal values which should not, as a rule, be averaged.

For the use of his indicator values in this specific study the most challenging note of caution comes from Ellenberg himself. He states that pioneers or early successional species may behave in a completely different way from that suggested by their published indicator values (Ellenberg *et al.*, 1991: 48). This is due to the fact that the indicator values describe the ecological behaviour of plant species after prolonged coexistence and competition with other plant species in the landscape. Since, by the nature of succession, the plants involved in re-colonising recently deglaciated terrain do not experience the same competition with other plant species their ecological behaviour might be expected to differ from that of the same species growing in mature-phase vegetation types. Despite the above cautions it was nevertheless decided to investigate the usefulness of Ellenberg's indicator values in a combined approach of gradient analysis and phytosociological research.

The value of Ellenberg indicator values in combination with ordination has been shown by Persson (1981). He used Ellenberg indicator values successfully to interpret ordinations of data from Swedish park-meadow vegetation. It is the incorporation of this additional information about the ecological behaviour of the plants from the Ellenberg indicator values and its influence on the interpretation of ordination diagrams, which will be investigated and explored in this thesis.

Pattern Analysis and Spatial Statistics

The distribution of vegetation is inherently clumped at different scales. The existence of these kinds of patterns (pattern is here defined as: non-random heterogeneity in vegetation which exhibits a certain periodicity) has led researchers to investigate the non-randomness of the distribution of plants in ecology and biogeography (e.g. Anderson, 1967; Carpenter & Chaney, 1983; Galiano, 1983; Usher, 1983; Gibson & Greig-Smith, 1986; Dale & MacIsaac, 1989; Ver Hoef & Glenn-Lewin, 1989; Dale, 1990; Dale & Blundon, 1990; Argyropoulou, Stamou & Iatrou, 1994; Dale, 1999). Research has focused on first, the scale of different patterns, i.e. the average size of patches with high and low densities, and second, their intensities, i.e. the difference between the average patch and gap density. By studying the vegetation patterns and their changes over time it is the expectation that important processes controlling ecosystem development can be identified (e.g. Watt, 1947). This is another aspect of glacier foreland succession that has not been addressed in any great detail. By investigating the development of distribution patterns over time it was envisaged to gain some indication of the processes involved in the colonisation of forelands.

Spatial Indices

Spatial properties of species distributions can be described in their most basic way by the area/perimeter index (e.g. area being the number of 0.25m² cells and perimeter the number of 0.5 m long border segments of a given area). The index can be used for different species at the same location to assess dominance. Furthermore, it allows for the direct comparison of the fragmentation of the distribution of a species in a given area. When the values are compared for the same species in blocks of increasing age, any

change of these indices during successions can be used to estimate underlying ecological and geophysical processes.

Spatial Autocorrelation

For the analysis of spatial data, Palmer (1988) points out that:

> .."quadrats should be spatially independent if they are to be considered statistically valid replicates."
>
> **(Palmer, 1988: 99)**

There are, however, indications that vegetation data exhibits spatial dependence at various levels of scale, resulting in distribution patterns different from the ones that would be expected if the distribution were random. For example, areas close to each other can be more similar floristically than areas further apart. The reason for this can be found in dispersal strategies of plants where seeds or propagules will be present in higher availability around the parent plant than further away from it. Similarly, biological processes like competition and allelopathy can influence spacing between individuals of the same or different species. Another reason for small-scale patterning of the vegetation can be found in small-scale variation of the environment (e.g. Kershaw & Looney, 1985; Matthews, 1992). The analysis of spatial dependence is therefore not only important to avoid improper use of statistics on vegetation data, but it can also give us interesting information about the patterns of different vegetation types. Autocorrelation is the propensity for data values to be similar to surrounding data values. It therefore represents a way of analysing spatial dependence. In a raster image, the autocorrelation statistic describes the degree to which values in any cell will be similar to the cells surrounding it. A common measure of autocorrelation is Moran's I, with a range from -1 to 1 (Eastman, 1987-1995). A value close to 1 indicates a smooth surface, with each cell containing a value very similar to the cell next to it. A value close to -1 indicates a very rough or fractured surface, with each cell quite different from its neighbours. In parts of this thesis Moran's I values are used to evaluate the spatial dependence of plant communities at different successional stages. If the processes outlined above change in importance over time I would expect a corresponding change of the associated measures of spatial dependence. Other ways of evaluating spatial autocorrelation for nominal data is the calculation of join counts (Sokal & Oden, 1978)

or percentage of similar neighbouring cells (Cortina Borja, 1998). Due to its ease of calculation this was used for the calculation of the autocorrelation measure used in the logistic regression models.

Fractal Dimension

Fractal geometry is another way of analysing the spatial dependence of vegetation data and of assessing the homogeneity and heterogeneity of vegetated areas at varying scales. The techniques now used for the analysis of variation in vegetation have been developed in geostatistics by commercial geologists (Clark, 1979) where they were used to predict the amount of ore in unsampled locations. They have since been used successfully by ecologists to describe spatial patterns of plant communities or to measure complexities of environmental gradients (e.g. Phillips, 1985; Palmer, 1988; De Cola, 1989; Palmer & Dixon, 1990; Gautestad & Mysterud, 1994). For linear transects, the principal geostatistical tool is the semivariogram. It represents graphically the summary of the variance of a dependent variable (e.g. species richness, DCA-Axis scores, etc.) in units of semivariance, as a function of scale (where both axes are log-transformed). The fractal dimension D can be calculated from the slope m of the double logarithmic plot of the semivariogram by the function:

$$D = \frac{(4-m)}{2} \qquad \text{Equation 2-1}$$

The use of this approach for data in a plane is somewhat restricted by the (often flawed) assumption that the variance is isotropic, meaning that it varies similarly in all directions (Dr. M. Palmer, personal communication). In the present study, the working hypothesis opposes this assumption: variance is expected to be anisotropic, which means it is influenced by the orientation of the plot in relation to the glacier foreland. Factors like time since deglaciation, temperature gradients brought about by cold glacier winds, or nitrogen and pH gradients, will increase the variance generally in relation to the long axis of the glacial valley.

Virkkala (1993) used another approach to calculate the fractal dimension of the distribution patterns of passerine bird species in Finland . He counted the presence of each species within a 160 by 160 km block at increasing scales (10 x 10 km to 80 x 80 km). The fractal dimension was then estimated by the slope of the regression line between the log of scale and the log of the inhabited squares. Gautestad & Mysterud

(1994) point out a problem in the calculation of Virkkala's *D*. They show that his approach is flawed with the assumption that a fractal Dimension of $D = 2$ means that all cells are occupied by the species (see Virkkala, 1993: 220). Since $D = 1 - b$, all distribution patterns with the same proportion of occupied cells in different scales of resolution (i.e. the same slope for log number of cells - log scale of resolution) will have the same fractal dimension *D*.

The use of pattern analysis in successional contexts is in identifying periodicities of high or low densities in the distribution of species and relating them to environmental influences (allogenic or environmentally determined patterns; see Greig-Smith, 1961) or life history traits of the plant species involved (autogenic patterns; Watt, 1947; Anderson, 1967). Kershaw (1957) and Greig-Smith (1961) put forward a hypothesis in which the pattern during primary succession was expected to intensify early on at the scale of primary establishment. This was thought to reflect the growth of individual plants. Later in the succession, the coalescence of patches was expected to lead to the loss of some scales of pattern while others may appear with the establishment of later-colonising plants. They finally proposed, that in approaching a "climax" vegetation, the intensity of the patterns will decrease and become more and more irregular due to the senescence and break-up of patches. Dale & Blundon (1990) found partial support for this hypothesis with their data from the Mt. Robson moraines. In this thesis the analysis of pattern is to be used to test these hypotheses for the study sites in Norway. Greig-Smith's (1961) hypothesis, however, appears to be too general in its prediction of pattern development during primary succession. In this thesis the influence of dispersal mechanisms on the pattern development of certain plants during primary succession on glacier forelands is to be investigated.

Environmental Modelling of Succession

Models are representations of real objects, systems or processes in varying degrees of realism, using a variety of media and procedures (e.g. trains of amateur modellers, animal models in clinical research, drawings, paintings, etc.). In its mathematical form modelling is a means of representing natural phenomena in a simple equation, which is designed to facilitate prediction and calculation (Brown & Rothery, 1993: 1).

For practical purposes different forms of models can be distinguished (for examples for different forms of models see Brown & Rothery, 1993). **Deterministic** and **stochastic** models differ in that, given a certain input, deterministic models always produce the same output, whereas stochastic models contain a randomly varying component. This random element represents stochastic, non-controllable influences, which cannot be predicted with any certainty in any individual case. Deterministic models are therefore usually the simpler versions of more complicated stochastic models. Another way models can be arranged is their classification as **descriptive** or **mechanistic**. Both forms of models are opposing endpoints of a continuum. Almost all models can be thought of as being descriptive. It is the level of concern about the mechanisms that lead to processes or relations between parameters, which determines the distinction between the two forms of models. Finally there is a distinction between **dynamic** and **non-dynamic** models. Dynamic models include models that are concerned with processes unfolding in time, whereas non-dynamic models describe a relationship at a fixed time. As with spatial phenomena scale plays a paramount role in the determination of the dynamism of the system. There are usually different time scales at which a system can vary (short term, e.g. animal movements, mid term, e.g. climatic variation, long term, e.g. evolutionary development). The focus on a certain time scale determines if a system might be regarded as being dynamic or non-dynamic.

Approaches used in the environmental sciences to model spatial distributions of organisms include the use of regressions to fit organism responses to one or more biotic and/or abiotic variables (e.g. O'Brien, 1998; Ostendorf & Reynolds, 1998), the use of GIS often combined with regression analyses (Ostendorf, 1998; Ostendorf, Mayr & Tappeiner, 1998; Ostendorf *et al.*, 1998) and the more mechanistic cellular automaton approach (e.g. Silvertown *et al.*, 1992; Clarke & Olsen, 1995; Ruxton, 1996).

A consideration for the proper use of Generalised Linear Modelling (GLM) is the normality of the data. When this assumption is satisfied, GLMs have been used successfully on quantitative data (e.g. Margules, Nicholls & Austin, 1987; Guisan, Theurillat & Kienast, 1998). But Austin (1976) reported non-normal vegetation response curves as early as 1976. Bio, Alkemade & Barendregt (1998) investigated the influence that more complex response shapes can have on the goodness-of-fit and significance of various models. In their study on wetland vegetation in The Netherlands they found that Generalised Additive Modelling (GAM), an extension of GLM, is a

useful and practical technique for improving current regression-based vegetation models, by allowing both for linear and alternative, complex response shapes.

For the special case where binary data (e.g. presence/absence) provides the source for the regression modelling, the data distribution is binomial and the log odds form of the logistic-binomial model for proportions (also called logit-model) can be used (Brown & Rothery, 1993: 130; Jongman, ter Braak & van Tongeren, 1995: 43). The result of a logit-regression is the probability of an event happening to the probability of it not happening. One example of a study where this method has been used successfully is Smith's (1994) investigation into the distribution of *Oxyria digyna*.

In connection with the development of modelling techniques the appearance and development of bootstrapping methods over the last 20 years is also important. First introduced by Efron (1979), they are mainly used as ways to estimate the statistical distributions of parameters when classical estimates are not available. They estimate those distributions by re-sampling (with replacement) from a reference sample and calculating the desired statistic for each of the re-sampled data sets (see Efron & Tibshirani, 1986 for review and examples). The empirically derived distribution of the parameters from the calculated statistic is a good estimate of the distribution of the original parameter. Due to their high demand on computer time bootstrapping methods are only slowly becoming more frequently used (e.g. Lamarre, Townshend & Shah, 1992; Wilson & Whittaker, 1995).

To develop mathematical models a number of ways to use original data exist. A well known and tested way of developing models is to use parts of the original data sets for the calibration of the model (data partitioning; see Fielding & Bell, 1997 Table 1 for list of methods) although doubts about the validity of this approach have been raised (Chatfield, 1995). The rest of the data set, which was not used in the calibration of the model, can subsequently be used to evaluate the performance of the model, by comparing predicted values of occurrence with observed values of the original data set. Since the size of the proportion of the original data set used as a training set influences the accuracy of the model, different data partitioning methods will lead to either low or high estimates of the error probabilities (Fielding & Bell, 1997: 39). The optimal way of calibrating a model, however, is to use the complete data set and collect new data for the validation of the model.

Estimation of the accuracy of the model is usually done using prediction errors. Following Fielding & Bells (1997) classification they can be placed into two categories. "Algorithmic" errors, which stem from the classification algorithm and the data-gathering process and "biotic" errors, which are related to the ecology of the organism under investigation. Many different error measures for the assessment of the accuracy of models have been devised. Fielding and Bell (1997) give an excellent overview of the available methods for the assessment of prediction errors. The calculation of prediction errors and the estimation of the performance of the model enables the scientist to make some inferences about the quality of the data entering the model. Good prediction rates will confirm that the parameters selected for the model are sufficient to predict the distribution of the response variable reasonably well. But besides this more mechanistically oriented analysis of the performance of the model, some of the more specific error measures allow the scientist to evaluate theories about processes and patterns in different environments.

Specific Objectives and Rationale

The study of glacier forelands has long been recognised as a very good way, if not *the* best way (Ellenberg, 1986: 581), to examine successional processes. The well known case studies from Glacier Bay, Alaska and South-Central Norway are particularly good examples of successful studies of this type (Matthews & Whittaker, 1987; Walker & Chapin III, 1987; Chapin III *et al.*, 1994; Fastie, 1995). The reasons why scientists regard those areas in front of glaciers as excellent natural laboratories are as follows (Matthews, 1992). Firstly, they are fairly contained in their spatial extent; secondly, they usually provide a series of moraines which delineate substrates of different age, thereby enabling a chronosequence approach to study successions; and thirdly, their location in arctic or alpine environments restricts the diversity of the plant species involved to a manageable number.

The first focus of this study lies in the development of successional trends for the vegetation and the physical environment. Description and analysis of cover, species diversity and life-form changes as well as soil depth and pH changes is intended to improve our knowledge about these trends. In order to make direct comparisons

between a low- and a high-altitude glacier foreland, data were gathered from Nigardsbreen (low-altitude) and Storbreen (high-altitude) forelands.

J. A. Matthews and R. J. Whittaker added another dimension to the previous, more descriptive studies when they used numerical methods to analyse the plant communities on a specific glacier foreland in South-Central Norway (Storbreen) and correlated the identified plant communities with a set of recorded environmental factors (Matthews, 1978; 1979a; 1979b; 1979c; Whittaker, 1989; 1991; 1993). Apart from their multivariate analyses, however, the potential for detailed analysis of vegetation-environment relationships and spatial patterns in primary succession has yet to be realised. It was one objective of this study to investigate the general validity of the postulated influence of time and associated environmental factors on the successional development of plant communities in these areas (cf. Matthews & Whittaker, 1987 on the Storbreen foreland). Several studies of succession on glacier forelands are limited by the chosen scale, which is based on isolated quadrats (Matthews, 1978; 1979a; 1979b; 1979c; Walker & Chapin III, 1987; Whittaker, 1989; 1991; 1993; Chapin III *et al.*, 1994). To be able to investigate biogeographical and other small-scale processes and the influence that they have on the development of patterns during primary successions on glacier forelands, the scale of the investigation and the sampling design needed to be altered. In 1995 therefore a regular grid sampling approach at two different scales (100m between sampling plots and 10m between sampling plots) was used on two of the forelands (Nigardsbreen and Storbreen). Large-scale sampling transects along the time gradient were used to investigate the major influence of time since deglaciation on the development of plant communities. The small-scale data were collected in homogeneous areas of different age and it was expected that if age was a major correlate of the vegetation on these forelands similarity of the vegetation from terrains of similar ages would be detected by ordination and cluster analysis.

Average Ellenberg indicator values, calculated to describe the environmental conditions of the sampling quadrats, are one of the new methods used in this thesis. They are used in ordinations of the data to facilitate plant-environment correlations for factors otherwise difficult to measure in the field (Ellenberg, 1974; Persson, 1981). This comes at a time when divisions between the Central European school of phytosociology and the Anglo-North American school of gradient analysis seem to be becoming less important (Kent *et al.*, 1997). Hence, the use of Ellenberg indicator values in ordinations

is an attempt to evaluate their usefulness and compatibility with the gradient analysis approach. The results will hopefully convince the reader of the importance and viability of both approaches (with their respective limitations kept in mind).

By including Nigardsbreen, a foreland previously not investigated in detail, this study also adds new information on succession and its general development in this region of South-Central Norway. The data from this sampling design could also be used to test the hypothesis that spatial heterogeneity masks the clear temporal gradient that might be expected from previous studies.

With the analysis of the 1995 data, new questions about the spatial pattern of the vegetation development emerged. It was decided that a change of the sampling design for 1996 to a grid-block sampling (see later chapters for explanation), would provide a better basis for the use of spatial statistical methods for the investigation of these questions. With the advent of fractal geometry and other spatial statistical methods in ecology (Palmer, 1988), new sets of analytical tools are now available that have been used only indirectly on the spatial aspect of successions on glacier forelands (Matthews, 1992: 169). Their use, however, enables us to address questions about the development of spatial patterns during succession and relate them to biogeographical processes. For example, one hypothesis tested was whether the fractal dimension of the patterns of individual species during primary succession would be different for species with different modes of dispersal. Animal-dispersed species were hypothesised to start from individual patches which, over time, coalesce into larger areas, thereby reducing the fractal dimension over time. Wind-dispersed species on the contrary, are hypothesised to advance in a more uniform front, starting with a low fractal dimension and breaking up into smaller fragments due to competition or other factors, thereby increasing their fractal dimension over time. The different pattern development on low- and high-altitude forelands was another focus of interest. Other spatial statistical tools and a variety of indices were used in addition to the fractal analysis.

Finally, a more practical aspect of this work is the estimation of the sampling effort scientists have to exert on glacier forelands to describe adequately the plant communities in such environments. To this end logit models were employed to investigate the relationships of dominant woody plant species with the diversity of other dominant woody species within the same quadrats, the environment and geographical location variables. By assessing the accuracy of the predicted distribution maps of those

models, estimates of the minimal sampling effort have been made. Investigation in the ways of producing different logit models using forced entry of selected variables and stepwise selection of variables were also used to highlight some potential problems with these approaches.

Within the general aim of contributing to the understanding of vegetation succession the objectives of this thesis may be summarised as follows:

- To investigate cover, plant diversity, plant life-forms, soil depth and pH of quadrats along the time gradient on the Nigardsbreen and Storbreen forelands and compare with results from literature.
- To demonstrate the influence of age related factors on the vegetation development on Nigardsbreen and Storbreen forelands.
- To test the hypothesis that physical factors such as nitrogen availability, light, temperature, moisture and soil-pH change predictably over time, by using Ellenberg indicator values in ordinations for data from Nigardsbreen and Storbreen forelands.
- To investigate the influence of dispersal mode on pattern development of animal- and wind-dispersed woody species, using spatial statistics.
- To test the hypothesis that low- and high-altitude forelands differ in the pattern development of their woody species.
- To develop predictive models of the dependence of the distribution of selected woody species on the woody species richness of the area and on an environmental favourability index.
- To estimate how much of an area has to be sampled to adequately describe the woody plant communities of such an environment.
- To test the hypothesis that the amount of unoccupied safe sites, as estimated by false positive predictions of the logit-regression model, will decrease with increasing time since deglaciation.

3. The Study Areas

"Knowledge is little; to know the right context is much, to know the right spot is everything."

- HUGO VON HOFMANNSTHAL, *The Book of Friends,* 1922

In this study, three glacier forelands in the Jostedalen and two glacier forelands in the Jotunheimen regions of South-Central Norway, were selected as study areas (Figure 3-1). Other research has shown that regional differences occur in successions on glacier forelands (e.g. Matthews, 1992: 221). By investigating three low- and two high-altitude forelands, it should be possible to take into account any fundamental differences in the successions in the region. That these forelands have been the destination of the annual Jotunheimen Research Expeditions for 20 years also contributed to their selection. Over this time an extensive body of supporting literature on varying aspects of these environments has been built up (Matthews, 1996b).

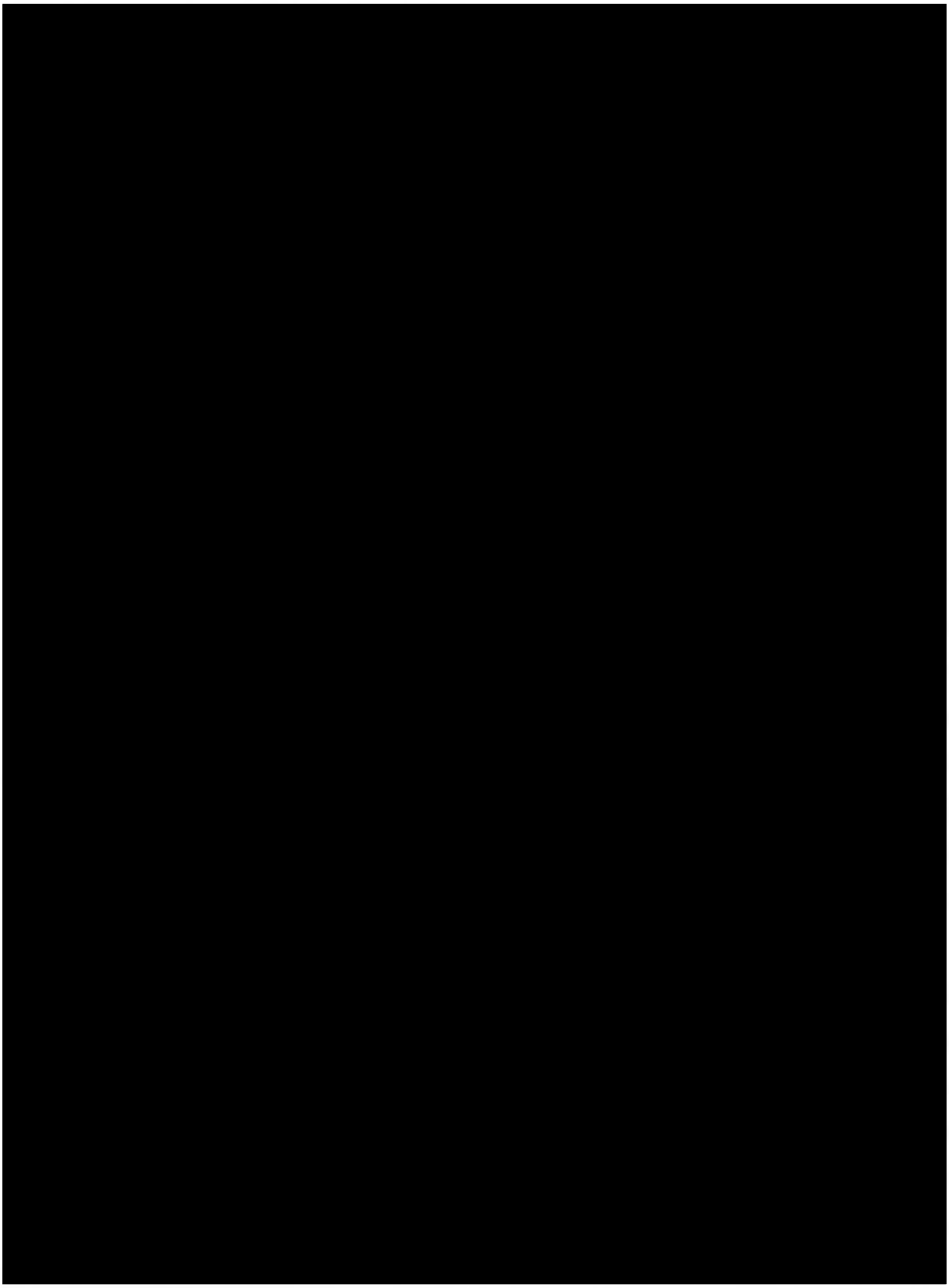


Figure 3-1: Location of the five study sites in South-Central Norway.

Low-Altitude Glaciers

The three low-altitude glacier forelands are all situated in front of outlet glaciers off the Jostedalsbreen ice cap (Figure 3-1). Their climate, physical environment and vegetation are described in more detail below.

Nigardsbreen (Figure 3-3)

Nigardsbreen is an outlet glacier on the eastern side of the Jostedalsbreen ice cap in South-Central Norway (long. 7°15' E, lat. 61°40' N, see Figure 3-1). The foreland covers an area of about 3.2 km^2 and an elevational range from 250 m to 355 m a.s.l. The estimated annual rainfall is 1100 mm/year, and the mean annual temperature for the foreland is about +3.66°C (Messer, 1988).

The bedrock in the Jostedals area is predominantly Precambrian gneiss with a few outcrops of ultrabasic rocks (Sigmond, Gustavson & Roberts, 1984). The moraine sequences found on the foreland have been extensively investigated and lichenometrically dated by Bickerton & Matthews (1992; 1993; Figure 3-2). There are 18 recognised moraine ridges on the south-western side of the foreland and 19 on the north-eastern side, typically 2-5 m high. Their estimated ages range from 1750 AD (moraine A delineates the "Little Ice Age" maximal extent of the glacier) to 1940 AD along the sides of the glacial lake (moraine X) and they are thought to have been dated to an accuracy of 10% (Bickerton & Matthews, 1992).

The foreland lies below the sub-alpine *Betula pubescens* treeline and is covered by a vegetation mosaic consisting of sub-alpine heath species as well as pre-alpine *Alnus glutinosa* forest fragments. Parts of the foreland have been and continue to be used as grazing areas for sheep and this is known to influence the vegetation development (see Matthews, 1992: 152). In addition to the life-stock grazing by native wild animals including reindeer, voles and lemmings has to be considered. This is true for all the other forelands in the study.

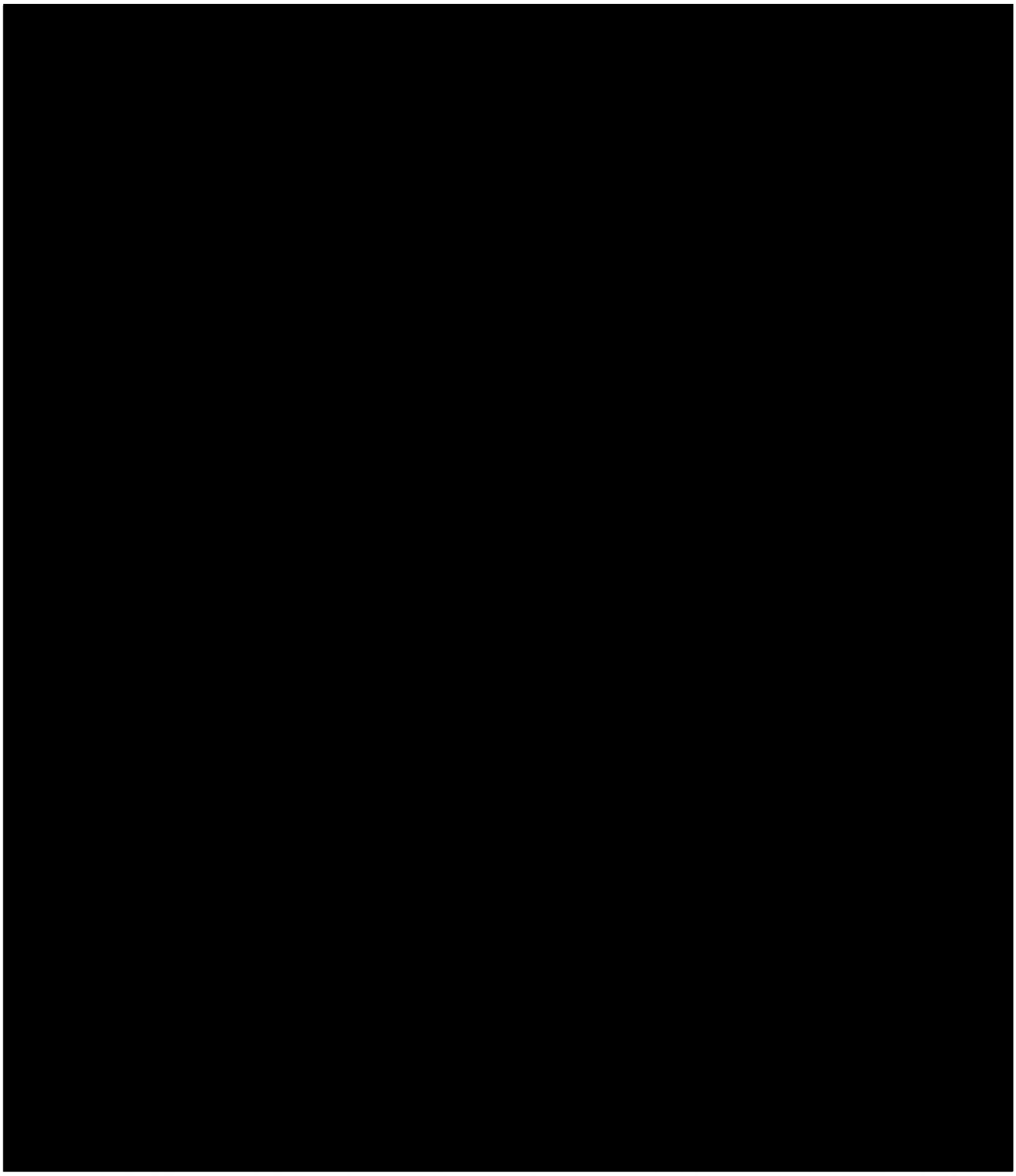


Figure 3-2: Nigardsbreen foreland: a) the end moraine sequence (from Bickerton & Matthews, 1992); b) vertical aerial photograph (Fjellanger Widerøe AS, 27.8.1993).

Figure 3-3: The Nigardsbreen foreland from the southern valley side looking towards mouth of valley (1995).

Austerdalsbreen (Figure 3-5)

Austerdalsbreen is an outlet glacier at the southern rim of the Jostedalsbreen ice cap (long. 7° E, lat. 61°36' N, see Figure 3-1). The foreland covers an area of about 3 km^2 and an elevation range from 310 m to 400 m a.s.l. Despite its relative proximity and comparable location to Nigardsbreen its mean annual temperature and precipitation values are higher than the one of the Nigardsbreen foreland, estimated at +5°C and 2250 mm/year (Mellor, 1985).

Precambrian gneiss with a few outcrops of ultrabasic rocks make up the underlying bedrock of the area (Sigmond, Gustavson & Roberts, 1984). The foreland in front of the Austerdalsbreen shows at least 15 moraine ridge complexes (Erikstad & Sollid, 1986; Bickerton & Matthews, 1993). The estimated dates for the moraines range from 1762 AD to 1927 AD. A sandur has developed around these moraines. Most of the valley floor between the moraines is covered with gravel and boulder bars and abandoned melt water streams (Maizels & Petch, 1985; Petch & Whittaker, 1997), which form a mosaic of surfaces of different age. Petch & Whittaker (1997) point out that on this foreland, dating of intermoraine areas is not consistent with the chronosequence of estimated ages of

moraine ridges and that more reliable dates for intermoraine areas can only be obtained when geomorphological investigations of the foreland are employed in combination with lichenometric methods.

In the past, the foreland was subject to grazing from domestic animals, mainly sheep, cattle and some goats (Whittaker, pers. comm.). With the decrease of the importance of this landuse over the last decade grazing densities have gone down and other, connected uses of the foreland (trees and shrubs were cut as fuel wood for the production of cheese) partially stopped. It is expected that this and accessibility have an important influence on the development of vegetation (see Nigardsbreen foreland). Grazing pressure varies within the foreland (which is also true for all other forelands) and differences between parts of forelands may be attributed, at least in part, to this. The vegetation on the right (eastern) foreland side consists of a sub-alpine *Betula* forest interspersed with pre-alpine *Alnus glutinosa* forest fragments and the other side is dominated by a sub-alpine heath.

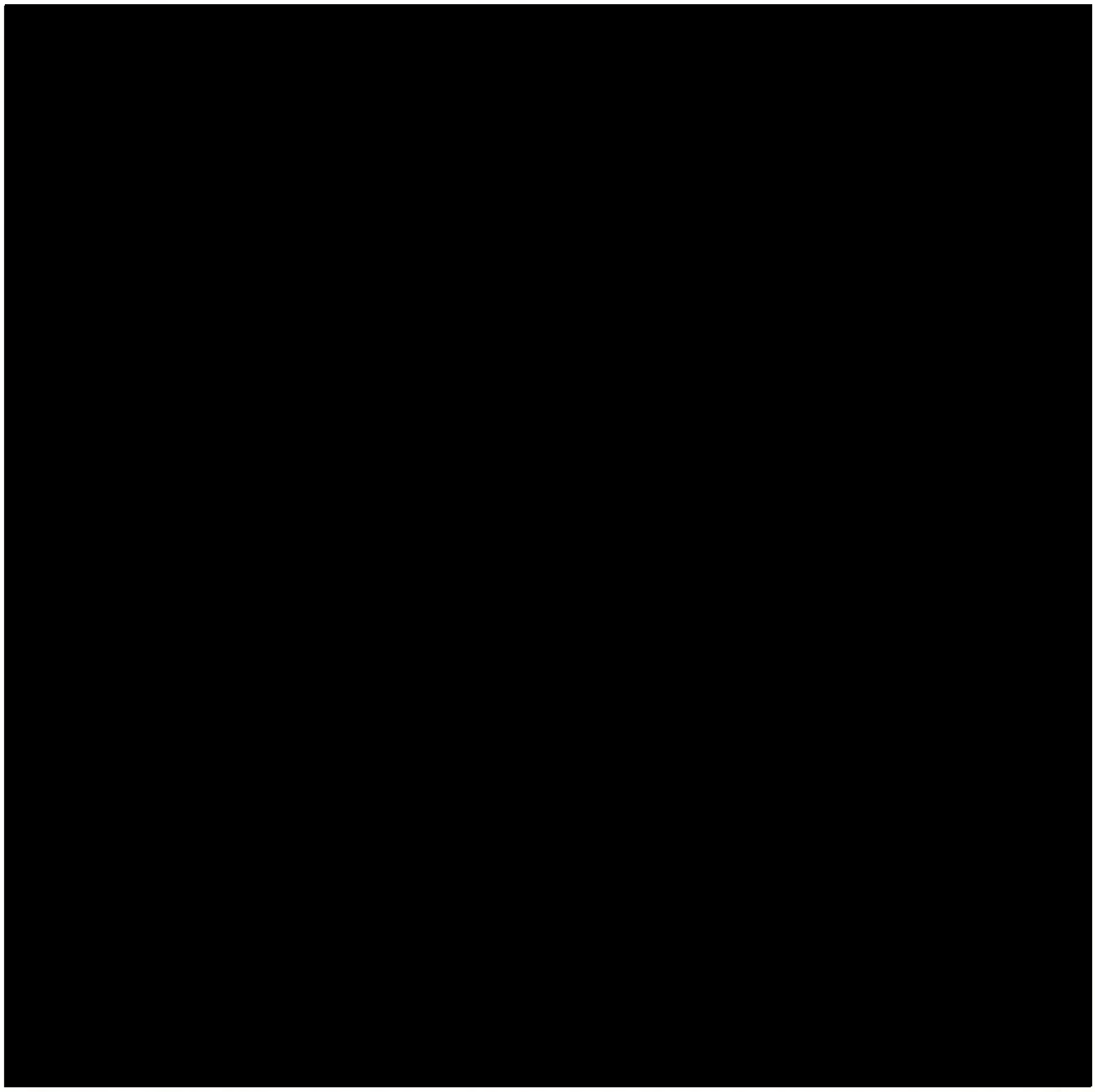


Figure 3-4: Austerdalsbreen foreland: a) the end moraine sequence (from Bickerton & Matthews, 1993); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1981).

Figure 3-5: The Austerdalsbreen foreland in 1996 with view towards the glacier.

Bødalsbreen (Figure 3-7)

Bødalsbreen is another outlet glacier of the Jostedalsbreen ice cap. It is situated at the northern rim of the ice cap (long. 7°7' E, 61°46' N, see Figure 3-1) and its foreland occupies an area of about 0.45 km^2 at an elevation of about 600 m a.s.l. Its location places it in the sub-oceanic climate regime with an annual rainfall of ca. 1100 mm/year (Vetaas, 1994). The mean annual temperature for the locality is estimated to be +2.46°C (Messer, 1988).

The bedrock of the glacial valley consists of granite and gneiss and the valley floor is covered by glacio-fluvial deposits. There are five discernible terminal moraines of a peculiar "saw-tooth" form, created by intermittent glacier retreat after the "Little Ice Age" maximum extent in about 1750 AD (Figure 3-6). They consist of derived fluvio-glacial deposits of well rounded clasts of cobbles and boulders in a matrix of sand and silt (Matthews, Cornish & Shakesby, 1979).

Figure 3-6: Bødalsbreen foreland: a) the end moraine sequence (from Bickerton & Matthews, 1993); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1981).

The glacier foreland lies below the treeline and is surrounded by sub-alpine *Betula* forests (up to 800 m a.s.l. on the surrounding steep slopes). The valley floor is covered by a pre-alpine *Alnus incana* forest. Both of these mature forest types are commonly found at this altitude in western Norway (Odland, 1981; Moen, 1987). The area was and is being used for grazing cattle and sheep, which is expected to have an influence on the development of the vegetation.

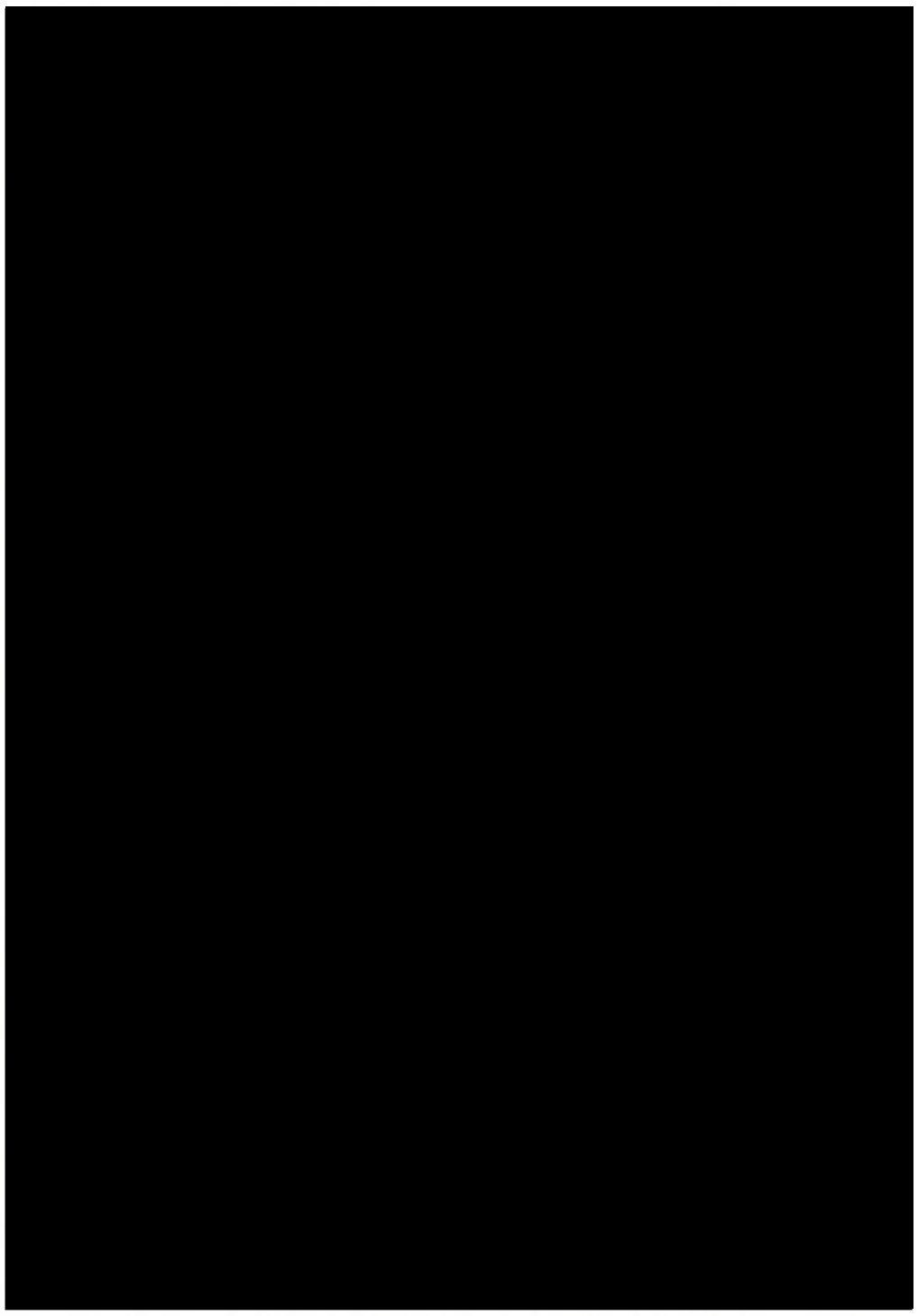


Figure 3-7: The Bødalsbreen foreland in 1996.

High-altitude Glaciers

Both high-altitude forelands lie in the Jotunheimen area of South-Central Norway (Figure 3-1).

Storbreen (Figure 3-9)

The Storbreen foreland (long. 8°10' E, lat. 61°35' N, see Figure 3-1) spans an altitudinal range from 1150 m to 1550 m a.s.l. It covers an area of approx. 2 km^2 in front of Storbreen. There are two main sources for the climate data for this area, from the meteorological stations at Elveseter (long. 8°17' E, lat. 61°42' N, 647 m altitude) and Fanåraken (long. 7°58' E, lat. 61°32' N, 2062 m altitude; Haines-Young, 1983). Mellor (1985) estimated the mean annual temperature as -1°C using the mean altitudinal temperature gradients for Southern Norway calculated by Green & Harding (1980). Similarly to the mean annual temperature, a value for mean annual precipitation can be estimated, the value being 1500 mm/year. (Mellor, 1985, after Østrem & Ziegler, 1969). Using a correlation analysis of 12 and 23 weather stations in the region, Messer (1988) calculates the mean annual temperature as -2.04°C and the precipitation as 740 mm/year, respectively. The discrepancy between the values is very large and is not being explained by Messer (1988). But because the estimates from her publication involve interpolation of many more weather stations Messer's values are considered to be truer representations of the real mean values.

The bedrock underlying the Jotunheimen area has been described by Battey & McRitchie (1973; 1975) as pyroxene-granulite gneiss. The moraine sequence covering the foreland has been dated using lichenometry in combination with dendroclimatology and dendroglaciology (Matthews, 1974; 1977a; 1977b) and renders 20 identified past ice-margins as indicated by their corresponding moraines, ranging in age from 1750 AD to 1986 AD (Figure 3-8).

Figure 3-8: Storbreen foreland: a) the end moraine sequence (from Matthews, 1992: 23); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1968).

The foreland lies entirely above the tree-line in the alpine vegetation zone and is dominated by heath communities with e.g. *Betula nana*, *Arctostaphylos alpina*, *Vaccinium myrtillus* and several species of *Salix* (Matthews, 1979b; 1979c; Moen, 1987). During the field seasons grazing has been noted by sheep, lemmings and voles.

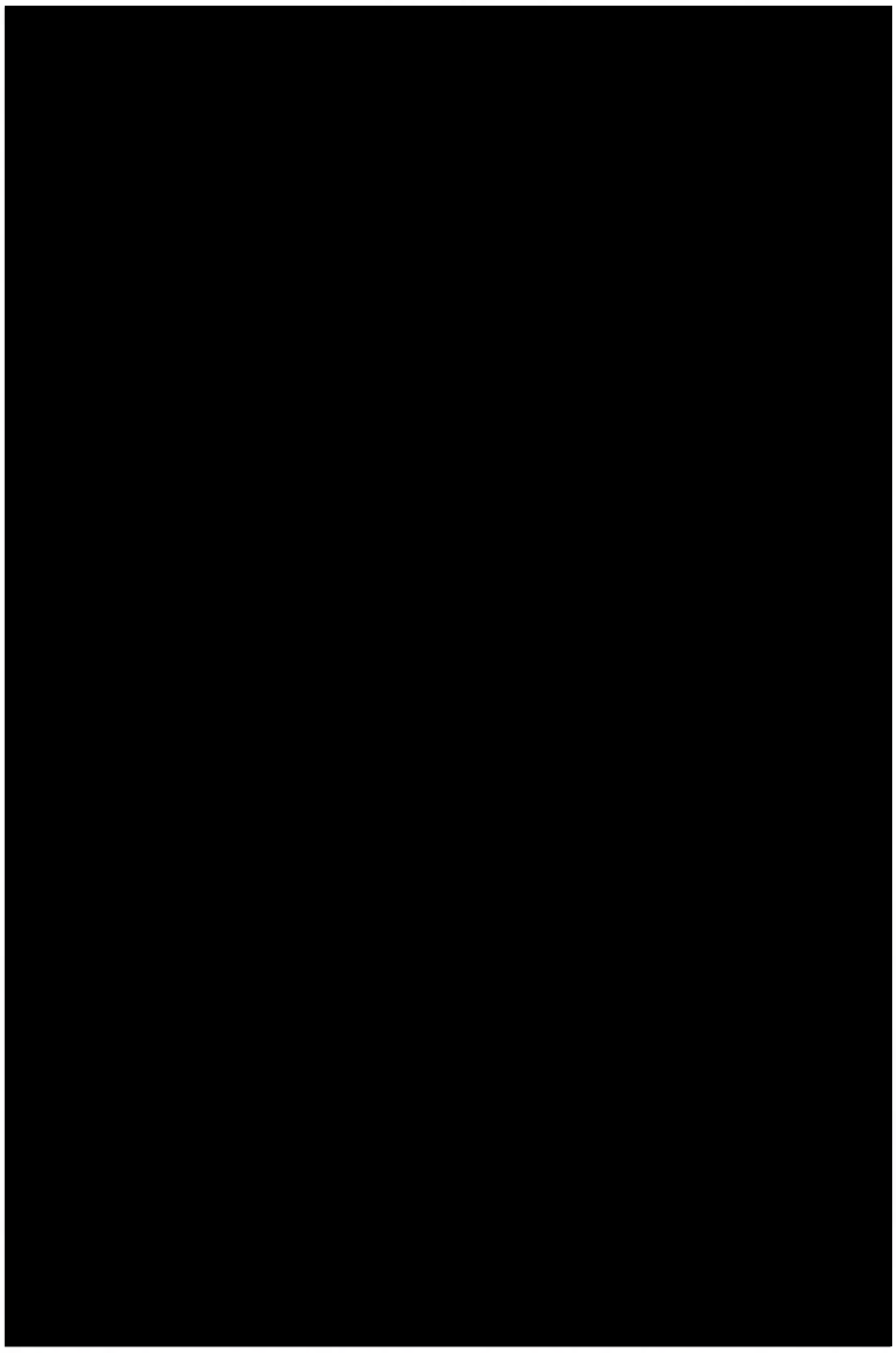


Figure 3-9: The Storbreen foreland from eastern Leira valley side (1996).

Høgvaglbreen (Figure 3-11)

The Høgvaglbreen foreland (long. 8°22' E, lat. 61°31' N, see Figure 3-1) covers an area of about 0.8 km^2 and spans an altitudinal range from 1400 to 1600 m a.s.l.

Mean annual temperature and mean annual precipitation values have been estimated from the meteorological stations at Elveseter (long. 8°17' E, lat. 61°42' N, 647 m altitude) and Fanåraken (long. 7°58' E, lat. 61°32' N, 2062 m altitude; Haines-Young, 1983) and amount to 0°C and approximately 1500 mm/year. As with the values for the Storbreen foreland, Messer (1988) provides quite different estimates for the mean annual temperature and the mean precipitation, with -2.73°C and 700 mm/year, respectively. Since the number of the weather stations used for the estimation of these values is much greater in Messer's study, her values are assumed to be closer representations of the true mean values.

The bedrock underlying the foreland is pyroxene-granulite gneiss (Battey & McRitchie, 1973; 1975). Erikstad & Sollid (1986) dated and mapped the moraine sequences. The estimated age of the moraines range from 1750 AD to 1933 AD (Figure 3-10).

Figure 3-10: Høgvaglbreen foreland: a) the end moraine sequence (from Erikstad & Sollid, 1986); b) vertical aerial photograph (Widerøe's Flyveselskap A.S., 1968).

The foreland lies entirely above the tree-line in the alpine vegetation zone and is patchyly covered by a very species poor heath community dominated by *Salix herbacea* and *Loiseleuria procumbens*. Since it is relatively inaccessible and far removed from any human habitation, the influence of life-stock grazing is absent. The grazing which nevertheless occurs is restricted to wild reindeer, voles and lemmings.

Figure 3-11: Part of Høgvaglbreen foreland. View from 1750 moraine towards the glacier (1996).

Sampling plot locations 1995 and 1996

The following figures document the sampling plot location of the 1995 and 1996 field season. For the 1995 field season sampling plots transects along which at 10 m intervals 4x4 m quadrats were surveyed are shown. The location of the small-scale sampling areas is highlighted.

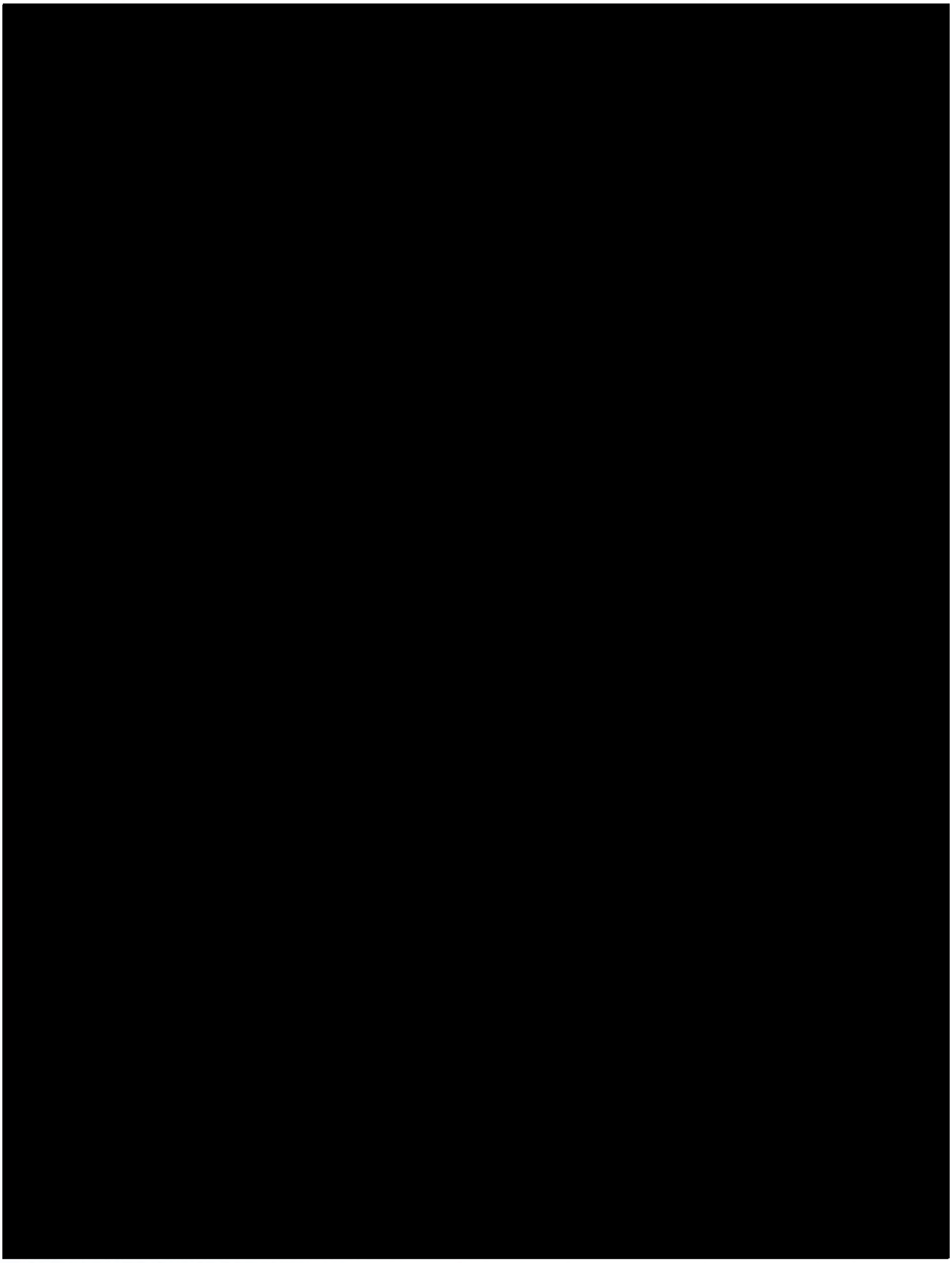


Figure 3-12: Location of the 1995 sampling plots, superimposed on the relevant aerial photographs.

The location of the 1996 plots was established using a subjective placement of the sampling blocks in areas of differing age since deglaciation. The three low altitude

forelands are shown in the first row and the two high altitude forelands in the lower row of the figure.

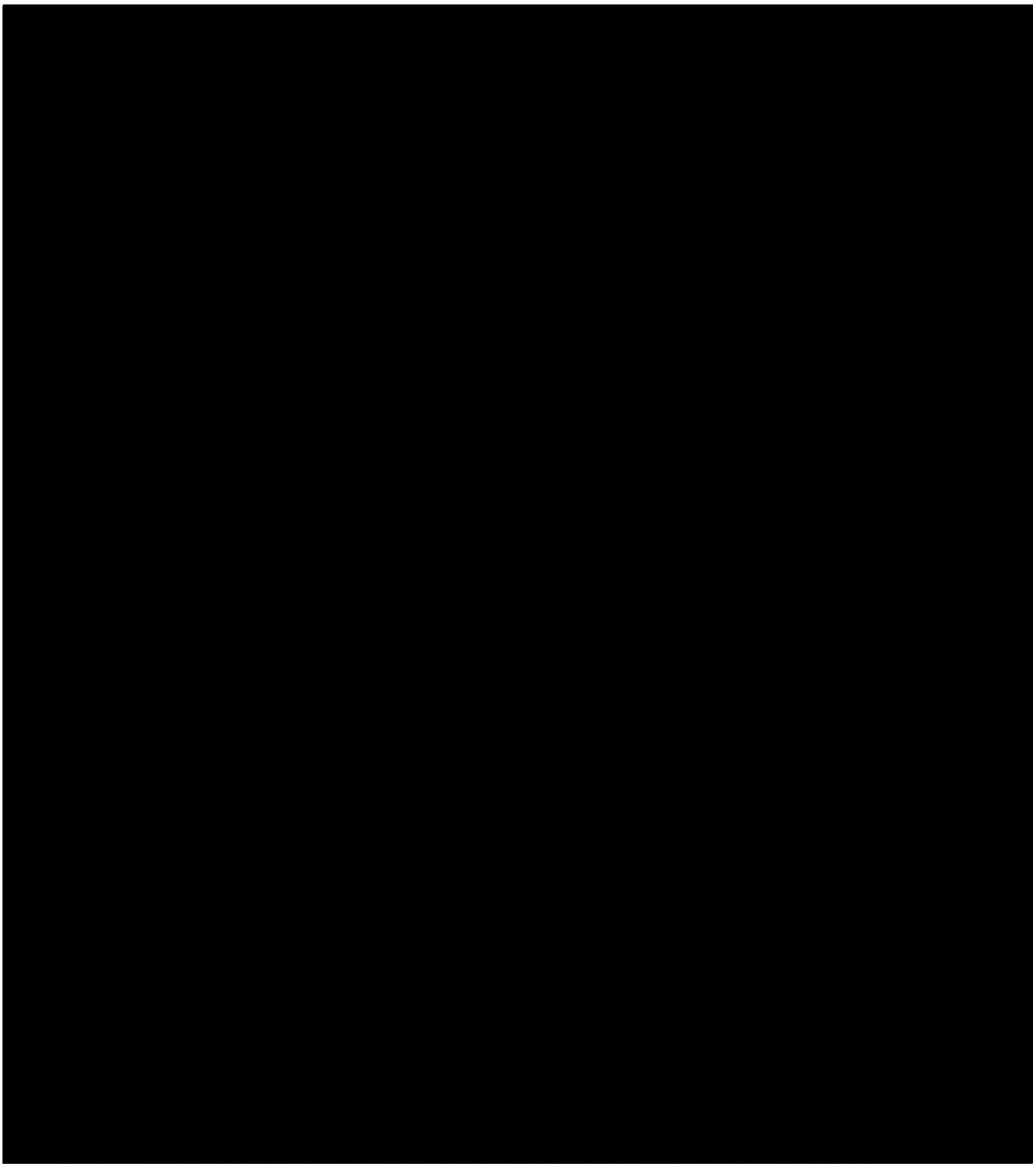


Figure 3-13: Location of the 1996 sampling blocks on the relevant forelands.

4. Trends in vegetation cover, richness, life-form , soil depth and soil-pH

"If you shut your door to all errors truth will be shut out."

- RABINDRANATH TAGORE, *Stray Birds*, 1916

Preface

This chapter is based on the 1995 field season on two glacier forelands in South-Central Norway (Nigardsbreen and Storbreen). Some prevalent hypotheses in succession theory, including the increase of vegetation cover and plant richness, changes in the representation of different life-forms, and predictable changes of the physical environment, are addressed. The selection of one low- and one high-altitude foreland allows for the comparison of the variation of these trends between glacier forelands.

An introduction to the literature on these trends in succession on glacier forelands is followed by a description of the geometrical sampling design implemented at two scales. Since spatial processes are known to be scale dependent an objective was to determine the scales at which the trends and processes are working. The methods section includes a new approach used to estimate soil-pH from the Ellenberg indicator values of the plant species in the sampling plots. These estimates are subsequently compared to pH-estimates from a previous study by Messer (1988). The results section presents the findings in tabular and graphical form. This is followed by a discussion of the results in the light of the previously described and postulated trends.

Introduction

Since the beginning of succession studies on glacier forelands, description and analysis of apparently general trends in succession represented a major part of the research. Studies in the Swiss and Austrian Alps, northern Sweden and perhaps most famous of all, in Glacier Bay, Alaska, demonstrated a progressive increase in vegetation cover (see Matthews, 1992: 168). The usual temporal progression of this increase in vegetation cover tends to be sigmoidal in form (Figure 4-1; Zollitsch, 1969). For

example during the typical development on the Pasterzer Gletscher, cover increases slowly for the first years after deglaciation, but shows a rapid increase between 20 to 100 years. After about 100 years it reaches approximately 100% cover.

Figure 4-1: Vegetation cover chronofunctions for three successional pathways (A, B and C) characteristic of respectively more favourable habitats, Pasterzer Gletscher, Austrian Alps. Large filled circles represent all three pathways (from Zollitsch, 1969).

Similar to the increase in vegetation cover, local plant species richness was shown to increase almost universally in many studies. The general speed of the increase in species richness depends on the severity of the environment, with arctic and alpine sites showing the slowest increase (see Matthews, 1992: 182). The study of Zollitsch (1969) on the Pasterzer Gletscher in the Austrian Alps provides us again with an idealised representation of the temporal development of species richness (Figure 4-2). It demonstrates the peak, found by many investigators early in succession, followed by a decline (e.g. Matthews, 1978; Sommerville, Mark & Wilson, 1982; Vetaas, 1986). The hypothesis developed from this pattern is that the initial increases in species numbers represents colonisation of the glacier foreland first by pioneer species and a subsequent overlap with the arrival of later colonisers. The ensuing decline in species numbers is commonly accounted for by increased competition between the species in later successional stages.

Figure 4-2: Species richness in three successional pathways (A, B and C) characteristic of respectively more favourable habitats, Pasterzer Gletscher, Austrian Alps. Large filled circles represent all three habitats (from Zollitsch, 1969).

Another trend which has received some interest in previous investigations is the change in the proportional representation of different life-forms on glacier forelands. Various stages of a succession tend to be dominated by different life-forms. The definition of the life-forms is based on the system of Raunkiaer (see Table 2-3) and represents a classification of plant species according to their physiognomy. This very basic classification has nevertheless proven to be successful in combining plant species, which behave similarly during successions. It is thought that the physiognomy of species is an expression of many other physiological and genetical properties of the plants. It is, however, much easier to assess and therefore a helpful way of characterising groups of plants. The general idea of the progressive change of life-forms during succession is demonstrated by Lüdi's study on the Grossen Aletschgletscher, Swiss Alps (Lüdi, 1945). Initial dominance of cryptogams is reduced over time and the relative importance of phanerogams increases with time.

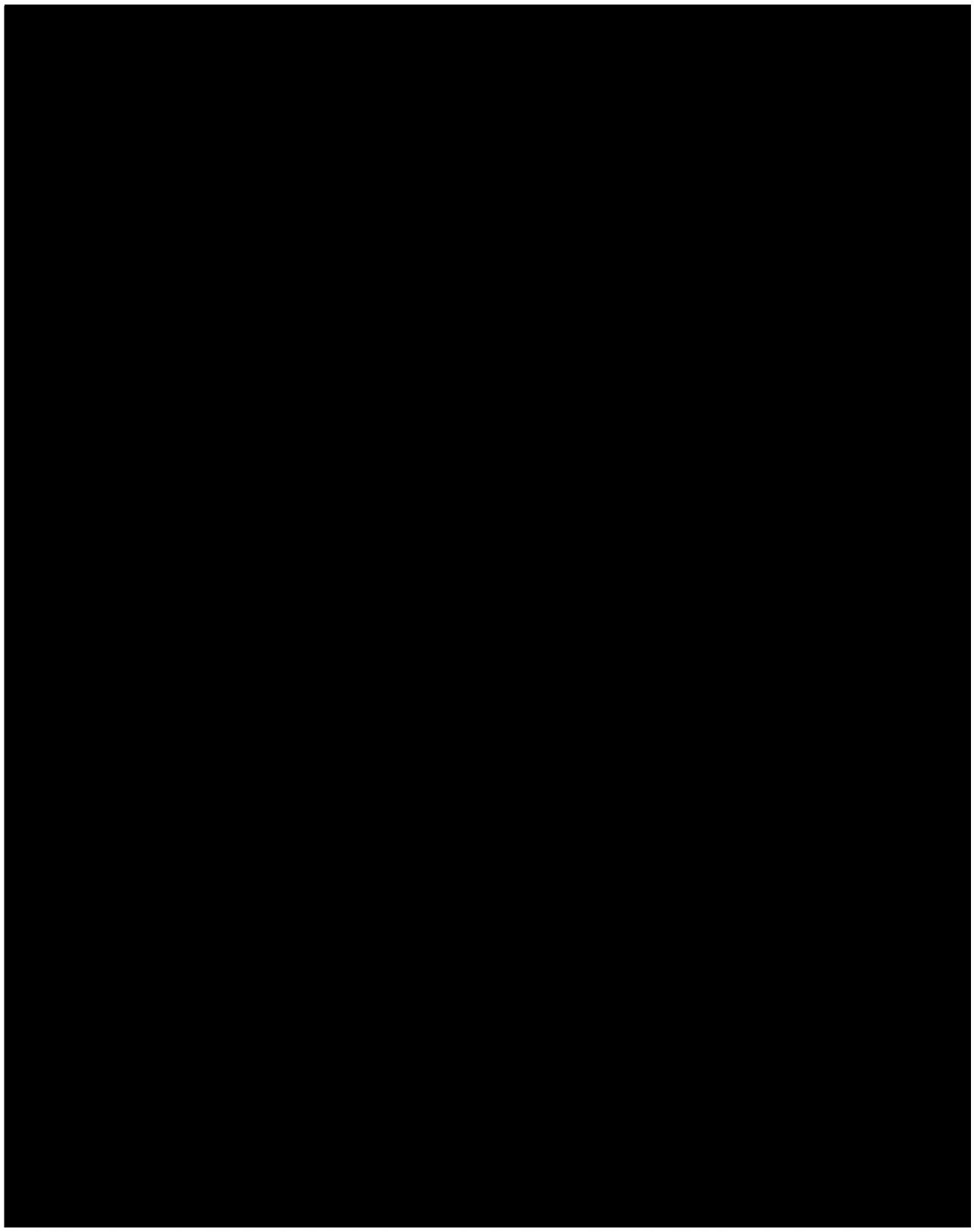


Figure 4-3: Percentage cover of various life-forms on terrain of increasing age, Grosser Aletschgletscher, Swiss Alps (from Lüdi, 1945).

The predictable change of the physical environment has also received considerable attention in previous research and constitutes another avenue followed in this thesis. One of the more obvious developments on recently deglaciated terrain is the formation of soils during succession. All important aspects of this development are excellently summarised in chapter 4 of Matthews (1992). The formation of soils in these areas is the prerequisite for the colonisation of those terrains by higher plants. Despite the very basic way of assessing the development of soils by recording the average soil depth within the study quadrats, this concept is nevertheless thought to represent an important part of the development of the physical environment. A more detailed investigation of the formation of soils, with their stratification and horizon formation was not possible in this study.

The goal of this analysis in this study is to compare the soil depths recorded on the two forelands with predicted soil depths from Messer's (1988) study.

Mellor (1985) and Messer (1988; 1989) have each studied the soil development of the Storbreen foreland in some detail. Due to time restrictions no detailed investigation of this particular soil property could be done in the present study, but with the abundant vegetation data it was expected that Ellenberg indicator values could be used to estimate the average pH conditions of the study quadrats and then compare those values to the values from the previous study. An evaluation of this new approach gives plant ecologists an indication on how efficient this way of estimating environmental conditions from vegetation data, using Ellenberg indicator values, is.

For all these successional trends on recently deglaciated terrain, large spatial variations within- and between-glacier forelands exist, which make the generalisation of any results difficult. The sampling strategy adapted in the 1995 field season of this study provides data from two glacier forelands experiencing different environmental conditions. They were collected in exactly the same way, so that a simple comparison of the results is possible. This was expected to shed some light on the differences in successions between low- and high-altitude forelands. The additional aspect of data from large and small-scale areas in the forelands permits the estimation of the scale at which the temporal trends are important and adds new information to the knowledge base of the trends on glacier forelands in different geographical regions.

Methods

The location of the 16m² sampling quadrats is shown in Figure 4-4. 121 and 86 quadrats were surveyed on the Nigardsbreen and Storbreen forelands, respectively. For the small-scale, investigation another 253 quadrats (1m²) were surveyed in three blocks of decreasing age on the Nigardsbreen foreland (block I n=55, block II n=132, block III n=66). On the Storbreen foreland 161 quadrats (1m²) were surveyed in three blocks (block I n=66, block II n=66, block III n=29). During the 1995 field season, vegetation cover was determined as the percentage of the sampling quadrat covered by a certain plant species in a perpendicular projection. Species richness is calculated as the sum of all identified higher plant species within a quadrat and the life-form attributes for the species were taken from Ellenberg *et al.* (1991) and Oberdorfer (1983).

At the time when the vegetation parameters within the quadrats were recorded, soil depth (in cm) was determined with a metal rod. The mean of 20 stratified random probings within a quadrat was recorded. The probings were restricted to the areas of well-developed soils within the quadrats. The deepest of the probings was individually recorded as the extreme value.

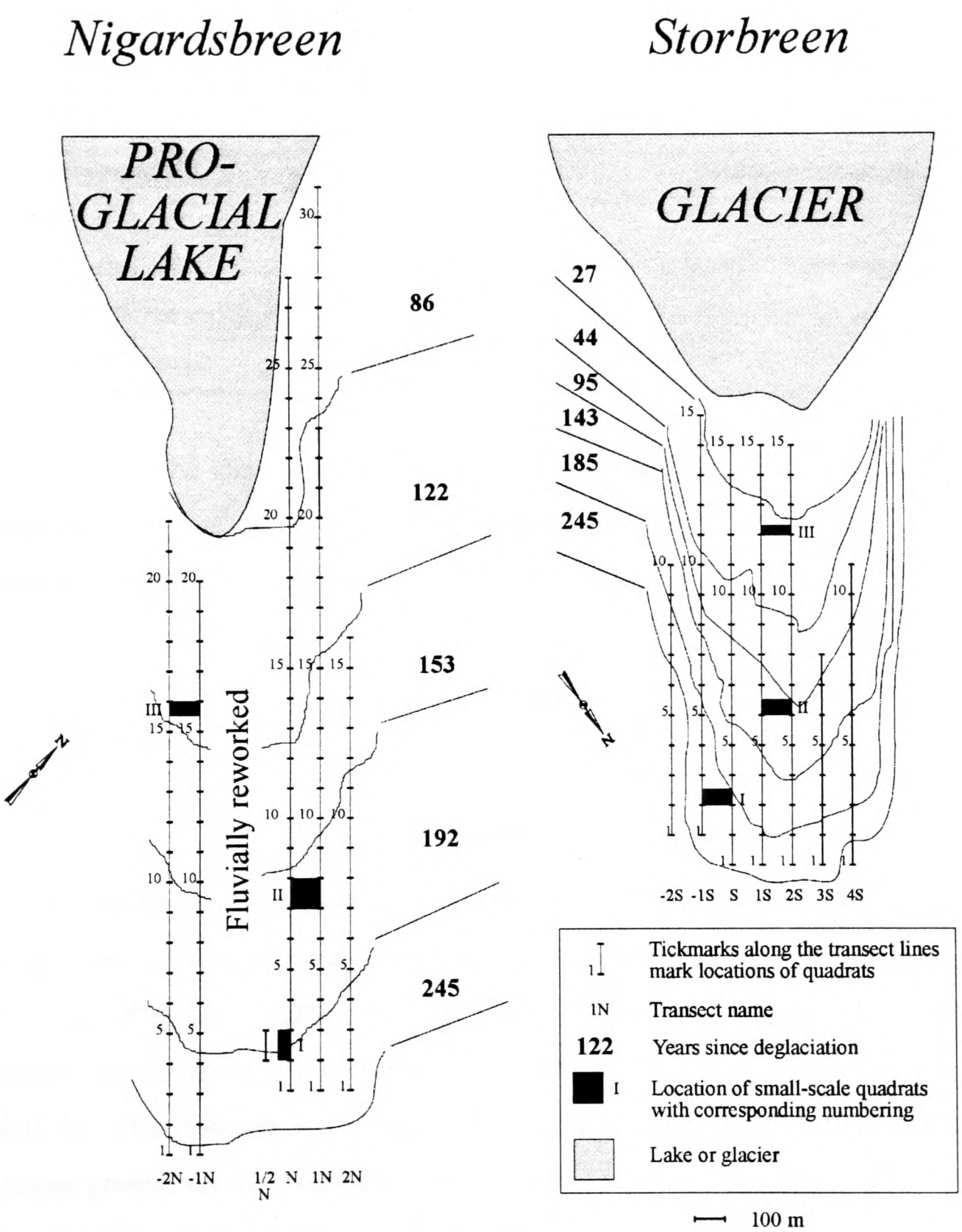


Figure 4-4: Location of plots recorded in 1995 with their respective numbers on the forelands.

The soil depth measurements from the present study were to be compared to estimates of soil depth from Messer (1988). Her regression equation for the estimation of

the soil depth and pH values on the Storbreen and Nigardsbreen forelands are given in (Table 4-1). Average soil pH conditions within a quadrat in this study were estimated using Ellenberg indicator values (Ellenberg *et al.*, 1991) and the average of the value was calculated with all the present species entering with the same weight. This qualitative way of calculating the average of the values for certain sampling plots was suggested by Ellenberg *et al.* (1991) and is thought to be a true representation of the average condition for the variable within the sampling area.

Table 4-1: Regression equations for the estimation of soil depth and pH for the Storbreen and Nigardsbreen forelands (from Messer, 1988)

Soil property	Regression equation
Storbreen soil depth	x = -0.4 + 0.0188 * agemax
Storbreen pH	x = 5.527 - 0.001 * agemax
Nigardsbreen soil depth	x = -1 + 0.092 * agemax
Nigardsbreen pH	x = 5.037 - 0.00042 * agemax

The way the temporal trends of the investigated features are analysed is by using histograms and bar graphs. ANOVA analysis (SPSS-Inc., 1989-1997) provided the means to determine the significance level of any trends.

Results

Vegetation Cover

As can be seen in Figure 4-5, only the values from the 86 large-scale quadrats on the Storbreen foreland show a significant increase in vegetation cover ($p < 0.01$; ANOVA, SPSS-Inc., 1989-1997). The data from the Nigardsbreen foreland (121 quadrats) do not show any significant trend across the surveyed time-span ($p = 0.655$; ANOVA). The histograms in Figure 4-6 illustrate that all quadrats sampled on the youngest ground on the Storbreen foreland show very low cover values (< 10%). With increasing age cover increases with a marked step between 185 and 245 years since deglaciation. This period marks the time when plant cover in the sampled quadrats first reaches 100%. It is notable that there are nevertheless quadrats with very low cover values (< 10%) for the oldest age groups on this foreland. Even outside the foreland, quadrats with very low cover values (< 25%) appear.

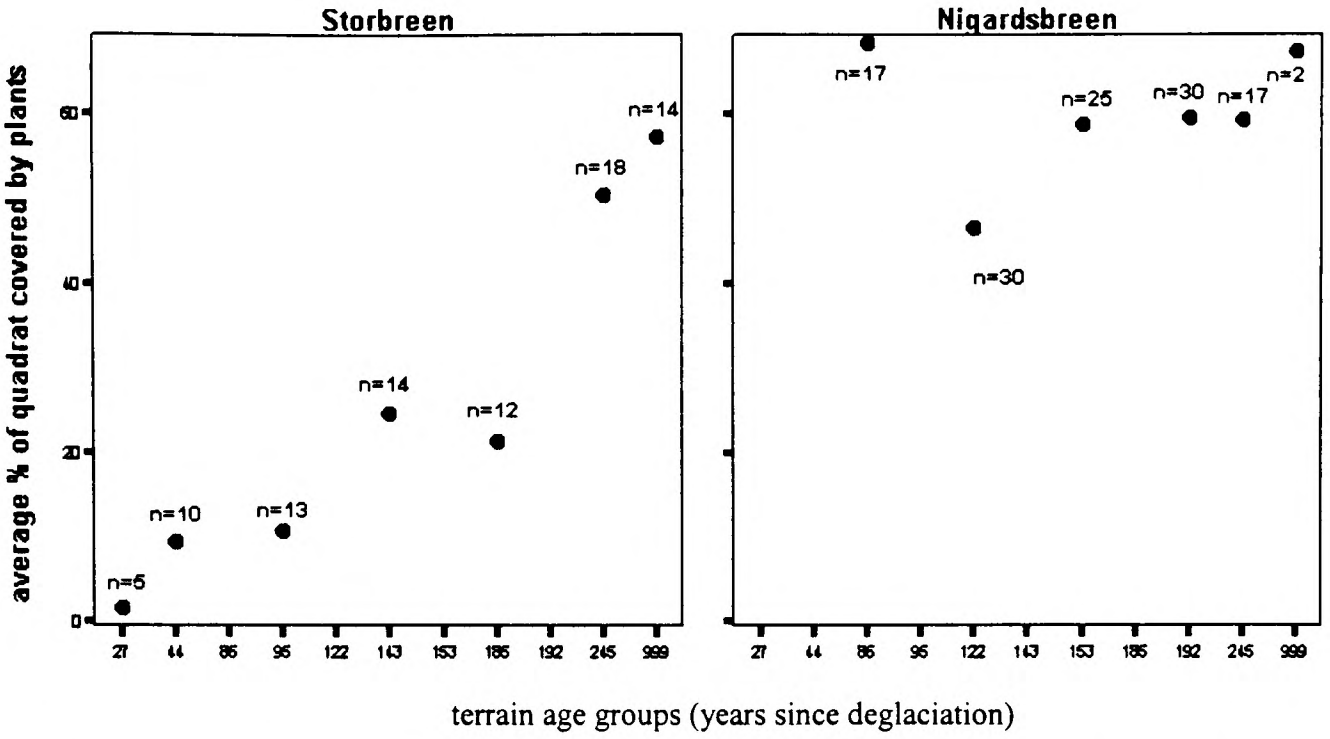


Figure 4-5: Average amount of plant cover for *n* quadrats (quadrat size = 16m²) of the large-scale sampling design in relation to age groups since deglaciation on the Storbreen and Nigardsbreen forelands.

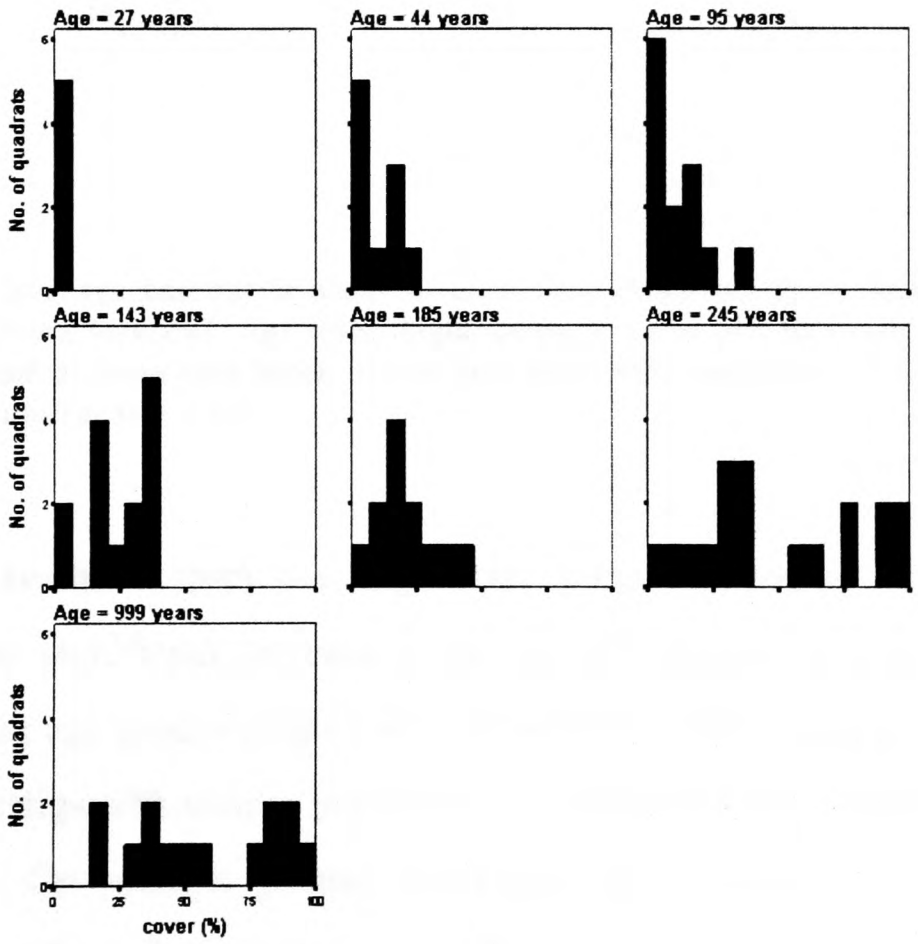


Figure 4-6: Histograms of the frequencies of recorded plant cover values on the Storbreen foreland, according to the time since deglaciation. Figures represent site age, 999 refers to quadrats from outside the foreland boundary. Quadrats from large-scale sampling design, quadrat size = 16m².

The 1995 sampling design also allows investigation of the vegetation cover of the small-scale blocks and comparison between the average plant cover values obtained

from the large-scale data. The plant cover values for all 1m² quadrats within the three age blocks on the Storbreen foreland were averaged. These averages from the small-scale sample grid, show a trend of increasing cover with time since deglaciation.

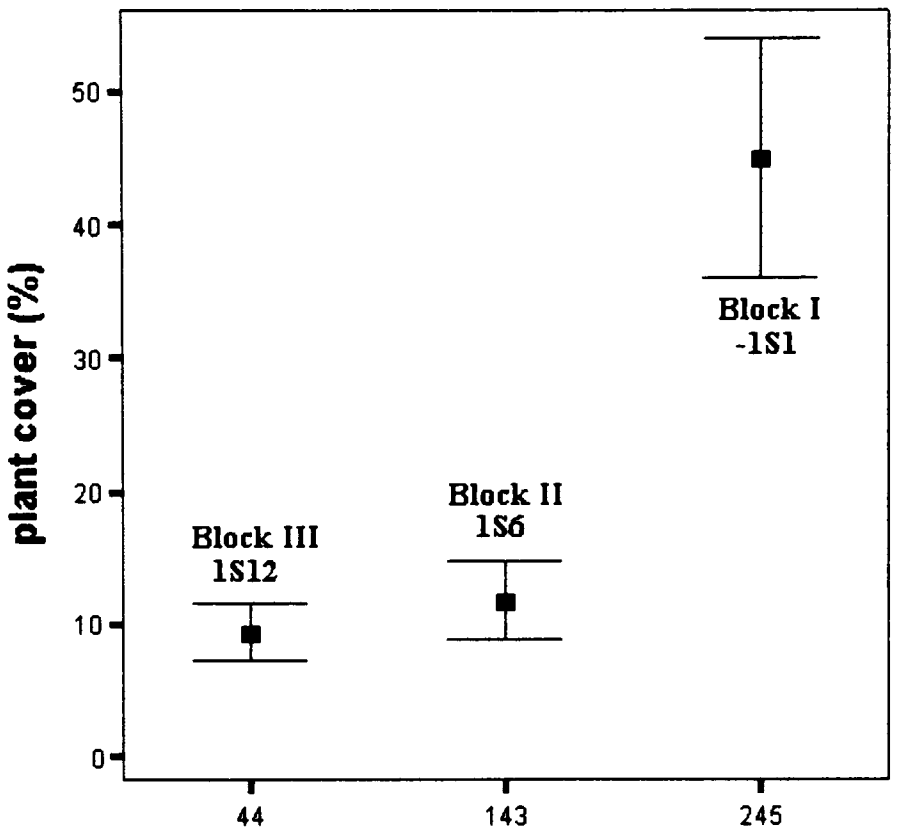


Figure 4-7: Average amount of plant cover of quadrats from three small-scale blocks on the Storbreen foreland. Age since deglaciation is a conservative estimate, using the youngest quadrat from each block. Error bars show 95% confidence intervals of mean. Individual quadrat size = 1m².

The data available from the large-scale sampling design on the Nigardsbreen foreland show no significant increase in the overall amount of plant cover within the quadrats of certain age groups (Figure 4-5). When the different age groups of those 16m² quadrats are investigated a similar picture to the one seen for the Storbreen data emerges (see Figure 4-8). On younger ground, the values for vegetation cover span the whole range, whereas on the oldest ground on the foreland very low cover values (< 10%) for quadrats are missing.

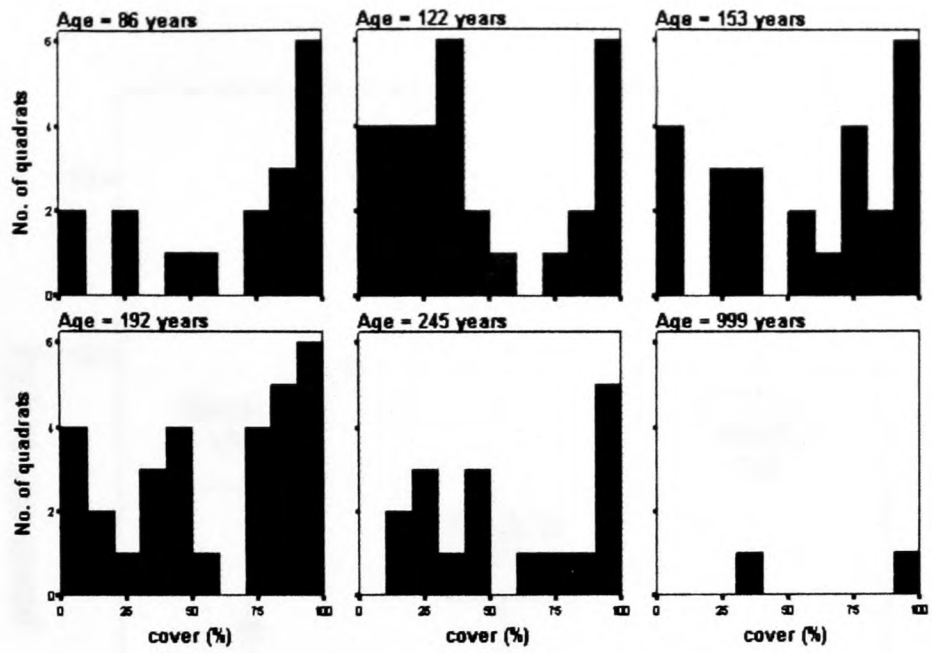


Figure 4-8: Histograms of the frequencies of recorded plant cover values on the Nigardsbreen foreland, according to the time since deglaciation. Figures represent site age, 999 refers to quadrats from outside the foreland boundary. Quadrats from large-scale sampling design, quadrat size = 16m².

The small-scale data from the Nigardsbreen foreland shows an increase in plant cover after 145 years (Figure 4-9). The mean plant cover value for the 66 1m² quadrats in the block which was deglaciated approx. 122 years ago (block III; see Figure 4-9) also corresponds very well with the large-scale plant cover average of quadrats in that age group (44.5% and 46.6%, respectively). Blocks I and II (n = 55 and n = 132, respectively), however, show big differences to the mean plant cover values calculated from the large-scale data for the corresponding age groups (40.6% and 58.8% for block II and 65.4% and 59.5% for block I). The average plant cover values for the small-scale investigations are less variable than the average values from the large-scale data (smaller CIs).

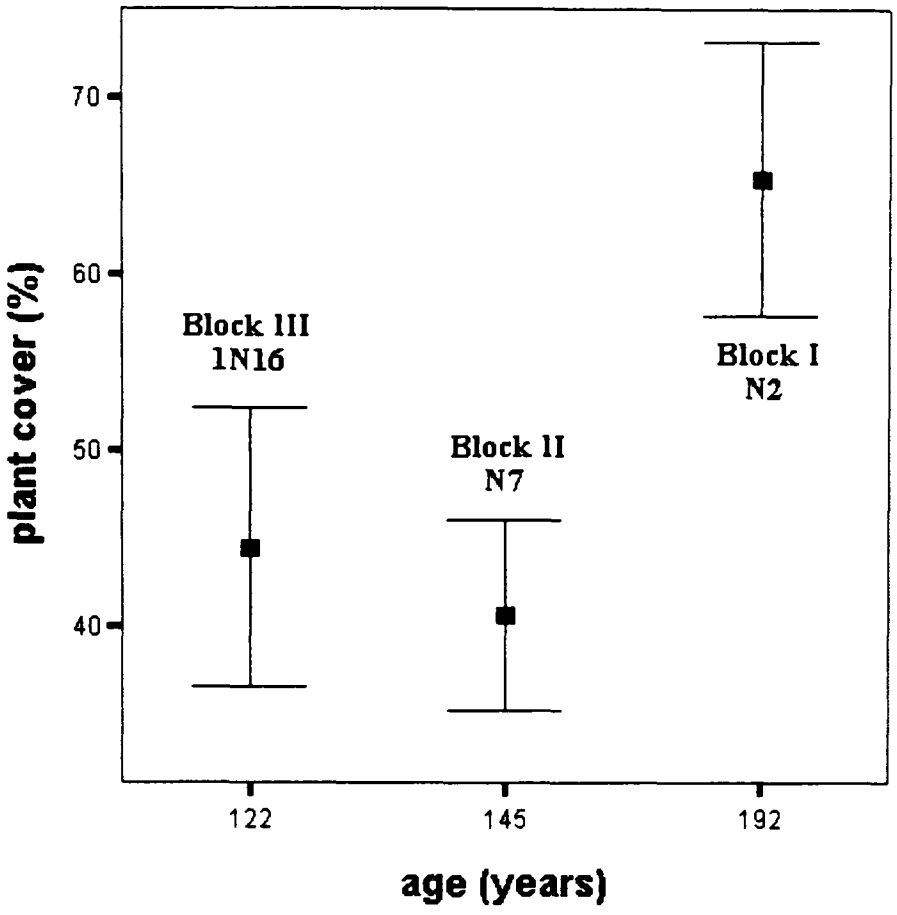


Figure 4-9: Average amount of plant cover of quadrats from three small-scale blocks on the Nigardsbreen foreland. Age since deglaciation is a conservative estimate, using the youngest quadrat from each block. Error bars show 95% CI of mean. Individual quadrat size = 1m².

Species Richness

Another trend in primary successions on glacier forelands is an increase in the number of plant species with terrain age (see Matthews, 1992: 182).

The richness of the vegetation on the two glacier forelands is represented by the number of species in an area of a set size (i.e. 1 sampling quadrat). Figure 4-10 shows that on the Storbreen foreland the number of species stays at a similar level for the first 185 years after deglaciation (approx. 10 species per quadrat). Then there is a significant increase to 16 species per sampling quadrat ($p < 0.01$; ANOVA). This is in keeping with the postulated increase of richness during primary successions. On the Nigardsbreen foreland, however, there appears to be a steady decline of species numbers in quadrats from 17 to 10 (86 to 192 years since deglaciation) with a slight increase to 12 species at 245 years after deglaciation ($p = 0.17$; ANOVA).

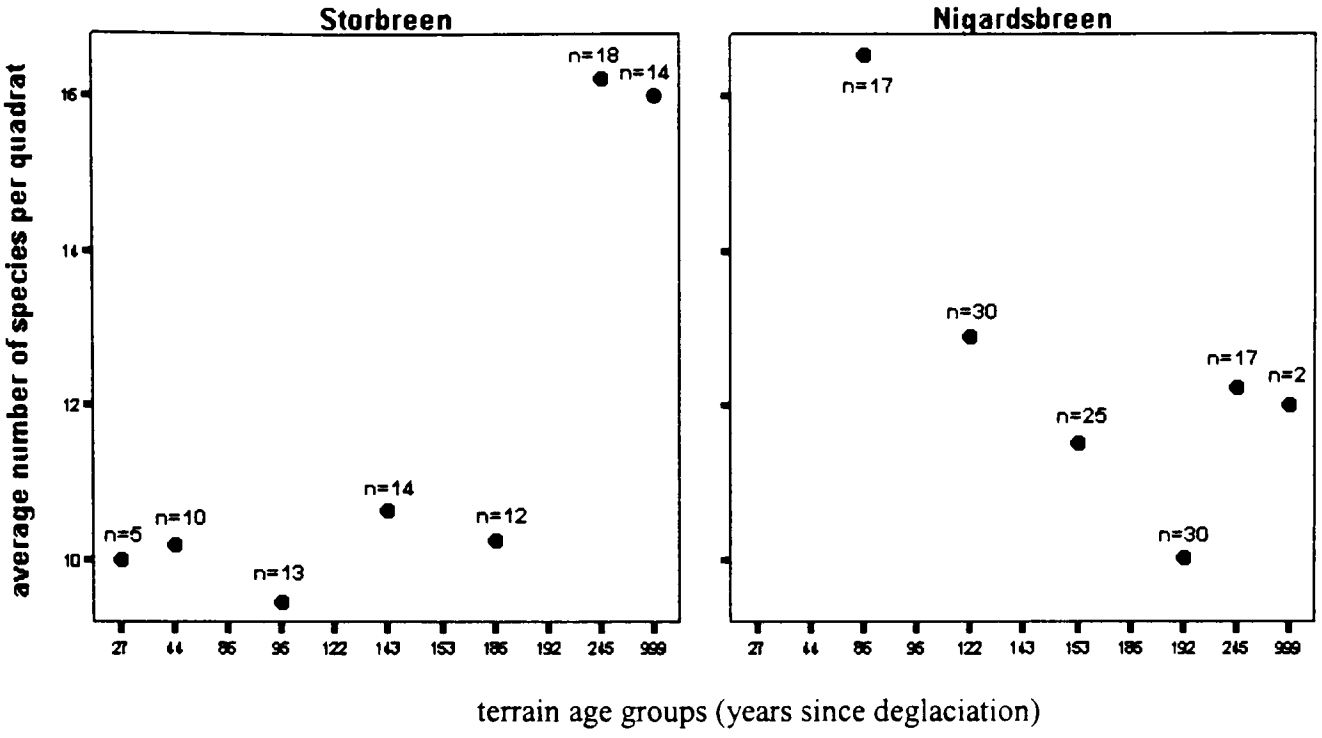


Figure 4-10: Average number of species in large-scale quadrats (quadrat size = 16m²) on terrains of increasing age.

Life-form Changes

The shift in the proportional representation of life-forms is yet another trend observed in primary successions on glacier forelands. Figure 4-11 illustrates the changes in the proportions of the Raunkiaer life-forms for the Nigardsbreen foreland. It follows, in general, the predicted changes, with life-forms like nanophanerophytes and hemicryptophytes decreasing in importance over time. Chamaephytes, therophytes and geophytes don't show any discernible trend over the sampled age range.

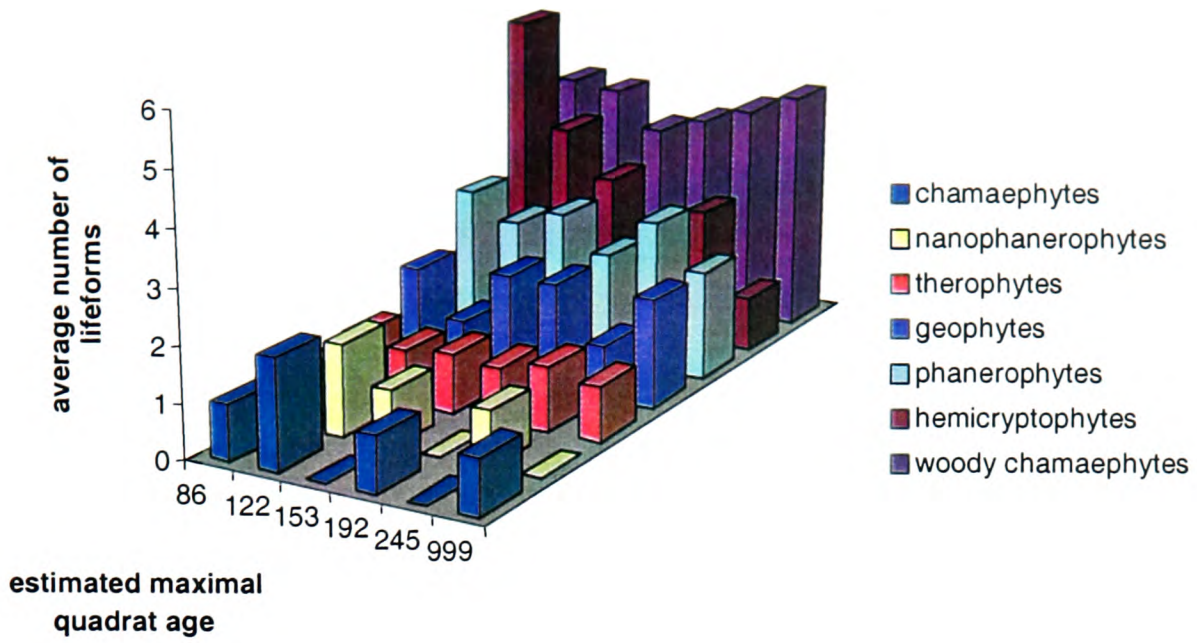


Figure 4-11: Average number of life-forms represented in sampling quadrats in relation to terrain age groups on the Nigardsbreen foreland.

On the Storbreen foreland on the other hand the number of hemicryptophytes increases on older ground (Figure 4-12). Woody chamaephytes show a similar trend and both life-forms dominate the foreland on older ground. Although on a lower level there is also an increase of geophytes as a life-form on older ground. As on the Nigardsbreen foreland phanerophytes do not increase in importance with substrate age.

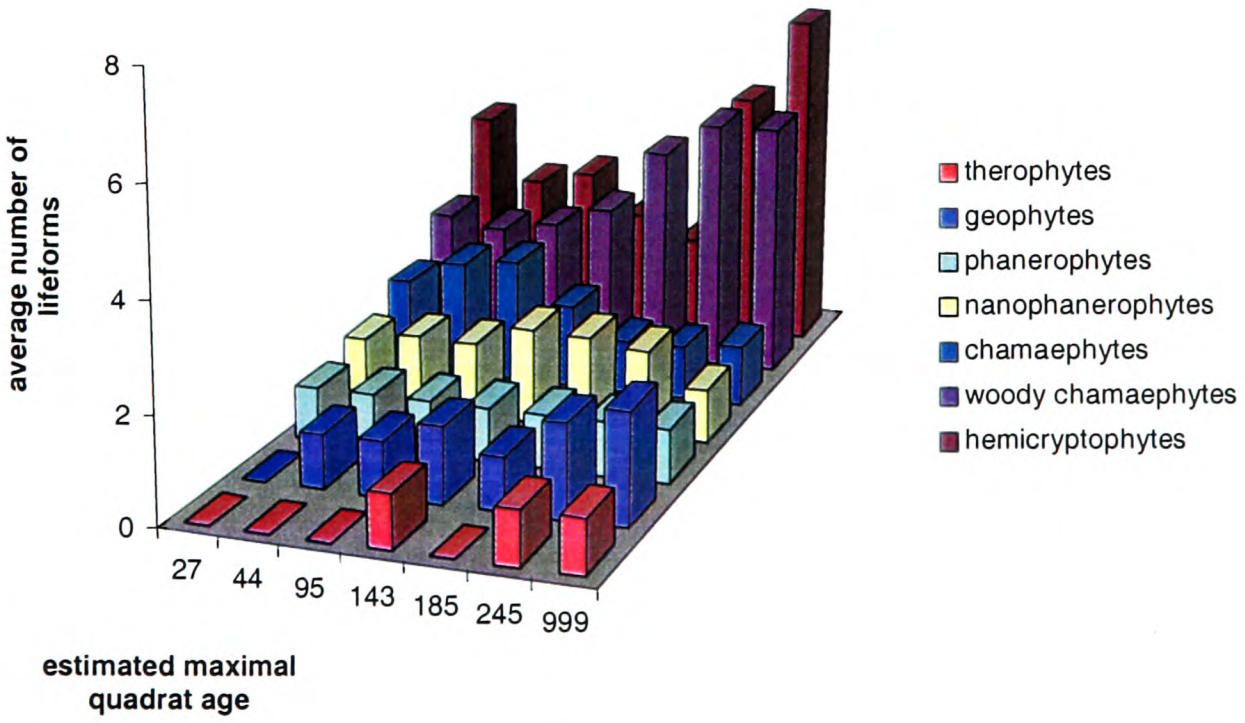


Figure 4-12: Average number of life-forms represented in sampling quadrats in relation to terrain age groups on the Storbreen foreland.

Soil Development

As pointed out in the methods section, soil depth measurements were made at the time of the investigation of each quadrat. These measurements could be regressed on the predicted soil depths from Messer (1988; note the difference in determining soil depth. Messer uses maximum depth of staining). Table 4-2 shows that for the Storbreen large-scale data set Messer's prediction have the highest regression coefficient with the extreme soil depth values measured by me. The other highly significant regression coefficient is for the correlation of the extreme soil depth measurement in the Nigardsbreen small-scale quadrats with Messer's predicted values for those ages.

Table 4-2: Regression coefficients for measured soil depths (mean and extreme relate to the soil depth measurement method used in the regression; see Table 5-4 for explanation of the methodology) and predicted values from Messer (1988)

data set	Regression coefficient r	significance (p)
Nigardsbreen large-scale (mean)	0.19	0.05
Nigardsbreen large-scale (extreme)	0.08	0.40
Nigardsbreen small-scale (extreme)	0.27	<<0.01
Storbreen large-scale (extreme)	0.52	<< 0.01
Storbreen small-scale (extreme)	0.12	0.15

pH Trends

Another generally accepted trend in primary successions on glacier forelands is the decrease of pH with increasing terrain age (Mellor, 1985; Messer, 1988; Foskett, 1998). With the characterisation of sampling quadrats by Ellenberg indicator values for reaction it was possible to predict the average pH of the sampling plots using the regression in Ellenberg *et al.* (1991: 30) and then correlate them to the expected pH-values from Messer (1988). The regression coefficients are all highly significant (Table 4-3).

Table 4-3: Regression coefficients for estimated pH-values from qualitatively calculated Ellenberg values for reaction (Ellenberg et al. 1991) and predicted values from Messer (1988)

data set	regression coefficient r	significance (p)
Nigardsbreen large-scale	0.26	< 0.01
Nigardsbreen small-scale	0.13	< 0.05
Storbreen large-scale	0.48	<< 0.01
Storbreen small-scale	0.27	< 0.01

Discussion

The general trend of an increase in vegetation cover for the large-scale quadrats is consistent with the findings in the literature (e.g. Matthews, 1992: 168). It could be shown that in the oldest large-scale quadrats on the Storbreen foreland, quadrats with very low cover values (< 10%) exist. Even the quadrats from outside the foreland can show very low cover values. This is an indication of the patchiness of the environment as well as the severity of the environment at Storbreen, which keeps the overall vegetation cover in the area relatively low. The difference in time since deglaciation between sites on the foreland and outside the foreland boundaries (an order of magnitude is assumed) is, however, enough to lead to the observed pattern, that all sites outside the foreland boundaries show at least 10% plant cover.

Quadrats of the small-scale sampling design also show an increase in plant cover with time. It was, however, expected that the average values of the 161 small-scale quadrats divided between the three blocks in different age zones coincide more closely with the values from the large-scale quadrats of the same age zones. The small-scale quadrats represent an increased sampling effort for three age groups on the foreland. The mean values of these age groups therefore include a greater variety of environments and vegetation types (e.g. a certain altitudinal range is covered within the blocks), but due to the large number of replicate measurements, it is thought that these values are truer representations of the real cover values, than the values from the large-scale quadrats.

The lack of trend in the cover development of the large-scale quadrats on the Nigardsbreen foreland may be due to its location. As a low-altitude foreland, with less severe environmental conditions, colonisation and increase in cover values may well be quicker than on the Storbreen foreland. Also on this foreland very young areas have not

been sampled. This shortfall of the sampling design will have an influence on the detection of an increase in cover values.

As for the small-scale quadrats on the Storbreen foreland, on the Nigardsbreen foreland only the average values of one age block (block III, age approx. 122 years, n = 66, quadrat size = 1m²) corresponds well with the cover value from the large-scale quadrats of the same age (see Figure 4-5). The other two age blocks show different cover values from the ones calculated from the large-scale quadrats of the same age. This might be because of the great variation of cover values within the quadrats used to calculate the average for the small-scale blocks (compare error bars in Figure 4-9). More small-scale samples from different areas of the same age group would be necessary to account for the variation. However, increased sampling efforts might not necessarily reduce the confidence intervals since it would also mean that more diverse environments from a even greater range of elevations and microclimates would be likely to contribute to the mean values.

It was shown that the overall mean values for quadrats of the same age on the Storbreen foreland (both small- and large-scale) are significantly lower than the ones on the Nigardsbreen foreland ($p<0.01$; Figure 4-5). On the Storbreen foreland younger terrains were sampled, starting with very low levels of plant cover. The difference between the youngest terrain ages sampled on Storbreen and Nigardsbreen is 59 years and this time could be enough for the vegetation cover on the Nigardsbreen foreland to already have reached a relatively high level. Another factor is that Nigardsbreen foreland lies below the treeline in an area much less severe than the Storbreen foreland. The difference is more pronounced for the younger terrain ages than for the older ones, which could be due to restriction in colonisation or establishment. The data suggest that after about 190 years since deglaciation both forelands reach a similar level of plant cover. The smaller confidence intervals of the small-scale values from the Storbreen foreland also suggest that despite the greater severity of the environment, cover of the quadrats is more homogeneous than on the Nigardsbreen foreland (see Figure 4-7 and Figure 4-9).

The increase in species numbers on the Storbreen foreland after 185 years is in keeping with the postulated increase of richness during primary successions. The increase of species numbers on this high-altitude foreland could however be due to an artefact. Since the oldest terrains on this foreland are also considerably lower in altitude this drop in altitude and its correlated improvement of environmental conditions could

account for the increase in species numbers. To evaluate this influence on the observed trend in species numbers a more sophisticated analysis, in which the influence of altitude is accounted for, would be necessary. For the Nigardsbreen foreland, however, species numbers decline between 86 and 192 years since deglaciation with only a slight increase to 12 species for terrain 245 years old. Since, on the Nigardsbreen foreland, the youngest terrains have not been sampled, it is not possible to examine the whole range of the trend. When the number of species at the start of the succession is assumed to be zero, the observed species numbers of this study are in keeping with an early peak, as demonstrated by Zollitsch and several other investigators (Zollitsch, 1969; Matthews, 1978; Sommerville, Mark & Wilson, 1982; Vetaas, 1986). This peak is traditionally thought of as an indication that a large number of pioneers are able to colonise in the early stages of the succession and that with the advent of later colonising species there might be a period in the time gradient in which both sets of species coexist. Another factor specific to the Nigardsbreen foreland could be that with the approach towards the glacier (i.e. going towards younger ground) the valley narrows. The sampling design with the regular grid therefore means that on younger ground more quadrats will lie closer to the steep valley sides. This increases the chance of covering areas on younger ground where clumps of soil and vegetation from outside the foreland boundaries can fall onto the foreland, introducing plant species into the species lists one would usually expect only on much older ground. These species don't necessarily establish themselves and survive on the young ground, but may be seen as temporary additions to the species inventory. During the field season, several of those areas with species from the valley sides were encountered, and in at least one large-scale quadrat a clump of *Geranium sylvaticum*, *Aegopodium podagraria*, *Alchemilla vulgaris*, *Angelica archangelica*, *Campanula rotundifolia*, *Coeloglossum viride* and *Ranunculus acris*, generally only found on older ground or outside the foreland boundary, was found.

The observed life-form changes on the Nigardsbreen foreland follow in general the predicted changes. The decrease in nanophanerophytes and hemicryptophytes presumably reflects the development of the vegetation towards a more layered type where small plants are overshadowed by larger species. This subsequently leads to the loss of these life-forms from older quadrats. There is, however, no significant increase in the proportion of phanerophytes. One reason for this might be that on this low-altitude foreland the tree species are able to invade from an early stage (there is an average of

three tree species in the quadrats on ground deglaciated 86 years previously). Quadrats on younger ground would therefore already show the maximum number of phanerophytes available in this region. The overall importance of woody chamaephytes as a dominating life-form illustrates the fact that the foreland is mainly covered by a pre- to subalpine heath vegetation.

In comparison to the development on the Nigardsbreen foreland, hemicryptophytes on the Storbreen foreland do not lose their importance as a life-form on older ground (Figure 4-12). Their importance rather increases with the age since deglaciation. Woody chamaephytes show a similar trend and both life-forms dominate the foreland on older ground, exemplifying the fact that this foreland lies in an area covered by an alpine heath. The increase of geophytes as a life-form on older ground might be explained with the development of the soil on the foreland and the increase of favourable habitats for this life-form on older ground. Chamaephytes include species like *Silene acaulis*, *Arabis alpina* and *Cerastium uniflorum*. The decrease in importance of this life-form with substrate age confirms their role as early pioneers on the high-altitude glacier foreland. As on the Nigardsbreen foreland phanerophytes do not increase in importance with substrate age. It becomes clear that the predicted changes in life-form dominance have to be interpreted in the light of regional as well as local conditions. The previously mentioned fact that species at Nigardsbreen species can enter the foreland from the steep valley sides is also likely to have affected this trend.

The correlation between soil depth measurements and Messer's predictions works well for the Storbreen large-scale data set. Keeping in mind that Messer demonstrated a high correlation between time and soil depth on this foreland (Messer, 1988; $r^2 = 0.7$, $p < 0.1$, $n = 19$), my measurements from 86 locations on the foreland therefore support the hypothesis of increased soil development over time (also confirmed by linear regression of extreme soil depth with age, $r^2 = 0.27$, $p << 0.01$). This also supports Foskett's (1998:132) finding that terrain age is the most important influence on soil texture.

The values for the Nigardsbreen foreland in this study show little correlation between my soil depth measurements and Messer's predicted values. This could be due to the difference in measuring soil depth (see above) or differences in the site location between the two studies (Messer included 18 sites on the Nigardsbreen foreland in contrast to the 121 large-scale and 253 small-scale quadrats visited in this study).

The relationship between Messer's estimated pH values and the average Ellenberg indicator values is highly significant for all scales on all forelands. The regression coefficients for the large-scale data sets are twice the value of the small-scale data sets (see Table 4-3). This might be an indication that larger areas (16m² quadrats from the large-scale investigation and 1m² quadrats from the small-scale investigation) provide a better basis for the calculation of qualitative Ellenberg indicator values for reaction (it is conceivable that this calculation based on a larger area gives more accurate values than from smaller areas, where the risk of missing important indicator species is increased). The fact that the regression coefficient of the large-scale data set at Nigardsbreen is less significant and only about half of the value at Storbreen is in keeping with Messer's finding that the correlation between pH-values and time on the Nigardsbreen foreland is less strong and less significant than for the same relation on the Storbreen foreland (Messer, 1988: 36, Table 2). It also has to be kept in mind that the Ellenberg indicator values were first designed for use in Central Europe and the fact that the study area lies at the border or even outside the accepted value area for the indicator values explains some loss of their accuracy.

5. Plant Community Ordination And Vegetation and Environment Correlations

"Every moment Nature starts on the longest journey, and every moment she reaches her goal."

- GOETHE, *Maxims and Reflections*, early 19th century

Preface

In the previous chapter the main focus lay on the development of the physical environment and the individualistic trends associated with vegetation development during primary succession on glacier forelands. The next logical step in analysing the processes and patterns of plant succession on recently deglaciated terrain is to investigate the successional change of plant communities. It has been shown in many studies that the concept of plant communities and their change over time provides important insights into the workings of successions. By defining plant communities, progressive and retrogressive vegetation developments on glacier forelands can be easily summarised and conceptualised (see the many studies on successional pathways, e.g. Matthews, 1979a; Richter, 1994). The ability of these studies should not, however, prohibit us from appreciating a historical debate that is still very much alive. Are plant species forming identifiable plant communities or are they simply coincidentally coexisting in certain areas, with no rules for their association? By using a new sampling layout and including data collected at two different scales new evidence for the nature of plant communities and their successional development was sought. The investigation of a low- and high-altitude glacier foreland with comparable methodology also provides valuable information about the differences, if any, between the successions in different environments.

This chapter also introduces a new way of using Ellenberg indicator values for the estimation of average conditions in the sampling quadrats. Instead of costly and time-consuming direct investigation of certain soil and climatic factors, such as nitrogen availability, pH, moisture content, temperature and light conditions, these values allow the investigator to estimate the average conditions of those factors from the vegetation present in the quadrats.

Introduction

Since successions on high-altitude and low-altitude glacier forelands have been shown to differ greatly (Faegri, 1933; Matthews & Whittaker, 1987; Matthews, 1992) one high-altitude foreland, Storbreen (Jotunheimen, ~ 1150-1550 m), and one low-altitude foreland, Nigardsbreen (Jostedal, ~ 250-355 m), were investigated in the 1995 field season. By including the Storbreen foreland, which has been the focus of many investigations and much detailed research (e.g. Matthews & Whittaker, 1987), the approach used herein could be evaluated and compared to previous results. In many previous studies of vegetation development on glacier forelands the existence of plant communities was implicitly recognised, when the investigators presented the successional pathways in their study areas as changes in plant communities. Few scientists regard this use of plant communities as incompatible with the individualistic behaviour of plant species along gradients, first postulated by Gleason (1926). It will be shown in this study that the scale at which the investigation of the vegetation on the glacier foreland was undertaken and the methodology adopted influences the results of the plant community approach.

To characterise environmental factors on the forelands a lot of time and money is usually necessary. By using mean Ellenberg indicator values, calculated from the vegetation of the sampling quadrats, a new way of assessing the environmental properties described by the relevant indicator value was explored.

Methods

Field Sampling

For the purpose outlined above, 5 transects were surveyed in 1995 on the Nigardsbreen foreland and 7 on the Storbreen foreland. They are oriented to provide a decrease in the time since deglaciation along their length. The transects were placed 100 m apart and quadrats of 16m² were surveyed every 100 m along the transects. The layout of the transects and the sampling points is illustrated in Figure 4-4. Identification of the quadrat location was achieved in the field by establishing the transect direction with a compass and measuring 100 m intervals along this line with tape measures. Using the relative location to identifiable features like big boulders or the shape of the moraines,

the locations of quadrats in the field were checked against aerial photographs to avoid any major positioning errors. During the summer of 1995, data from 121 16m² quadrats on the Nigardsbreen foreland and 86 16m² quadrats on the Storbreen foreland were thus collected.

In addition to the large-scale grid a nested approach was used, examining selected areas in a more detailed fashion. The location of these areas was chosen so as to cover areas of differing age and some boundaries of landscape units (as defined in Matthews, 1992) and plant communities. The selected areas were sampled in a similar fashion to the large-scale approach, the difference being the distance between the transects, which was reduced to 10 m and the sampling plot size of 1m². The location of these areas is also shown in Figure 4-4. This investigation yielded data from another 231 quadrats (1m²) from Nigardsbreen foreland and 165 quadrats (1m²) from Storbreen foreland.

The layout of this sampling strategy does not follow the sampling strategy of the Braun-Blanquet methodology (Braun-Blanquet, 1964) in which the scientist identifies plant communities *a priori* and then places the sampling quadrats into homogeneous and representative areas of those communities. For the purpose of this research, where the influence of time-dependent parameters on succession was to be evaluated, the more objective, purely geometrically-arranged sampling scheme described above was necessary. Multivariate numerical analyses (e.g. PC-ORD) were used on these data to investigate the extent of spatial variability within the temporal development of plant communities.

For the characterisation of the physical environment and the overall vegetation development a variety of parameters were recorded, which are described in Table 5-1.

Table 5-1: Parameters of the physical environment and vegetation recorded in the 1995 field season

Parameter	Description
General aspect	main aspect of the plot in degrees, determined by using a compass
General slope	slope of the majority of area within the plot in degrees, determined by using a clinometer
Soil depth	in cm; determined with a metal rod; a mean of 20 stratified random probings and lowest and highest values were recorded
Water regime	two groups, water receiving or water shedding; were determined by evaluating the surrounding area and the likely water movements
Disturbance factors	solifluction, toppling, frost actions, frost churning, cryoturbation, trampling, grazing, mass movement, flowing water, stagnant water, as obvious at the time of investigation
Bare rock face	in percent of plot area
Plant cover	cover of shoots of higher plants in percent of plot area
Substrate size classes	recorded as a score in a triangle, with the corners of the triangle being 100% boulder, 100% rock and 100% fines
Ratio of green to brown lichens (only for Storbreen foreland)	a ratio to be used to estimate snowcover and wind action depending on the observation that brown lichens, *Umbilicaria spp.*, dominate exposed and windswept areas, whereas yellow lichens of the genus *Rhizocarpon* are more commonly found in more sheltered areas (Crouch, 1993)

The soil variables were selected because they are thought to be time-dependent. They have previously been identified as belonging to a terrain age factor complex, which was highly correlated to the successional development of vegetation, as mirrored in the variation extracted by DCA on the Storbreen foreland (e.g. Whittaker, 1989). I nevertheless think that erosion and the topography of the physical environment can exert a strong influence on the distribution of soil at the recorded scale. The soil variables might therefore not always necessarily correlate with the time component on the forelands. Exposure (general aspect and slope) and moisture (water regime) in connection with substrate size classes and disturbance are factors which can represent a microtopographic factor complex (loc. cit.). Due to time and money constraints more quantitative evaluations of parameters such as available soil moisture, pH-values, or available nitrogen were not possible on the scale required herein.

The vegetation data were recorded using a modified Braun-Blanquet scale. After establishment of the quadrat, a list of all the identifiable higher plant species was compiled and the %-coverage or abundance of the individual species was recorded using the key given in Table 5-2.

Table 5-2: Modified Braun-Blanquet scale for estimation of abundance and %-coverage of plant species within plots (after Braun-Blanquet, 1964)

Code	Description
r	Fewer than 5 individuals
+	more than 5 individuals but less than 1% cover
1	1-5%
2a	6-10%
2b	11-20%
3	21-50%
4	51-75%
5	76-100%

The inherent problems of the subjective estimation of the cover values are acknowledged (for discussion see Greig-Smith, 1983), but the fact that all the plots were investigated by the author, will have reduced the chance of introducing individual-based variation in the cover estimates.

It was initially intended to survey most of the transects on the forelands to record their topography for later construction of digital elevation models (DEMs), but this proved too time-consuming and it was subsequently abandoned. DEMs from digitised topographical maps were sufficient for the purpose of visualising plot locations and determination of plot age by comparison of plot location to the location of dated moraines.

It also became clear in initial trials that a Global Positioning System (GPS) used to establish and verify the exact location of the plots rendered unusable results. The average error of 200 m was too big to allow for a precise location of plots, which only lay 100 meters apart (see Fix & Burt, 1995 for discussion of related errors). The plan of using GPS as the sole information for the spatial arrangements of plots and the topographic description of the terrain was therefore abandoned. The establishment of transects were finally restricted to the use of good topographic maps, aerial photographs and compass bearings.

It has to be noted that the use of a compass also contained possible sources of errors. An influence on the accuracy of the compass readings was found to be exerted by some iron containing rocks on the Storbreen foreland. To reduce the influence of deflected readings only a few long distance bearings were taken per transect and when the reading was taken every effort was made to exclude the above mentioned disturbances. Landmark points were thus established in the medium to long distance,

which then were identified and checked on aerial photographs and subsequently used to establish the transect line.

Ordinations

For ecological interpretation of sparse vegetation and environmental data, **correspondence analysis** (CA) and its relatives, as performed by programs like CANOCO, DECORANA, MULVA and PC-ORD, have proven to be very helpful (Persson, 1980; Gauch Jr., 1982; Helm, 1982; Greig-Smith, 1983; ter Braak, 1987-1992; Whittaker, 1989; Eilertsen *et al.*, 1990; Birks & Austin, 1992; ter Braak, 1994; Vetaas, 1994; Zhang & Oxley, 1994; Johnson, 1996; Kent & Coker, 1996). CA is an extension of the method of weighted averaging (Whittaker, 1967). The software packages that provide a CA option and which were used in this study are PC-ORD and CANOCO (ter Braak, 1987-1992; McCune & Mefford, 1997). An assumption made by CA is that response curves of the species under investigation are bell-shaped in regard to environmental gradients. Analysis of the 1995 data showed that this assumption was satisfied for most of the data. In ordinations theoretical variables are constructed, which explain the variance within the species data best. They can be subsequently correlated with measured environmental variables. The algorithms used in the CANOCO software package (and PC-ORD) are summarised in Table 5-3.

Table 5-3: Two-way weighted averaging algorithm of CA (after ter Braak, 1995)

Iteration process		
Step 1	Assign arbitrary, but unequal, initial site scores (x_i, these can be for example plot numbers).	
Step 2	Calculate new species scores (u_k) by weighted averaging of the site scores.	$u_k = \sum_{i=1}^{n} y_{ki} x_i \Big/ \sum_{i=1}^{n} y_{ki}$
Step 3	Calculate new site scores (x_i) by weighted averaging of the species scores.	$x_i = \sum_{k=1}^{m} y_{ki} u_k \Big/ \sum_{k=1}^{m} y_{ki}$
Step 4	For the first axis, go to step 5. For second and higher axes, make the site scores uncorrelated with the previous axes by the orthogonalization procedure described below.	
Step 5	Standardize the site scores. See below for standardization procedure.	
Step 6	Stop on convergence, i.e. when the new site scores are sufficiently close to the site scores of the previous cycle of the iteration; ELSE go to Step 2.	
Orthogonalization procedure		
Step 4.1	Denote the site scores of the previous axis by f_i and the trial scores of the present axis by x_i.	
Step 4.2	Calculate.	$v = \sum_{i=1}^{n} y_{+1} x_i f_i \Big/ y_{++}$

Step 4.3	Calculate new site scores.	$x_{i,new} = x_{i,old} - vf_i$
Step 4.4	Repeat Steps 4.1 - 4.3 for all previous axes.	
Standardization procedure		
Step 5.1	Calculate the centroid, z, of site scores.	$z = \sum_{i=1}^{n} y_{+i}x_i \Big/ y_{++}$
Step 5.2	Calculate the dispersion, s^2, of site scores.	$s^2 = \sum_{i=1}^{n} y_{+i}(x_i - z)^2 \Big/ y_{++}$
Step 5.3	Calculate new site scores.	$x_{i,new} = (x_{i,old} - z)/s$

where y_{ki} **= abundance of species k at site i**
x_i **= site score of site i**
u_k **= species score of species k**

$$y_{+i} = \sum_{k=1}^{m} y_{ki}$$

$$y_{++} = \sum_{i=1}^{n} y_{+i}$$

The axes (= theoretical variables) are constructed so as to maximise the dispersion of the species scores. This maximised dispersion is equal to the eigenvalue (λ) of the ordination axis (in mathematics ordination axes are termed eigenvectors) and is a measure of the importance of the ordination axis in statistical terms. The first axis represents a theoretically constructed factor or a complex of factors which explain the variation within the data best, followed by the next axis which explains the next biggest source of variation within the data and so on. To display the site and species scores in the ordination diagram according to the importance of the axes, Hill (1980) introduced a procedure which is usually referred to as Hill's scaling. After convergence the site scores must be divided by $\sqrt{(1-\lambda)/\lambda}$ and all the species scores by $\sqrt{\lambda/(1-\lambda)}$. The scores so derived are expressed in multiples of one standard deviation (s.d.). Sites whose scores differ by more than 4 s.d. usually have few species in common (ter Braak, 1995). Despite the original high acclaim for the new technique it was subsequently shown that CA (as other ordination techniques then available) suffers from two major faults. First, the ends of the axes are compressed relative to the middle and second, the second axis often shows a systematic relation with the first axis (arch effect).

These two problems are intertwined and...

> "... arise from a discrepancy between the underlying model of RA [reciprocal averaging] and the mathematical properties of communities as exemplified in the Gaussian model of community structure."
>
> **(Gauch Jr., 1982: 150)**

(see Gauch Jr., 1982: 149; Jongman, ter Braak & van Tongeren, 1995: 104; Kent & Coker, 1996: 221 for discussion).

To avoid the "faults" of CA, **Detrended Correspondence Analysis** (DCA) was developed by Hill (1979; see also Hill & Gauch, 1980; ter Braak, 1988a; 1988b). The arch effect is eliminated by detrending so that for any segment along the first axis the mean values of the site scores of higher axes are about zero. There are different procedures for detrending and the one used in this thesis is detrending by segments. This means that the first axis is divided into a number of segments (26 segments is the default value in PC-ORD and was used here) and within each segment the site scores for the second axis are detrended by subtracting their mean (ter Braak, 1995: 106). The same procedure is used for higher axes, detrending them with respect to the corresponding previous axes.

The phenomenon that site scores at the end of the axes are compressed when compared to site scores in the middle of the axes results in species curves being narrower near the ends of the axes than in the centre. Non-linear rescaling of the axes, a procedure developed by Hill (1979), adjusts the width of the species curves so that they are practically equal (Hill & Gauch, 1980).

Tausch *et al.* (1995) and Oksanen & Minchin (1997) point out another problem with ordinations specifically with the older version of the software package CANOCO. The input data order seems to influence the results of the ordination, especially the scores on the second and higher axes. However, tests using the programs provided by Oksanen (1997) on his website showed that the results of the ordinations of the 1995 data do not suffer from this problem. PC-ORD Ver. 3.0 has been corrected for this problem, since a previous bug in the rescaling algorithm has been rectified. It also applies Oksanen and Minchin's "super strict" criteria of tolerance = 0.0000001 and maximum number of iterations = 999. Comparison of the CANOCO and the PC-ORD results showed that, for the data set in this thesis, both software packages produced very

similar ordinations and it was mainly for the superior quality of graphical output that PC-ORD was chosen in this study.

Two-Way INdicator SPecies ANalysis (TWINSPAN)

As indicated in chapter 2 TWINSPAN is the most widely used member of the polythetic divisive classification methods. It is polythetic in the sense that all the species information is being used in the analysis. It is based on ordination techniques and essentially is a form of partitioning ordination space. This takes the form of progressively dividing a single ordination axis from reciprocal averaging or CA into pairs of groups of quadrats and species. The method is explained in some detail in Kent & Coker (1996: 290-303).

Data Selection, Data Transformation and Pre-Analysis Preparation of the Data

In addition to the vegetation data and the environmental variables recorded at the time of the survey of the quadrat (see Table 5-1), some additional factors, which were calculated from the GIS maps and from the Ellenberg indicator value list (Ellenberg *et al.*, 1991) complete the data sets for the DCA analysis (Table 5-4).

Table 5-4: Number and names of environmental variables and factors either recorded in the field (denoted by asterisk) or calculated from the original data, with short descriptions
† denotes an environmental variable only recorded on the Storbreen foreland
†† denotes the environmental variables only used in the large-scale investigations

Number of environmental variable	Name of environmental variable	Short description of environmental variable
	quadrat-name	complete quadrat name (restricted to 8 characters by CANOCO)
1	aspectgr *	orientation of the main plane of the quadrat
2	slope *	slope of the main plane within the quadrat, in degrees
3	soilmini *	minimal depth of any area covered with soil in the quadrat
4	soilmean *	average of soil depth (determined by randomly probing 20 times with an iron rod in the quadrat area which showed soil development)
5	soilextr *	maximal depth of any soil in the quadrat
6	waterreg *	classified in water receiving (1) and water shedding (2)
7	disturbn *	classified into 5 groups according to severity of disturbance[1]
8	bare_roc *	amount of bare rockface found within the quadrat in %
9	plant_co *	amount of plant cover (estimated area of the quadrat covered by plants or pieces of plants) in %
10	substrat *	estimate of clast size and composition
11	X-reduce	UTM X-coordinate reduced by 400000 (Nigardsbreen) and 450000 (Storbreen)
12	Y-reduce	UTM Y-coordinate reduced by 6800000
13 ††	X-grid	X-coordinate on an artificial grid over foreland (from valley side to valley side
14 ††	Y-grid	Y-coordinate on an artificial grid over foreland (from terminal moraine to glacier snout)
15	absdist	distance from the glacier snout in meters
16	reldist	distance from glacier on the artificial grid
17 ††	agegrp	zones of same age as outlined by moraine ridges
18 ††	agemax	maximal possible age for the zone, using the date of the moraines
19	Light	average Ellenberg light value of the species present in the quadrat as far as numbers are available for species
20	Temp	average Ellenberg temperature value of the species present in the quadrat as far as numbers are available for species
21	Conti	average Ellenberg continentality value of the species present in the quadrat as far as numbers are available for species
22	Moist	average Ellenberg moisture value of the species present in the quadrat as far as numbers are available for species
23	React	average Ellenberg reaction value of the species present in the quadrat as far as numbers are available for species
24	Nitro	average Ellenberg nitrogen value of the species present in the quadrat as far as numbers are available for species
25 †	lich_rat *	a ratio summarizing the local abundance of brown lichens, *Umbilicaria spp.*, and yellow lichens of the genus *Rhizocarpon* (see Table 5-1)

For aspect, a four point ordinal scale was devised. It seems a reasonable assumption that south-facing quadrats receive more energy in the form of sunlight and

[1] Disturbances encountered include: mass movement, grazing, solifluction, running water, sedimentation, trampling, cryoturbation, frost sorting, treefall, avalanches and snowcover.

therefore should be ranked higher in the scale than east and west facing quadrats, which are still more favourable than north facing quadrats. Quadrats lacking any slope were assigned an aspect group of 3 to reflect an intermediate energy influx level.

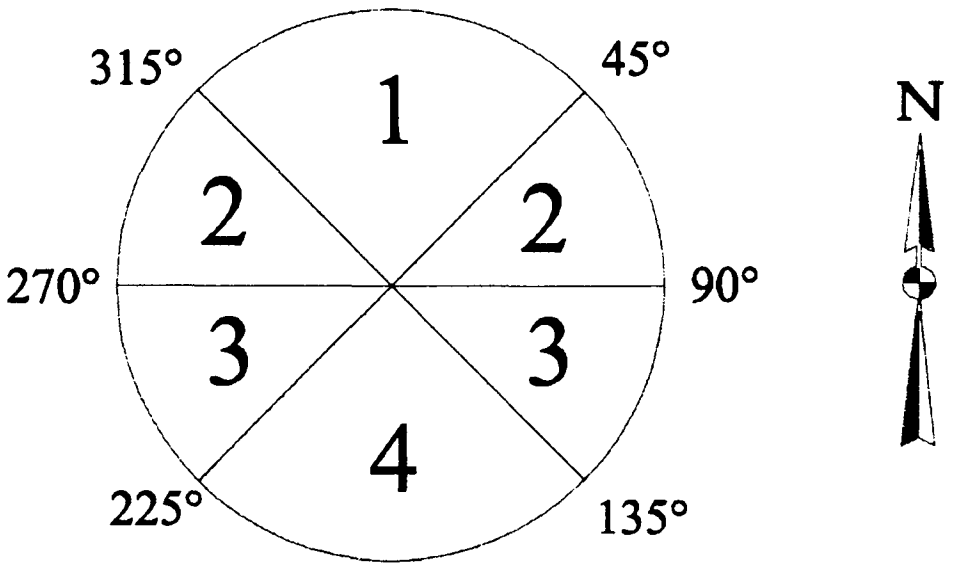


Figure 5-1: Grouping of different aspects into four classes.

At the time the quadrat was visited the types of (recognisable) disturbances acting on the vegetation and environment were noted. A disturbance number was calculated per quadrat according to the number of different disturbances. Low values of the disturbance number reflect little disturbance in the quadrat and high values a high disturbance regime. This does not consider varying qualities of different disturbances and assumes that the overall effect is additive.

Substrate properties and composition were recorded as proportions of three clast sizes. The proportions of the three classes shown in Table 5-5 were recorded in the field in a graphical representation of a triangle, each corner representing substrates consisting of 100% of the respective class (after Petch & Whittaker, 1996). An example of this way of denoting varying proportions of clast sizes is given in Figure 5-2.

Table 5-5: Clast sizes for the characterisation of substrate

Description	Size range
Fines (F)	0 - 5 cm
Rocks (R)	6 - 50 cm
Boulders (B)	> 51 cm

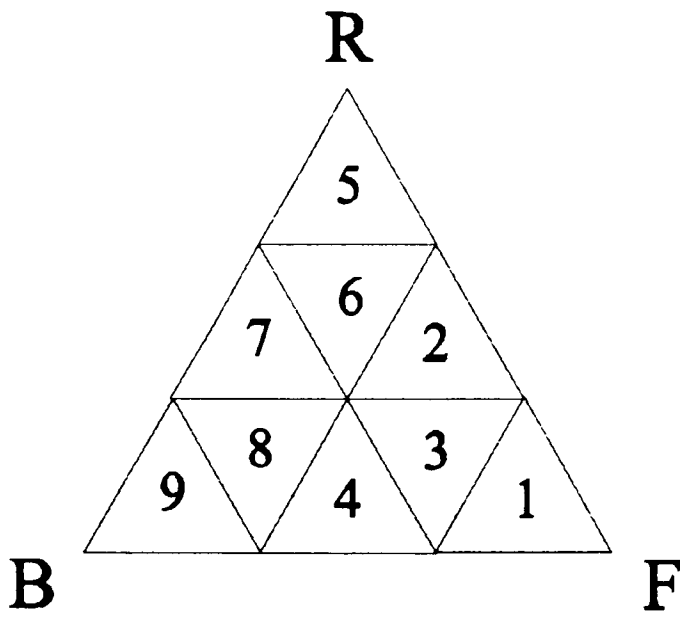


Figure 5-2: Representation of varying proportions of clast sizes of substrate.

The numbers in the main triangle correspond to differing proportions of the three clast sizes (e.g. substrate classified as number 5 consists mainly of rocks with very little fines and boulders). The substrate numbers were chosen to form an ordinal scale along which the water hoding capacity (availability of water for the plants) of the substrate decreases due to the increased proportion of bigger clast sizes.

The Ellenberg values were taken from the literature (Ellenberg *et al.*, 1991; Lindacher, 1995). Other Ellenberg indicator values provided by Firbank *et al.* (2000) could be viewed as more appropriate for the study area in Norway. These have been adapted and developed from the original indicator values for Central Europe to represent the ecological behaviour of species on the British Isles. Similarly to the situation in England, the study sites in Norway are sometimes at the edge of the distribution ranges of the species involved. However, analysis of the correlation between both sets of values (Table 5-6) and comparison of the relevant indicator values from both publications with the actual ecological behaviour of the plants in the study areas led to the belief, that the original values give a truer representation of the realised niches in Norway. One factor in this might be the alpine character of the study sites. There are more similarities between the study sites in Norway and central European alpine environments than with the coline and montane environments on the British Isles. It was therefore decided to use the original Ellenberg indicator values for Central Europe.

Table 5-6: Spearman rank correlation between original Ellenberg indicator values (Ellenberg *et al.*, 1991) and Firbank *et al's* (2000) indicator values for the species present in the study sites. $p < 0.0001$ for all values.

Light	Reaction	Moisture	Nitrogen
0.77	0.86	0.86	0.71

Mean values for each Ellenberg value within each quadrat were initially calculated in two different ways. The qualitative way only uses the presence/absence of species to decide whether to include their indicator value in the calculation of the average indicator value for the quadrat. In the quantitative approach the Ellenberg indicator value for each plant species is multiplied by the cover value recorded for this species within the quadrat and is then averaged over the quadrat. This way more weight is given to the more abundant species (e.g. used by Persson, 1981). Regressions between the quantitative average Ellenberg characteristic indicator values (CIVs) and the corresponding qualitatively derived Ellenberg indicator values calculated for the Nigardsbreen large-scale investigation shows strong correlations between both (Figure 5-3). It was therefore decided to use the qualitative average Ellenberg indicator values in the ordinations, as recommended by Ellenberg *et al.* (1991: 27).

These Ellenberg indicator values were used in the ordination analyses in the environmental variables data set, where they represent estimates of the corresponding environmental factor within each quadrat.

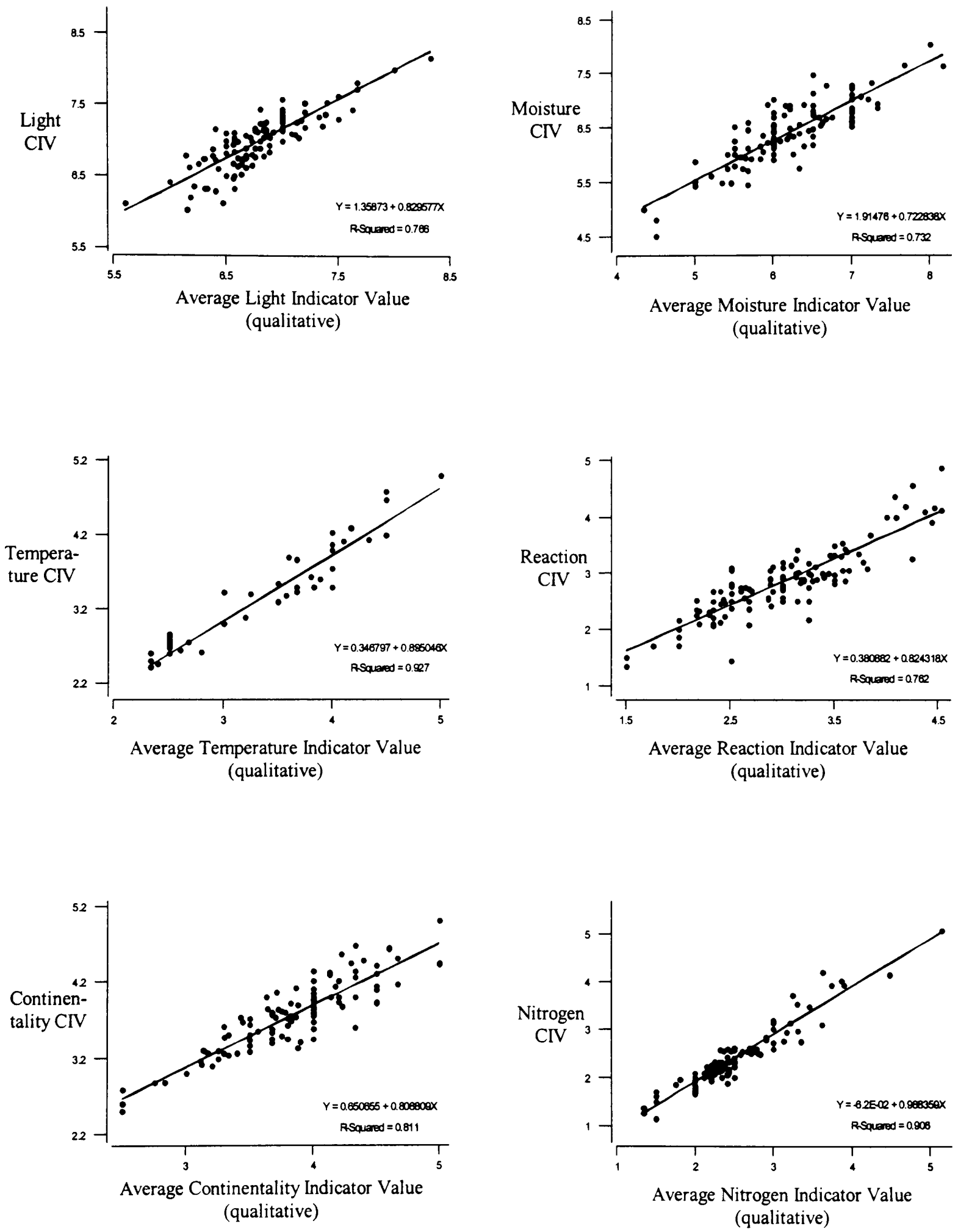


Figure 5-3: Regression plots of qualitatively and quantitatively calculated average Ellenberg indicator values calculated for the Nigardsbreen large-scale data.

The UTM-coordinates were taken from ARC-INFO coverages of the study sites (20 m contour lines were digitised from 1:50000 topographic maps) and had to be

reduced by 40000 and 680000 for the longitudinal and latitudinal values respectively, due to a restriction for the number size in the PC-ORD software package.

The X-foreland and Y-foreland values correspond to the location of the quadrats on an imaginary grid overlaying the foreland. The Nigardsbreen foreland is symmetrically divided into two parts by the meltwater stream. For the left side of the foreland the X-foreland values are negative decreasing with distance from the meltwater stream, whereas the right side of the foreland has positive X-foreland values, increasing with distance from the meltwater stream. Similarly, at Storbreen the artificial grid was divided symmetrically. But rather than being associated with the occurrence of a meltwater stream at the centre of the foreland this symmetrical division is not based on a naturally occurring feature and only relates to the relative location of the quadrats to the valley sides and their distance from the glacier snout.

The variable *absdist* was calculated from ARC-INFO maps (called coverages) and represents the actual distance in meters of the quadrat to the tip of the glacier tongue. This variable was included to test for the influence of factors such as temperature, which may be influenced by the proximity of the ice mass (glacier winds have been shown to influence temperatures considerably (Matthews, 1992). *Reldist* is a distance measure that corresponds to the location of the quadrats on the artificial grid. Although these two distance measures are strongly correlated, as can be expected ($r^2 = 0.99$; Figure 5-4), *reldist* is used to see if a cruder resolution could still give interpretable results.

Agegrp and *agemax* were obtained from ARC-INFO coverages by locating the quadrats in relation to dated moraine ridges (digitised from Bickerton & Matthews, 1992). In *agegrp*, the quadrats are assigned to classes of ages (class number increases with presumed age), whereas *agemax* uses the age estimates of Bickerton & Matthews (1992) to assign maximal ages to the quadrats. The two measures show a strong correlation ($r^2 = 0.99$; Figure 5-5), but both are nevertheless included in the analysis to give a comparison of their ecological interpretability. It has to be kept in mind that these ages are maximal estimates because of the problems associated with the dating of intermoraine areas. It is not always possible to derive exact ages of intermoraine areas by interpolating from moraine ages, as shown by studies of the Austerdals foreland (Maizels & Petch, 1985; Petch & Whittaker, 1997). The areas between the moraine ridges are subject to major disturbances in the form of extensive reworking by the episodically changing stream channels. The time the substrate has had to consolidate and the time

available for plants to colonise these areas is therefore thought to be considerably shorter than the time since the retreat of the ice would sometimes imply. The comparable geomorphological situation with a major meltwater stream running through the centre of the Nigardsbreen foreland suggests that, at least in parts of the foreland, similar drastic reworking has taken place or is likely to have happened.

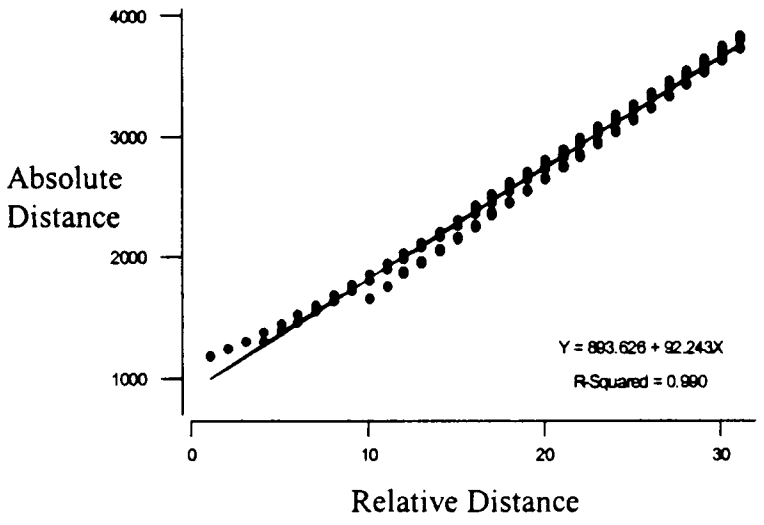


Figure 5-4: Regression plot of relative distance and absolute distance of quadrats from glacier snout. Nigardsbreen large-scale data.

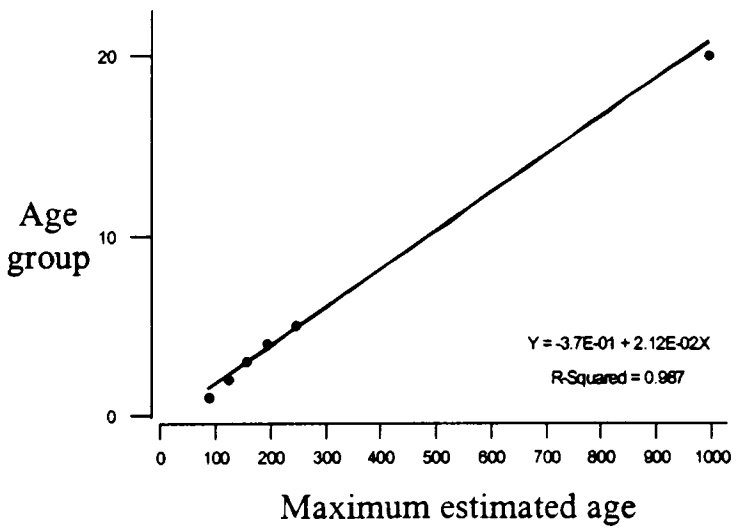


Figure 5-5: Regression plot of maximum estimated age using the dates provided by Bickerton & Matthews, 1992 and age group. Nigardsbreen large-scale data.

For the Storbreen foreland, one additional variable was recorded. The ratio of green to brown lichens on rocks was estimated and noted (Table 5-1). This number has

been shown by Crouch (1992; 1993) to correlate with snow-cover and wind exposure due to differential adaptation of the two lichen groups involved. Since the vegetation cover on the Nigardsbreen foreland was much greater and most of the quadrats did not have a reasonable amount of the two genera of lichens this ratio could not be recorded in all the quadrats.

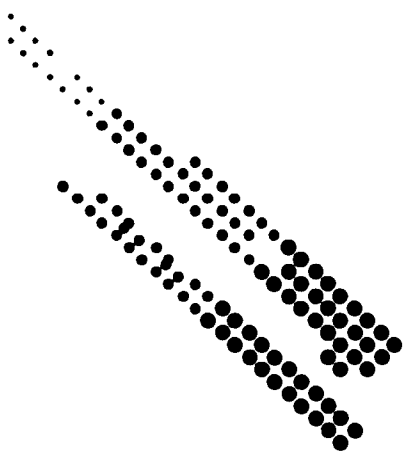
Time-dependent (e.g. a terrain age factor complex), as well as time-independent factor complexes (e.g. a snow melt/exposure/moisture factor complex), have been identified as the major correlates of vegetation compositional pattern on the Storbreen foreland in South-Central Norway (e.g. Whittaker, 1987). Using the 1995 sampling design described earlier, the importance of such factor complexes on the successional development of vegetation was investigated on the Nigardsbreen and Storbreen forelands visited in 1995. According to the chronosequence approach, each large-scale transect on either foreland is seen to represent a gradient along a time axis, with the youngest terrains closest to the glacier snout. The data were analysed using ordination techniques, which lead to the ordering of sample sites along mathematically constructed axes. If the data support the hypothesis of the importance of similar to the above mentioned factor complexes, it is expected that these axes will correlate strongly with the environmental and geographical variables, which represent the time gradient (y_reduced, agemax, agegrp, absdist and reldist; Figure 5-7 and Table 5-4) and time-independent factors (e.g. disturbance levels, soil variables and the occurrence of bare rockface within the quadrat). It is thought that the latter variables, although sometimes influenced and changed throughout time, are primarily controlled by meso- and microtopography or geographical location (see Figure 2-6 and Figure 5-8, see for Kendall's tau correlation coefficients and significance levels).

Figure 5-6: Kendall's tau correlation coefficients, significance levels and number of paired variables for the non-parametric correlation of various variables with time on the Nigardsbreen foreland (agemax). Italicised variables are referred to in the text as time-dependent

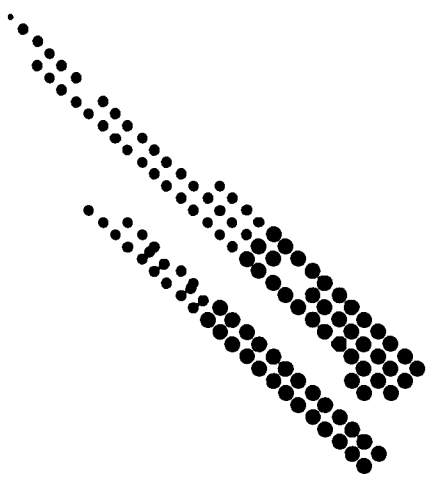
	aspect gr	slope	soilmi ni	soilme an	soilex tr	waterr eg	distur bn	bare_r oc	plant_ co	substr at	*X-reduce*	*Y-reduce*	X-forela	*Y-forela*	*absdist*	*reldist*	*agegrp*
Correlation Coefficient	-0.113	-0.207	-0.338	-0.297	-0.221	0.055	0.163	0.106	0.026	0.008	0.808	-0.821	-0.021	-0.886	0.867	0.886	1
Sig. (2-tailed)	0.177	0.022	0	0	0.002	0.504	0.027	0.12	0.701	0.906	0	0	0.778	0	0	0	0
N	102	73	117	117	117	120	121	121	121	121	121	121	121	121	121	121	121

In this connection the use of the Ellenberg indicator values as representations of the average conditions of the relevant factor within the quadrats, provides a new means for the analysis of vegetation development on glacier forelands. They were therefore included in the DCA-analyses as environmental variables, which at the end of each ordination are correlated to the extracted DCA-axes. The strength of the correlation of the different variables can be used as an indication for which of the factors or factor complexes form the dominant influence on the vegetation variation.

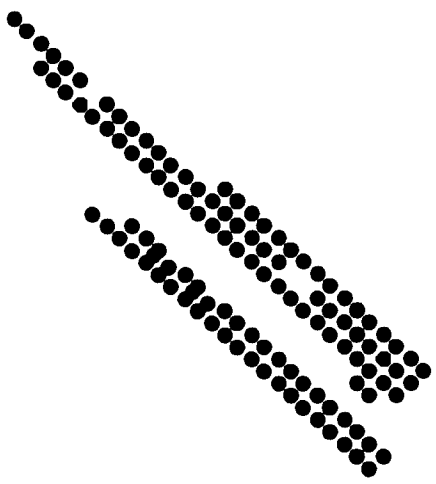
a) Variable reldist



b) Variable absdist



c) Variable y-reduced



d) Variable agegrp

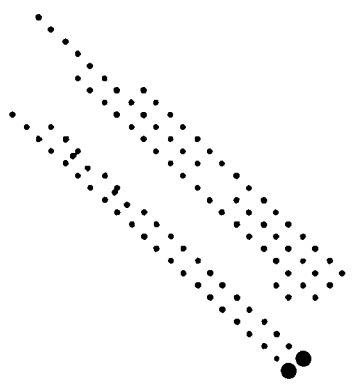


Figure 5-7: Location plots of time-dependent variables used in the DCA. Top of page is north, distance between quadrats is 100m (see Figure 3-12 for quadrat location). Size representation of the variables is relative for each figure.

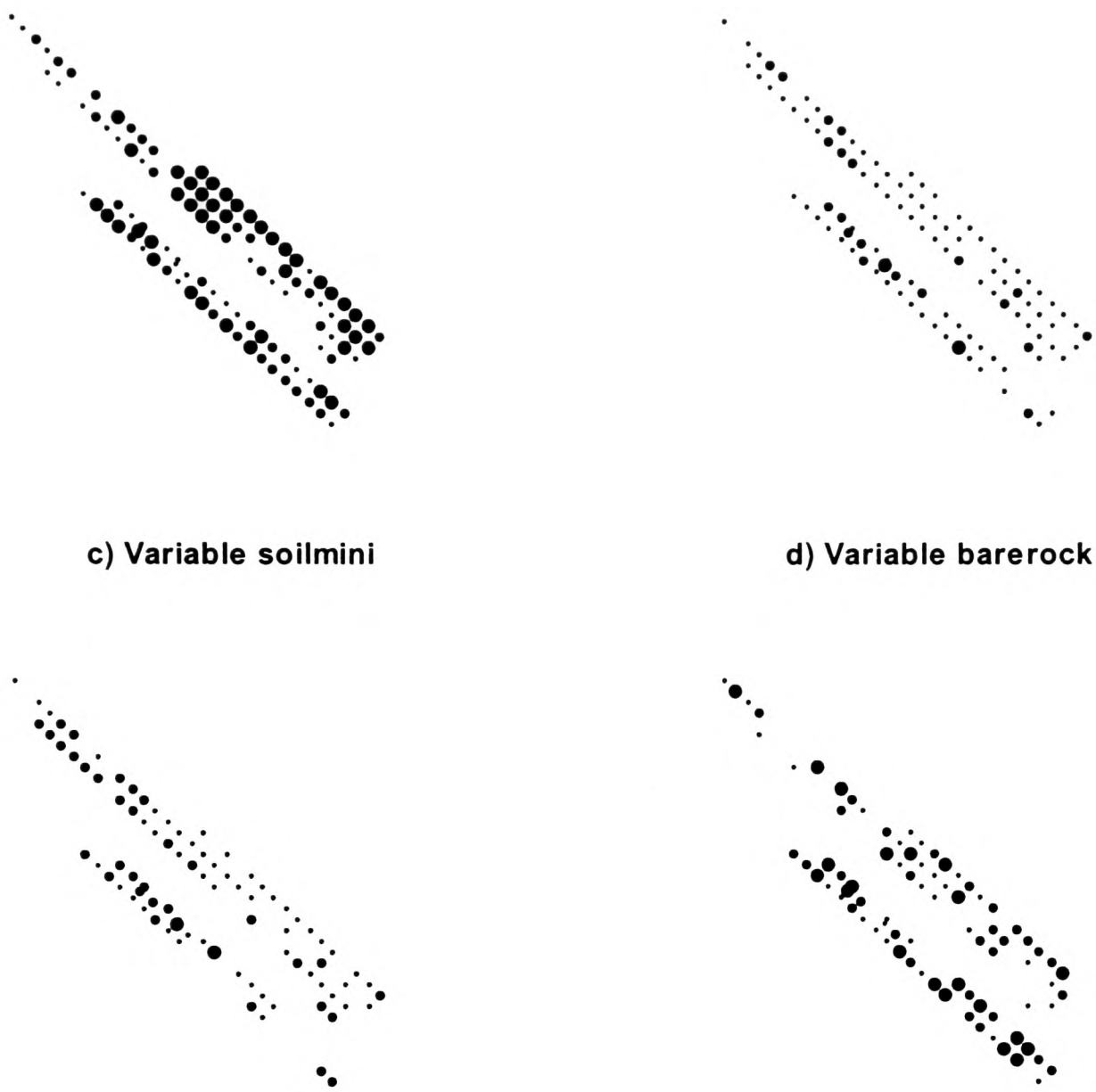


Figure 5-8: Location plots of time-independent variables used in the DCA. Top of page is north, distance between quadrats is 100m (see Figure 3-12 for quadrat location). Size representation of the variables is relative for each figure.

The inclusion of small-scale sampling grids on terrain of different ages, is another approach to test the hypothesis of the influence of time on the development of plant communities on glacier forelands. The small-scale sampling design provides a reasonable number of independently sampled sites from different terrain age groups on each foreland. If the vegetation on the terrains of different age reflect a change of plant communities controlled by time, ordination and classification of these sets should result in a clear distinction of the sets of different ages. The change of sampling scale also allows investigation of the importance of environmental variables at large and small-scales. It is expected that the geographical variables such as the soil variables, which can

be highly variable over short distances may be important to succession at small-scales. A comparison of the factors identified as the ones to influence the succession for the large- and small-scale investigation is also expected to shed some new light on the importance of scale in succession studies on glacier forelands.

The influence of data transformations on ordination analyses has been investigated by many scientists (e.g. Tüxen & Ellenberg, 1937; Orlóci, 1978; van der Maarel, 1979; Jongman, ter Braak & van Tongeren, 1995: 21). Different transformations tend to stress different aspects of the vegetation data when these data are used in ordination analyses. The presence/absence scale for example emphasises rare species by considering their presence to be of equal importance to the presence of common species. The transformation suggested by Tüxen & Ellenberg (1937) on the other hand takes the centres of the Braun-Blanquet cover classes, hence giving strong importance to dominant species. Van der Maarel (1979: 112) states that:

> "In all examples classification and ordination results obtained with intermediate transformations were superior to those obtained with either a strong weighting on mere presence, or an emphasis on dominance."

As a result of van der Maarel's work an intermediate transformation, which balances the importance of presence and dominance of species is used in this thesis.

Table 5-7: Transformation table with symbols used in the field to record frequency and abundance of species and the corresponding values of the van der Maarel transformation used in the DCA

Modified Braun-Blanquet scale used in the field	Description of frequency and % shoot cover	Modified van der Maarel scale (van der Maarel, 1979:101)
r	very rare, less than 5 individuals	1
+	more than 5 individuals but less than 1%	2
1	1 - 5%	3
2a	5 - 10%	5
2b	10 - 20%	6
3	20 - 50%	7
4	50 - 75%	8
5	75-100%	9

Although presence and abundance of mosses and lichens were recorded during the 1995 field season it was decided not to include these data in the ordination analyses. These two plant forms were found in 100% (large-scale) and 97% (small-scale) of the

surveyed quadrats on the Nigardsbreen foreland, and they are therefore not thought to contain discriminative information about environmental gradients, but rather mask any ecological gradients by their dominant occurrence. Problems in plant sociological research associated with these plant forms arise firstly because of the broad environmental range of conditions mosses and lichens can tolerate, therefore differing in their ecological behaviour from higher plants. Crouch's (1992) findings support this point by showing that bryophytes and lichens exhibit rather different community patterns from higher plants on the Storbreen foreland. Secondly, the fact that these groups were surveyed as compound life-form classes, in which different species with a big range of environmental requirements and behaviours were pooled, might confound any gradients that may exist.

Outliers can unduly influence the correlation coefficients used in the interpretation of the ordination, introducing strong correlations that have little to do with the majority of the data (Jongman, ter Braak & van Tongeren, 1995; McCune & Mefford, 1997). The outlier analysis option of PC-ORD was therefore used to check the data sets for such "freak" occurrences. Where necessary the species and quadrats involved were removed from the ordination.

The downweighting option of PC-ORD was used to avoid excessive influence of rare species on the final ordination result (Jongman, ter Braak & van Tongeren, 1995). This option eliminates weak and obscuring gradients from the ordination due to rare species.

For the few quadrats where some of the environmental variables could not or have not been recorded, the average of the variable across all other quadrats was used. Since the exclusion of a variable with a few missing values seems to be a waste of hard earned data, this method of dealing with missing values provides a chance of still being able to use the variable in the analysis. It does not involve subjectivity and is therefore preferable to "educated guesses" or regressing the variable that contains missing values on other variables. Replacing missing values with the mean for a given variable does not change the overall average of this variable and usually has little effect on the outcome of the analysis. It will, however, reduce the variance of the variable and will often weaken the correlation structure slightly (McCune & Mefford, 1997).

Results

Nigardsbreen Large-Scale Data Set

A DCA analysis was performed for each transect on the Nigardsbreen foreland on the whole range of higher plants, living and recorded in the quadrats surveyed (with the restrictions outlined above). By incorporating all species in this analysis, uncommon species, which might be good indicators for certain environmental conditions, were still used in the ordination. This analysis was expected to lead to the extraction of meaningful, ecologically interpretable DCA-axes, since it uses most of the information which is available in the 1995 data sets.

The hypothesis tested with the ordination analyses of these data sets is, that the factor complexes which have been identified as being important for the determination of plant communities on high-altitude glacier forelands in South-Central Norway (Matthews & Whittaker, 1987), are also important for the development of the vegetation on low-altitude forelands such as for example Nigardsbreen.

The picture that emerges from the correlation coefficients of the environmental variables with the first DCA-axis suggests, that although no simple correlation of this axis with age or age related factors, like distance from the glacier snout, exists (Table 5-8), some age related factors show significant correlations with the first DCA-Axis. For example in transect 1, 3 and 5 the variable agegroup is significantly correlated with the first DCA-axis at the 95%-level. Although there is a very high correlation between the variable agegroup and agemax (r=0.99; as can be expected, since agegroup was constructed from the estimated maximal ages since deglaciation provided by Bickerton & Matthews, 1992), in transect 5 agemax fails to register as being significantly correlated with the first DCA-axis.

Transects 2 to 5 show significant correlation with the other three age dependent variables, y_reduced, absdist and reldist at least at the 95%-level. As will be explained later in this chapter, this strong correlation with these distance measures has to be interpreted with care, especially in transects 2 and 5. But why is transect 1 not correlated with those three variables?

The only variable consistently correlated with the first DCA axis of each transect at the 99% level is the number of species in the sample plots (Table 5-8; 0.85, -0.83, 0.80,

0.63 and –0.60, respectively). This lends support to the hypothesis of the paramount influence of age on vegetation development and is in keeping with the observation of increasing richness as vegetation develops during succession on other glacier forelands (e.g. Chapin III *et al.*, 1994). The increase of species numbers has nevertheless to be used with caution for the interpretation since all plots are, due to their location in arctic and alpine environments, relatively species poor (average species number per quadrat is 9.6, median = 9). One additional species, which does not have to appear anywhere else in the study area, will make a big difference in the richness of one plot. These additional species tend also to be the outliers which influence the ordination, forcing it to extract the corresponding factor as a dominant axis.

Table 5-8: Pearson's correlation coefficients for environmental and geographical variables with the first DCA Axis for individual transects. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level

Variable	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5
Soilmini	n.s.	n.s.	0.61	0.48**	n.s.
Soilmean	n.s.	n.s.	n.s.	0.42*	n.s.
Soilextr	0.46*	n.s.	n.s.	0.48**	n.s.
Disturbn	n.s.	0.51**	n.s.	n.s.	n.s.
Bare_roc	n.s.	0.60**	-0.51**	-0.35*	n.s.
Plant_co	0.41*	-0.45*	0.55**	0.39*	n.s.
X_reduce	n.s.	0.40*	-0.47**	-0.36*	0.52*
Y_reduce	n.s.	-0.41*	0.47**	0.36*	-0.52*
Absdist	n.s.	0.40*	-0.47**	-0.35*	0.51*
Reldist	n.s.	0.40*	-0.47**	-0.36*	0.52*
Agegrp	0.45*	n.s.	-0.39*	n.s.	0.48*
Agemax	0.48*	n.s.	-0.36*	n.s.	n.s.
Light	-0.57**	n.s.	-0.58**	-0.45**	n.s.
Temp	0.41*	n.s.	0.64**	0.55**	-0.67**
Conti	0.60**	n.s.	0.38*	n.s.	n.s.
Moist	n.s.	-0.43*	n.s.	n.s.	n.s.
React	0.40*	n.s.	0.54**	0.45**	-0.69**
Nitro	0.42*	n.s.	0.64**	0.92**	-0.71**
No.ofspe	0.85**	-0.83**	0.80**	0.63**	-0.60**

A correlation analysis of the DCA-scores of the first DCA-axis shows, that the 5 transects form two groups. Transects 1, 3 and 4 show positive and highly significant correlation coefficients and all three of them show negative correlation coefficients with transects 2 and 5, which in turn are themselves highly positively correlated with each other (Table 5-9).

Table 5-9: Kendall's tau correlation coefficients between the correlation coefficients of the environmental variables in Table 5-8. * and ** denotes significance at 95% and 99%, respectively

	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5
Transect 1	1				
Transect 2	-0.26	1			
Transect 3	0.46**	-0.52**	1		
Transect 4	0.42*	-0.40*	0.83**	1	
Transect 5	-0.22	0.52**	-0.67**	-0.71**	1

When the DCA sample scores for the first DCA axis are plotted on a map of the foreland it becomes clear that all transects except transect 5 show a rather complicated pattern. The DCA-scores cannot be translated straightforwardly into a temporal sequence of variation change. The size of the disks in Figure 5-9 corresponds to the relative location of the sample plots on the first DCA-axis, with smaller disks at the negative side of the axis and larger disks at the positive end of the axis. At this scale stochastically distributed factors like the highly fragmented nature of the environment (exemplified by the amount of bare rockface within a quadrat; Figure 5-8) and the ongoing disturbance by periglacial processes seem to exert more influence on the vegetation variation than strictly time-dependent components.

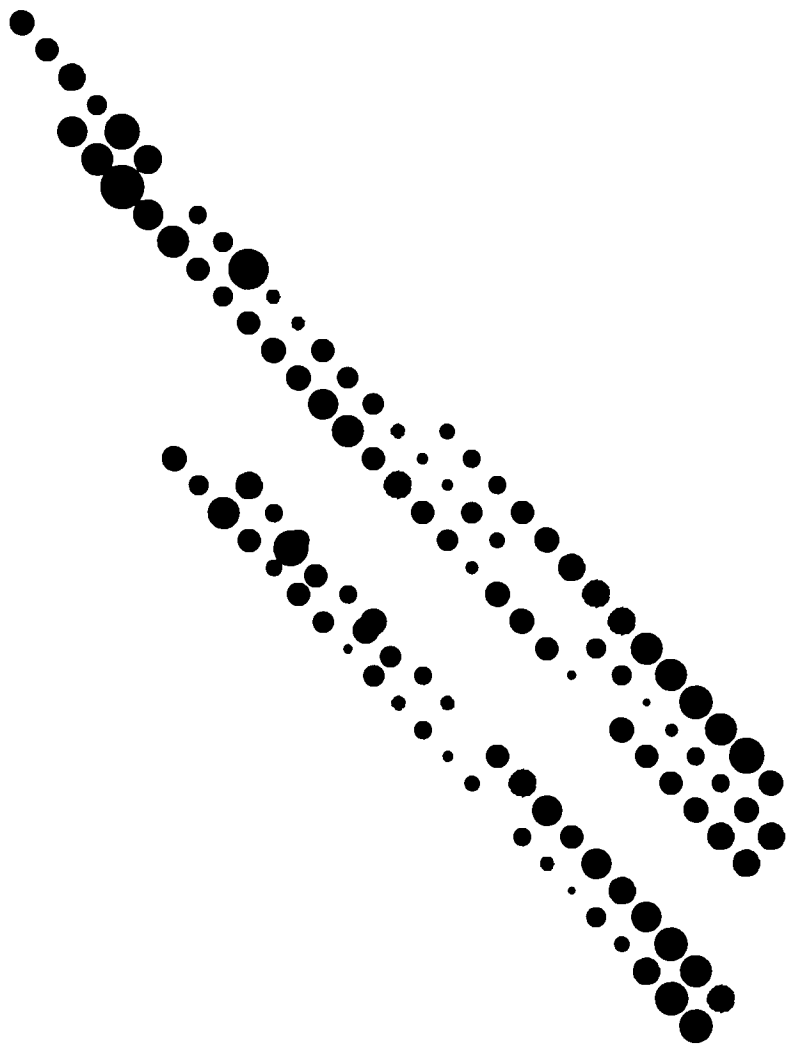


Figure 5-9: DCA sample scores of the first DCA axis for Nigardsbreen large-scale data set. Sample scores derived from ordinations on individual transects. Top of page is north, distance between quadrats is 100m (see Figure 3-12 for quadrat location). Size representation of the variables is relative.

Figure 4-4 shows that transect 2 lies close to the centre of the glacier foreland, which is constantly fluvially reworked by the large glacial stream. Some of the quadrats closest to the glacier were actually located in the meandering flood-plain of the stream, having very different species composition to the rest of the quadrats in the transect. The species found in those quadrats are indicators for wet soil conditions. The vegetation variation extracted by the first DCA-axis shows therefore a strong correlation to the Ellenberg indicator value for moisture ($r=-0.43$; $p \geq 0.05$). Since quadrats which lay in the area of the flood-plane were found towards the glacier, this also increased the directional vegetation variation along the length of the transect, making variables like absdist, reldist

and y_reduced significantly correlated with the first DCA-axis. This exemplifies that correlation of environmental variables with DCA-axes have to be interpreted very carefully and with the appropriate knowledge of the study area to avoid false conclusions.

The values for the species variance explained by the first two DCA axes are low when compared to values in the literature (Table 5-10). Jensen (1978) reports values of 51.5% and 24.4% for a comparable transformation scale on nymphaeid and elodeid vegetation and 46.6% and 19.8% on helophyte vegetation, whereas van der Maarel (1979) calculates values of 25.3% and 13.1% for *Arrhenatheretum* data and 24.3% and 20.0% for the *Spartinetea* data (all values for the first two axes, respectively). The lower percentage values of variance explained in this study might be a result of the specific sampling design. As explained earlier the area of the foreland was sampled using a strictly geometric placement of the sampling quadrats. This approach, at this scale, seems to encounter problems in detecting environmental gradients. The gradients for the measured variables are heavily fragmented by the physical disturbances on the forelands and therefore not continuous over space. By including sampling plots which lie in "unusual" environments the environmental gradients which might be present will be obscured. As can be expected attempts to use ordination on such a data set will not produce an ordering of species and quadrats along strong gradients. The use of a Braun-Blanquet or a stratified random sampling design (e.g. Matthews, 1979b) might have avoided some of the problems. By sampling only the homogeneous areas of "identifiable" communities or well vegetated patches there is a certain pre-selection of "favourable" environments, making the detection of environmental gradients more likely.

Table 5-10: Species variance explained by the first two DCA-axes (in % of total variance)

	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5
Axis 1	53.8	26.7	25.0	34.3	19.9
Axis 2	7.0	9.1	17.9	-1.9	10.5

Table 5-10 shows that the first axis of the ordination explains large amounts of the species variance in the data set. This suggests a dominant important factor or factor complex, which can be represented by the first DCA-axis. The correlation coefficients for the second axis show, that except for transects 2 and 4 none of the age dependent

variables are significantly correlated with the second DCA-axis (Table 5-11). This suggests that the primary influence on the vegetation development is indeed a complex of time related factors, modified by a set of geographical and location variables, which are micro- and meso-topographically controlled.

Table 5-11: Pearson's correlation coefficients for environmental and geographical variables with the second DCA Axis for individual transects. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level

Variable	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5
Soilmini	n.s.	n.s.	n.s.	n.s.	-0.50*
Soilmean	-0.51**	0.41*	n.s.	0.35*	-0.55*
Soilextr	-0.54**	0.47*	n.s.	0.37*	n.s.
Disturbn	n.s.	n.s.	0.37*	-0.47**	n.s.
Bare_roc	0.51**	n.s.	n.s.	n.s.	n.s.
Plant_co	n.s.	-0.49*	n.s.	n.s.	-0.52*
X_reduce	n.s.	-0.46*	n.s.	-0.36*	n.s.
Y_reduce	n.s.	0.45*	n.s.	0.36*	n.s.
Absdist	n.s.	-0.46*	n.s.	-0.34*	n.s.
Reldist	n.s.	-0.46*	n.s.	-0.36*	n.s.
Agegrp	n.s.	n.s.	n.s.	-0.34*	n.s.
Agemax	n.s.	n.s.	n.s.	-0.34*	n.s.
Light	0.64**	n.s.	-0.66**	n.s.	n.s.
Temp	n.s.	n.s.	n.s.	n.s.	n.s.
Conti	-0.45*	0.39*	0.52**	0.46**	-0.46*
Moist	n.s.	0.62**	n.s.	0.40*	-0.44*
React	n.s.	n.s.	n.s.	n.s.	-0.44*
Nitro	n.s.	0.48*	0.52**	n.s.	-0.46*
No.ofspe	n.s.	n.s.	n.s.	n.s.	n.s.

Eigenvalues of the ordination are a measure of the importance of the respective axis (e.g. Whittaker, 1989: 420) and represent the spread of the species along the ordination axes. The eigenvalues of the DCA-axes of this analysis are also low when compared to the values from the literature (Table 5-12).

Table 5-12: Eigenvalues of the first two DCA-axes for each transect

	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5
Axis 1	0.31	0.27	0.31	0.41	0.35
Axis 2	0.14	0.18	0.19	0.14	0.23

An ordination of the whole data set (not divided into individual transects) also reveals an indication of strong correlations with age related variables (see Table 5-13). The only time-dependent variables not correlated with the first DCA-axis at the 95%-level are agegrp and agemax. That the time-dependent variables should play a major role

in explaining the variance of the species in the whole data set is an indication that even within the whole data set age related factors exert a major control on the variation of the vegetation. Amongst other factors not necessarily related to time are nitrogen availability within the plots as demonstrated by the Ellenberg indicator value for nitrogen, which has a very significant correlation coefficient with the first DCA-axis ($r=0.70$; $p \geq 0.01$). As hypothesised earlier the nitrogen conditions on a glacier foreland may change with time, but they are also likely to be influenced by micro- and meso-topography.

Table 5-13: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the whole large-scale data set. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level

Variable	Complete data set
Soilmini	0.16*
Soilmean	n.s.
Soilextr	n.s.
Disturbn	0.15*
Bare_roc	-0.29**
Plant_co	0.40**
X_reduce	-0.15*
Y_reduce	0.42**
Absdist	-0.26**
Reldist	-0.31**
Agegrp	n.s.
Agemax	n.s.
Light	-0.53**
Temp	0.53**
Conti	n.s.
Moist	n.s.
React	0.53**
Nitro	0.70**
No.ofspe	0.61**

The results for the Nigardsbreen foreland suggest that time has an important role to play in the composition of successional vegetation on the low-altitude glacier foreland in front of Nigardsbreen in South-Central Norway. The analysis, however, also shows that time-independent factors, like disturbance levels and the distribution of suitable habitats influences the phytosociological mosaic on glacier forelands significantly. With this result the succession on low-altitude glacier foreland vegetation seems to be controlled by similar factors to the succession found on the Storbreen foreland by Matthews and Whittaker (1987). The apparent differences, with the Nigardsbreen foreland showing a less pronounced influence of time-dependent factor complexes on the succession, may be

explained firstly by the sampling design, which was less exhaustive and more objective than the one on the Storbreen foreland as well as, secondly, the slightly less severe environmental conditions which govern the low-altitude glacier foreland.

Nigardsbreen Small-Scale Data Sets

One aim for the use of the small-scale sampling design was to try and investigate the influence of scale on the detection of spatial variation in the vegetation and its relation to environmental factors. To investigate this aspect DCA site scores of the first DCA-axis in the three small-scale blocks were plotted in relation to their location within the block. The ordination scores represent differences between the sites in their vegetation composition (sites with similar scores vary little in their species inventory). Each block was analysed independently and the results of the ordinations are graphically represented in the following figures. For location of the blocks on the foreland see Figure 4-4.

Nigardsbreen Small-Scale Block I (N2-95, 192 and 245 years since deglaciation)

The first step of the investigation of the variance within the data set in block I aims to identify the factors which influence the vegetation development at this smaller scale. Within this block, 25 quadrats lie on substrate deglaciated 245 years ago and 29 quadrats in an area ice free for 192 years. The graph of the sample DCA-scores of the first DCA-axis in Figure 5-10 shows that there seems to be no variation in the data set which is attributable to the age of the substrate.

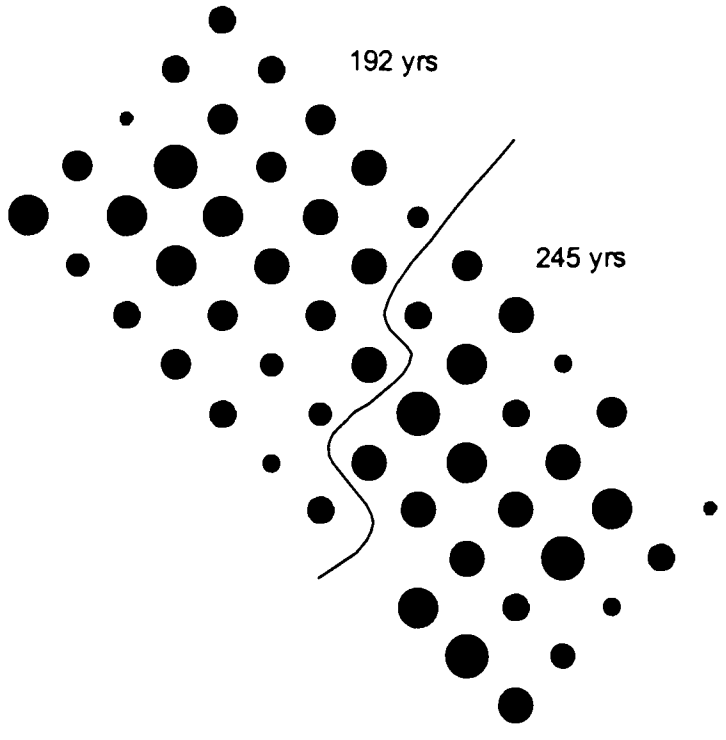


Figure 5-10: DCA sample scores of the first DCA axis for block I of the small-scale data set. Top of page is north, distance between quadrats is 10m. Size representation of the variables is relative. For location of block I on the Nigardsbreen foreland see Figure 3-12.

The environmental variables most significantly correlated with this axis are the Ellenberg indicator values for light, continentality, nitrogen, the number of species in the quadrats, the amount of plant cover recorded and the slope of the main plane within the quadrat (see Table 5-14). The use of DCA on this small-scale data set reveals, that at this resolution time-dependent variables don't seem to be of a major influence on the vegetation development in this particular area on the Nigardsbreen foreland.

Nigardsbreen Small-Scale Block II (N7-95, 192 years since deglaciation)

The DCA-scores of the first DCA-axis of the second block can be seen in Figure 5-11. In this block all the quadrats are from an area which should not show any age variation in terms of time since glacial retreat. The whole block lies completely in an area between the two moraines H and J of the Nigardsbreen foreland and could reasonably be expected to have been vacated by ice at around the same time. The systematic variation of the variance within the vegetation data therefore suggests, that other, time-independent variables, have an influence on the succession. The variation extracted by the first DCA-axis when graphically displayed as in Figure 5-11 shows a systematic trend in the scores form the Northeast to the Southwest of the block. This

reflects the overall locational conditions of the block with the northeastern quadrats approaching the proximal slope of the H-moraine. The quadrats are therefore slightly higher and show a difference in the orientation of their slope, which is reflected in the significant correlation of this variable with the first DCA-axis (Table 5-14).

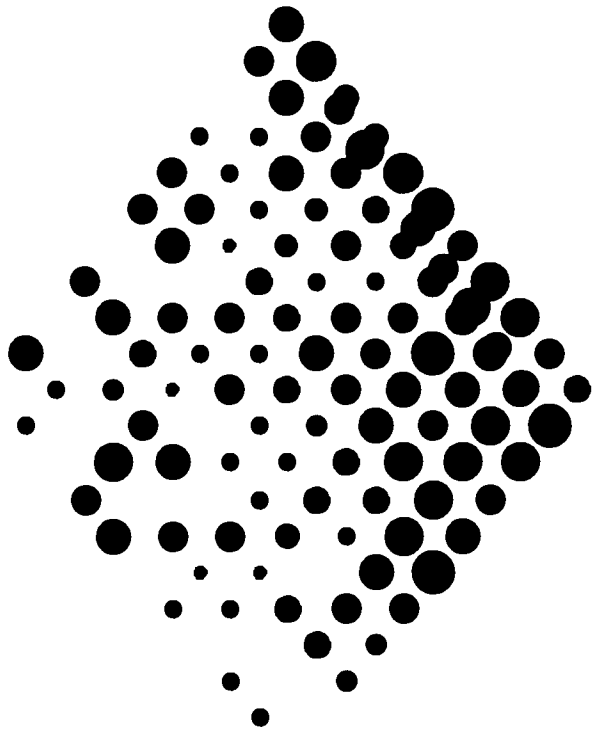


Figure 5-11: DCA sample scores of the first DCA axis for block II of the small-scale data set. Top of page is north, distance between quadrats is 10m. Size representation of the variables is relative. For location of block II on the Nigardsbreen foreland see Figure 3-12.

The coincidental orientation of this topographical variable along the length of the foreland determines also the significant correlation of the first DCA-axis with the distance variables reldist and absdist. With the assumption of no temporal change across the block in mind this indicates the care with which interpretation of the correlation matrices of environmental variables with the DCA-axes have to be made.

Nigardsbreen Small-Scale Block III (-1N16-95, 122 and 999 years since deglaciation)

The third block of quadrats from the Nigardsbreen foreland was most likely to produce a strong correlation between time-dependent variables and the ordination axes, since it contains quadrats from substrates differing in age by an order of magnitude. 54 of the quadrats lie in an area deglaciated since 122 years and 6 quadrats come from outside the glacier foreland boundary with an estimated time since deglaciation of more than 1000 years.

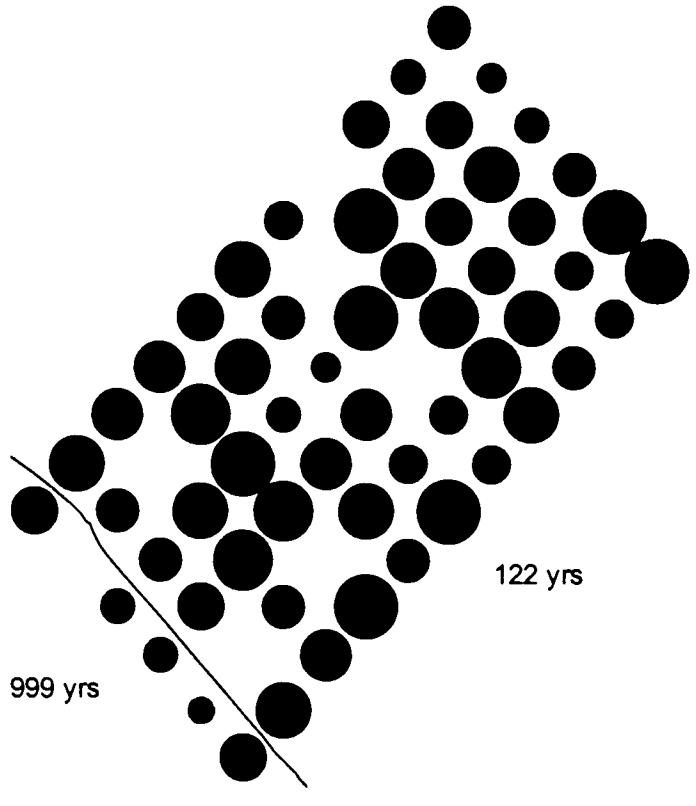


Figure 5-12: DCA sample scores of the first DCA axis for block III of the small-scale data set. Top of page is north, distance between quadrats is 10m. Size representation of the variables is relative. For location of block III on the Nigardsbreen foreland see Figure 3-12.

The location and orientation of the block is responsible for the fact that the age variables are not in line with the distance measures. This explains why the distance variables absdist, reldist and y_reduce show no significant correlation with the first DCA-axis despite the significant correlation of the age variables agegrp and agemax (see Table 5-14).

When all the three small-scale blocks are analysed in one ordination both age related factors as well as age independent factors are correlated significantly with the first DCA-axis (see Table 5-14).

Table 5-14: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the small-scale data sets. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level; NA = no age variation within Block II does not allow for correlation of agegrp and agemax with first DCA-axis

Variable	Block I	Block II	Block III	All Blocks in one ordination
aspectgr	n.s.	n.s.	n.s.	n.s.
slope	-0.41**	0.27**	n.s.	0.22**
soilmini	n.s.	n.s.	n.s.	0.13*
soilmean	n.s.	n.s.	n.s.	n.s.
soilextr	n.s.	0.18*	n.s.	n.s.
disturbn	n.s.	n.s.	n.s.	-0.11*
bare_roc	n.s.	n.s.	n.s.	n.s.
plant_co	-0.51**	n.s.	-0.26*	0.35**
X_reduce	n.s.	0.49**	n.s.	-0.15*
Y_reduce	n.s.	n.s.	n.s.	n.s.
absdist	n.s.	0.35**	n.s.	n.s.
reldist	n.s.	0.24**	n.s.	n.s.
agegrp	n.s.	NA	0.40**	0.17**
agemax	n.s.	NA	-0.40**	0.20**
Light	0.74**	-0.80**	0.67**	-0.79**
Temp	n.s.	-0.44**	n.s.	-0.16**
Conti	-0.71**	0.37**	-0.66**	0.58**
Moist	n.s.	n.s.	n.s.	n.s.
React	0.29*	n.s.	-0.25*	n.s.
Nitro	-0.42**	0.63**	-0.57**	0.70**
No.ofspe	-0.66**	0.58**	-0.54**	0.70**

A TWINSPAN analysis in PC-ORD does not produce a stringent division into groups dependent on their location in one of the blocks (and thereby different ages), but rather divides the data set into groups dependent on some indicator species like *Melampyrum pratense* and *Salix phyllicifolia*.

Storbreen Large-Scale Data Set

Following the rationale outlined in the previous sections the vegetation data of the 7 transects of the Storbreen large-scale data set excluding lichens and mosses were analysed in a DCA (for location of plots see Figure 4-4). Rare species were downweighted and the data were transformed using the modified van der Maarel scale. The same considerations apply to the use of this data set, which have been outlined in the previous section. In all transects the age dependent variables (y_reduce, absdist, reldist, agegrp and agemax) show a significant correlation with the first DCA-axis (Table 5-15).

This is in keeping with the results of Whittaker (1989), who identified an age factor complex as the main influence on the succession on this glacier foreland.

Table 5-15: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the whole large-scale data set. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level

Variable	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6	Transect 7
aspectgr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
slope	n.s.	0.64*	n.s.	n.s.	n.s.	0.71**	n.s.
soilmini	n.s.	n.s.	n.s.	0.73**	n.s.	-0.59*	-0.64**
soilmean	n.s.	n.s.	n.s.	n.s.	n.s.	-0.72**	-0.63**
soilextr	n.s.	-0.76**	n.s.	n.s.	n.s.	-0.81**	-0.62**
disturbn	n.s.	0.68*	n.s.	n.s.	-0.87**	n.s.	n.s.
bare_roc	0.71**	0.85**	n.s.	n.s.	n.s.	0.55*	0.70**
plant_co	-0.55*	-0.89**	-0.81**	-0.50*	-0.87**	-0.78**	-0.73**
X_reduce	-0.65*	-0.83**	-0.89**	-0.76**	-0.75*	-0.79**	-0.85**
Y_reduce	-0.65*	-0.83**	-0.89**	-0.76**	-0.75*	-0.79**	-0.85**
absdist	-0.64*	-0.83**	-0.89**	-0.76**	-0.75*	-0.79**	-0.85**
reldist	-0.65*	-0.86**	-0.88**	-0.78**	-0.75*	-0.79**	-0.85**
agegrp	-0.50*	-0.79**	-0.87**	-0.74**	-0.77*	-0.83**	-0.55*
agemax	n.s.	-0.79**	-0.86**	-0.76**	-0.77*	-0.84**	-0.54*
Light	0.67**	0.86**	0.96**	0.59*	n.s.	n.s.	n.s.
Temp	n.s.	n.s.	-0.79**	-0.65**	-0.70*	n.s.	-0.49*
Conti	n.s.	n.s.	n.s.	n.s.	n.s.	-0.72**	n.s.
Moist	n.s.	-0.65*	-0.69**	n.s.	-0.87**	n.s.	-0.46*
React	0.58*	n.s.	n.s.	0.69**	n.s.	0.69**	n.s.
Nitro	0.79**	n.s.	n.s.	0.61*	n.s.	0.82**	0.58**
No.ofspe	n.s.	-0.75**	n.s.	-0.59*	-0.70*	-0.59*	-0.56**

It is understandable that the amount of bare rockface in the quadrat shows a strong correlation with the DCA-axis. The transects which do not show this strong correlation (transects 3, 4 and 5) are the ones in the centre of the foreland showing a less strong gradient of this variable, than the transects which are in fact terminated by running into rocky outcrops, having started from outside the foreland boundary, thereby representing a much stronger gradient. That the variance in the vegetation extracted in the first DCA-axis is correlated with the distance measures and the location variables supports the general view of progressive development of the vegetation during succession on the Storbreen foreland.

Storbreen Small-Scale Data Sets

Storbreen Small-Scale Block I (-1S2-95; 245 years since deglaciation)

The first of the small-scale blocks on the Storbreen foreland is located on terrain deglaciated approximately since 1750 AD. The ordination of the data set (N=64) shows a highly significant correlation of soil variables with the first DCA-axis (Table 5-16). It has been pointed out before, that these variables may change over time, but are also influenced by periglacial erosion and deposition processes. On these grounds a strict correlation of the first DCA-axis to time-dependent variables is therefore not possible. There are a number of other significantly correlated variables, which include the amount of bare rockface found in the quadrats, the amount of plant cover, the number of species, some location variables (especially along the x-axis, i.e. orthogonal to the suspected time axis) and the Ellenberg indicator values for light, continentality and nitrogen. Most of these variables are thought to change with time. With the sample size of 64 quadrats within this block there is a reasonable scope for variance of the data. The block straddles the distal side of the B-moraine introducing a slope gradient into the data stronger than in the other blocks. This might be the reason why only in this block the variable for slope is significantly correlated with the first DCA-axis.

Storbreen Small-Scale Block II (1S6-95; 143 years since deglaciation)

The second block is located in the centre of the foreland and had approximately 100 years less time than the previously discussed one, to develop its vegetation cover. This block has a meltwater river running through it and this, with the objective sampling design accounts for the importance of the variables for the amount of bare rockface and plant cover in the quadrats. No other location variables shows a significant correlation with the first DCA-axis. The only other variables with significant correlations are Ellenberg indicator values for temperature, continentality, nitrogen and the lichen ratio of green to brown lichens on the rocks and boulders in the quadrats.

Storbreen Small-Scale Block III (1S12-95; 44 years since deglaciation)

Block III is the most homogenous area of the three blocks in terms of environmental variability. It is not surprising that neither the soil variables nor variables like the amount of bare rockface and the amount of plant cover are significantly correlated with the first DCA-axis. The only variables significantly correlated with the

first DCA-axis at the 99% level are the Ellenberg indicator value for continentality and the number of species in the quadrat.

Table 5-16: Pearson's correlation coefficients for the environmental and geographical variables with the first DCA-axis for the small-scale data sets. * and ** denotes significance at 95% and 99%, respectively; n.s. = not significant at either level; NA = no age variation within the Blocks does not allow for correlation of agegrp and agemax with first DCA-axis. Due to lack of data lich_rat could not be used for Block III

Variable	Block 1	Block 2	Block 3	All Blocks in one ordination
aspectgr	n.s.	n.s.	n.s.	0.15*
slope	0.27*	n.s.	n.s.	n.s.
soilmini	-0.41**	n.s.	n.s.	n.s.
soilmean	-0.53**	n.s.	n.s.	n.s.
soilextr	-0.33**	n.s.	n.s.	n.s.
disturbn	0.26*	n.s.	n.s.	0.21**
bare_roc	0.59**	0.36**	n.s.	0.27**
plant_co	-0.58**	-0.23*	n.s.	-0.59**
X_reduce	0.58**	n.s.	0.36*	-0.65**
Y_reduce	-0.60**	n.s.	-0.39*	-0.71**
X_grid	-0.68**	n.s.	-0.39*	-0.28**
Y_grid	n.s.	n.s.	n.s.	-0.21**
absdist	n.s.	n.s.	n.s.	-0.69**
agegrp	NA	NA	NA	-0.68**
agemax	NA	NA	NA	-0.68**
Light	-0.49**	n.s.	0.33*	n.s.
Temp	-0.24*	-0.73**	n.s.	-0.47**
Conti	-0.72**	-0.43**	0.57**	-0.31**
Moist	n.s.	n.s.	-0.39*	-0.21**
React	n.s.	n.s.	-0.38*	n.s.
Nitro	0.47**	0.41**	n.s.	0.45**
lich_rat	n.s.	-0.47**	NA	NA
No.ofspe	-0.61**	n.s.	-0.55**	n.s.

It is interesting to note that in the ordination of all quadrats of all blocks the variable for the aspect of the main plane of the quadrat is significantly correlated with the first DCA-axis. The vegetation of the three blocks seems to vary with the aspect of the blocks. It has been mentioned before that insolation seems to be the controlling factor for the longevity of snow-fields (Christiansen & Humlum, 1993) and the difference in the vegetation of the three blocks supports the hypothesis that the length of the snow-lie can alter the vegetation composition of certain areas on the foreland.

It is peculiar to find that the Ellenberg indicator value for continentality shows a highly significant correlation with the first DCA-axis in a study of this scale. Devised as

an indicator for the continentality gradient from the Atlantic coast to the centre of Central Eurasia (Ellenberg *et al.*, 1991: 68) it is surprising to find this large-scale indicator value to be of any importance on a small-scale glacier foreland study. However, in its definition it is mentioned, that it is especially based on the temperature changes experienced by the plants in different distribution areas (Ellenberg *et al.*, 1991: 68). It is conceivable that on the glacier foreland a gradient exists from locations which experience strong changes in temperature comparable to Central Eurasian locations, to more sheltered locations which experience less strong temperature changes, like the Atlantic coast locations. The vegetation of those locations on the glacier foreland reflect this difference in their respective values for the Ellenberg indicator value for continentality.

Discussion

It has been show that time-dependent factors are important for determining the successional pathway both on low- and high-altitude glacier forelands. There is, however, a reduced influence of age on the gradients extracted from the large-scale data sets by the first two ordination axes when compared to Matthews' and Whittaker's findings on the Storbreen foreland (e.g. Matthews & Whittaker, 1987; Whittaker, 1989), where an age-complex of environmental factors was found to be the most important factor for the differential development of vegetation. This can partially be explained by the effect the patchy environment has on the development of the vegetation on the two forelands. With the sampling design adopted in this thesis the quadrats from the large-scale investigations covered a great variety of environments. This variation in the environment is thought to reduce the significance of time-dependent factors in the ordination analyses. As has been shown in previous chapters and in other research, patchiness represented as both micro- and mesoscale variation of environmental conditions, is highly developed on glacier forelands (Foskett, 1998). Factors connected to a gradient of age include the decrease of pH, increase in biomass and plant cover, accumulation of nutrients (especially nitrogen), increased soil depth, decreased disturbance regime and decreasing influence of periglacial activities like frost churning (e.g. Whittaker, 1989). It is conceivable that over the area of the forelands this gradient is broken up by disturbances as described by Petch & Whittaker (1997) for the

Austerdalsbreen foreland or Ballantyne & Benn (1994) at Fåbergstølsdalen. If the number of sampling quadrats were therefore not big enough to provide independent replicate samples from the areas spanning the age gradient (as might have been the case in this study) the gradient will be obscured by the variety of disturbed and therefore not sequential quadrats.

It has also been shown that the Ellenberg indicator values can be used successfully in ordinations to help and try to explain the gradients extracted from the vegetational composition of the sample quadrats. It was surprising to find that the Ellenberg indicator value for continentality was of use in explaining gradients in such a small-scale investigation. It was conceived to describe the degree of continentality of the general climate with emphasis on the minimum and maximum temperatures (basically the macro-climate of an area). Since the sampling areas cover only very limited areas (0.8 to 2 km^2) it could not be expected to detect differences in the ecological behaviour of the investigated plants in those areas with reference to this macro-climate variable. The results however show, that on the forelands visited meso-climatic conditions seem to exist which reflect this large-scale gradient on a much smaller scale. This is in contrast to Persson's (1981) findings. He calculated CIVs for continentality for 153 quadrats (sampling area approximately 6 ha) and showed that their values varied very little between the quadrats.

Other Ellenberg indicator values like the indicator values for light, reaction and nitrogen on the other hand, could be expected to vary on a small-scale. Their use in the interpretation of ordinations was demonstrated in this study. The detection of a gradient in the "requirement" for light made it possible to explain the differences in the species composition of the quadrats in the Nigardsbreen small-scale area 1N2 due to gaps in the overstorey of a relatively dense *Betula* forest.

6. Spatial Analysis of 1996 Data sets

"God could cause us considerable embarrassment by revealing all the secrets of nature to us: we should not know what to do for sheer apathy and boredom."

- GOETHE, *Memoires*

Preface

Chapter 4 investigated the developments of plant cover, species richness, soil depth and soil-pH. They appear to be universal features of successions on glacier forelands with definite trends over successional time. In chapter 5 it was shown that plant community development on glacier forelands can be related to environmental factors using a new application of Ellenberg indicator values in ordinations and how these communities change over time. In addition to the relatively traditional approaches of these previous chapters a new, spatially explicit approach was expected to provide more information about the processes involved in primary succession on glacier forelands. By analysing the pattern of the distribution of dominant woody species on five forelands the importance of the dispersal mechanism on the development of the spatial pattern was investigated.

Introduction

Chronosequence studies have been very successful in elucidating some of the processes and pathways involved in primary successions on glacier forelands (Matthews, 1979b; Matthews & Whittaker, 1987; Walker & Chapin III, 1987). There is no doubt about the usefulness of this approach and the wealth of information it has produced on succession processes. However, in addition to the conventional correlation of vegetation to environmental factors and the idea of a sequential development of plant communities, the spatial arrangement of the plant species on glacier forelands may be viewed as another key to the understanding of primary succession. The patterns exhibited by colonising plant species would be expected to reflect some identifiable life history traits, which provide evidence for some of the phenomena conventional methods like gradient analysis could not address.

A variety of spatially explicit analytical techniques, some of which have only become available over the last 10 years to plant ecologists, were employed in this study to elucidate the role of spatial patterns in primary successions on glacier forelands. This chapter examines the spatial patterns exhibited by dominant woody plant species along the time gradient on the glacier forelands and specifically the hypothesis that animal-dispersed species enter the forelands with their biotic vectors, advancing large distances along the newly deglaciated terrain and establishing small, isolated nuclei, which grow and over time coalesce into larger more contiguous distribution areas. Wind-dispersed species on the other hand are expected to advance in a more homogenous front up the foreland and, as time passes, become more fragmented by competition with other species.

Methods

Field Sampling

Questions about the development of spatial patterns during succession posed here could not be adequately addressed with the 1995 sampling design. It was therefore decided in 1996 to change to a grid sampling design. This design permitted better capture of the small-scale spatial dimension of the dynamic development of vegetation on glacier forelands. The data so collected then allowed GIS and spatial statistics to be used for their analysis.

Five forelands were visited from 26 June - 2 August (for location see Figure 3-1) and, altogether, 30 blocks of vegetation were surveyed, ranging in size from 10 x 15 m to 21 x 30 m. Within these blocks, rankings of the dominant woody species and selected herbs (for a species list see Table 6-1) in 0.5 x 0.5 m cells were recorded (1 = most important to up to 11 = least important; for illustration see Figure 6-1 and Table 6-2). In total 59680 cells were surveyed, containing between 0 and 11 species per cell. Presence/absence of the species within the blocks was used to compile distribution maps. The scale of the investigation is a trade-off between a resolution fine enough to pick out individual plants but still coarse enough to be manageable within a field season. To be able to relate any observed patterns to biogeographical (dispersal and life history)

processes, it was important that the scale of investigation was fine enough to analyse the data in this respect.

The decision to record only dominant woody species was made according to the following rationale. Firstly, all those species are similar in their phenology, competing at the same levels for space and other resources. By building up woody structures they use comparable strategies to use their resources. Secondly, the restriction to dominant woody species considerably reduced the amount of time necessary to record the plots. Thirdly, the restriction of visiting the area at a specific time had the inherent risk of climatic phenomena, such as late snow melt, influencing the presence or absence of herbaceous species. Woody species with their semi-permanent structures, in those cases can nevertheless be identified and used for the purpose of compiling distribution maps. *Cassiope hypnoides* and *Dryas octopetala*, although woody species, were not included in the survey, due to their very low frequencies and their isolated occurrences. Selected herbaceous species were included as indicator species for certain environmental conditions (e.g. *Pinguicula vulgaris* for wet, nutrient poor patches).

Table 6-1: List of all recorded species in the 1996 survey. **P=Phanerophyte, tree or shrub with aerial dormant buds; C=Chamaephyte, perennial plant having buds at or just above ground level; H=Herb, seed plant with non-woody green stems**

Spec.No.	Species name	Life-form
1	*Alnus incana*	P
2	*Arctostaphylos alpinus*	C
3	*Arctostaphylos uva-ursi*	C
4	*Betula nana*	C
5	*Betula pubescens*	P
6	*Calluna vulgaris*	C
7	*Empetrum nigrum* ssp. *hermaphroditum*	C
8	*Juniperus communis*	C
9	*Loiseleuria procumbens*	C
10	*Lotus corniculatus*	H
11	*Phyllodoce caerulea*	C
12	*Pinguicula vulgaris*	H
13	*Pinus sylvestris*	P
14	*Rubus saxatilis*	C
15	*Salix herbacea*	C
16	*Salix phylicifolia*	P
17	*Salix reticulata*	C
18	*Silene rupestris*	H
19	*Sorbus aucuparia*	P
20	*Vaccinium myrtillus*	C
21	*Vaccinium uliginosum*	C
22	*Vaccinium vitis-idaea*	C

Table 6-2: Codes, names, dates visited, location and size of the 1996 blocks

Foreland	Name of plot	Date of visit (1996)	Location on foreland in relation to moraines[1]	Size of plots (m)	# of cells
Nigardsbreen	N1-96	1.7. + 3.7.	between F and G (left)	21 x 30	2520
	N2-96	4.7. + 5.7.	between G and H (left)	20 x 30	2400
	N3-96	7.7. + 8.7.	between A and B (left)	20 x 30	2400
	N4-96	21.8.	between I and J (left)	20 x 30	2400
	N5-96	22.8.	between H and I (left)	20 x 30	2400
	N6-96	23.8.	between A and B (left)	20 x 30	2400
	N7-96	24.8. + 25.8.	between I and K (right)	20 x 30	2400
	N8-96	25.8.	between G and H (right)	10 x 20	800
	N9-96	26.8.	between F and G (right)	10 x 20	800
	N10-96	26.8.	between F and G (right) 120m left of road	20 x 30	2400
Austerdalsbreen	A1-96	11.7. + 12.7.	between B and C (left)	20 x 30	2400
	A2-96	12.7. + 13.7.	between C and D	20 x 30	2400
	A3-96	15.7. + 17.7.	between H and I	20 x 30	2400
Bødalsbreen	B1-96	19.7. + 20.7.	between B and C (left)	20 x 30	2400
	B2-96	21.7.	between C and D (left)	20 x 30	2400
	B3-96	22.7. + 23.7.	between lake and moraine	20 x 30	2400
Storbreen	S1-96	25.7.	between A and B (low left)	13 x 30	1560
	S2-96	27.7. + 28.7.	between A and B (left, medium)	20 x 30	2400
	S3-96	29.7.	just inside B (medium)	20 x 30	2400
	S4-96	31.7. + 1.8.	inside B (low + stream)	20 x 30	2400
	S5-96	2.8.	between A and B (high)	20 x 30	2400
	S6-96	3.8.	between C and D (medium)	20 x 30	2400
	S7-96	6.8. + 7.8.	outside A (medium)	15 x 30	1800
	S8-96	8.8. + 12.8.	inside H (high)	15 x 30	1800
Høgvaglbreen	H1-96	15.8.	outside A	10 x 30	1200
	H2-96	15.8.	between A and B	20 x 30	2400
	H3-96	16.8.	between B and C	10 x 15	600
	H4-96	16.8.	between C and D	10 x 15	600
	H5-96	16.8.	between D and E	15 x 30	1800
	H6-96	17.8.	between A and B (near stream)	10 x 15	600

[1] Glacier forelands are characterised by a series of more or less distinct terminal moraine ridges which typically provide the dating framework of the foreland and which are assigned letters from A to Z from oldest to youngest.

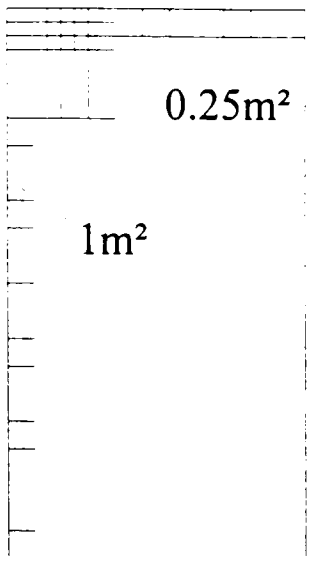


Figure 6-1: Schematic outline of sampling quadrats within one vegetation block.

Geomorphological sketch maps of the locations were produced for each block (except two) to record major geomorphological features, which were thought to be relevant in the interpretation of the distribution of the plants within the block (Table 7-1).

Two Dimensional Two-Term Local Quadrat Variance (TTLQV)

The pattern analysis procedure used in this thesis follows Dale (1990) and Dale & Blundon (1990), an improved and modified version of Hill's (1973) two-term local quadrat variance (TTLQV). It was used to calculate the scale-dependent mean variances across the rows ($V_x(b)$) and along the columns ($V_y(b)$) of a rectangular sampling grid at scale b. Used this way, TTLQV is based on transect data and compares the variances between different scales of investigation. The first step is to calculate the variance between all single cells of the transect (i.e. n/2 comparisons have to be made). In the second step, neighbouring cells are added up to create blocks of 2 cells width and the variance between the pooled 2-cell blocks is calculated. This is done for all possible starting points. The procedure of increasing the block size by 1 cell is repeated until the block size reaches n/2, which is the largest block size at which a comparison between two blocks can be made. Equation 6-1 is the mathematical representation of this procedure.

$$V(b) = \sum_{i=1}^{n+1-2b} \left(\sum_{j=i}^{i+b-1} \left(x_j - x_{j+b} \right) \right)^2 \Big/ 2b(n+1-2b) \qquad \text{Equation 6-1}$$

where b **= block size**
$V(b)$ **= variance at block size b**
n **= number of quadrats in transect**
x **= presence or absence**

The resulting scale-variance plot shows maxima at scales at which a pattern has been detected in the data. Since it has been suggested that the scale at which the variance peaks and the scale of the true pattern are not the same (Errington, 1973), Dale & Blundon (1990) suggest a correction term to obtain the true scale of pattern (B) from the variance peak block size (b):

$$B = b + \left[\frac{30b}{255}\right] + 1 \qquad \text{Equation 6-2}$$

where ***B*** **= true scale of pattern**
b **= scale at which variance peaks**

Campbell, Franklin, Gibson & Newman (1998) raise a note of caution on the use and interpretation of TTLQV variance peaks. As a general rule of thumb, the interpretation of variance peaks explicitly prohibits the use of variance peaks for block sizes larger than half the transect length and for block size 1. But Campbell *et al.* (1998) also caution against the use of variance peaks found at block sizes larger than 10% of the transect length and they show that variance peaks found at block sizes 1, 2 and 3 occur frequently by chance, not necessarily representing ecologically meaningful patterns. Their recommendation is the use of multiple replicate transects to reduce the probability of Type II error (accepting H_o even if it is not true). Here, according to Dale's (1990) recommendation, the one-dimensional TTLQV along rows and columns were averaged, which is in keeping with Campbell *et al.'s* (1998) suggestions. Spatial autocorrelation within the data sets and its influence on spatially close TTLQV transects was not considered to be a problem in this procedure.

$V_I(b)$, the two-dimensional variance, is the square of the difference between the density in a block of cells with the density of three contiguous blocks of the same size, averaged over all possible positions of such blocks (see Equation 6-3 and Equation 6-4). The initial cell for this variance is in the top left corner (Figure 6-2).

+	-1/3
-1/3	-1/3

Figure 6-2: The method used to calculate the two-dimensional variance. The data in the "+" square are added together and then the sums of the other squares, weighted as indicated, are subtracted. The variance is the average of the squares of such differences for all possible positions.

$$s_b(i,j) = \sum_{p=i}^{i+b-1} \sum_{q=j}^{j+b-1} d(p,q) \qquad \text{Equation 6-3}$$

where ***d(p,q)*** **= density of the quadrat in the p*th* column and the q*th* row of the sample array, an *m* x *n* matrix**
$s_b(i,j)$ **= sum of the data in a *b* x *b* square with its upper left corner at *(i,j)*.**

$$V_l(b) = \sum_{i}^{n+1-2b} \sum_{j}^{m+1-2b} \frac{\left[3s_b(i,j) - s_b(i+b,j) - s_b(i,j+b) - s_b(i+b,j+b)\right]^2}{18(n+1-2b)(m+1-2b)b^2} \qquad \text{Equation 6-4}$$

where ***b*** **= block size**
$V_l(b)$ **= variance at block size b with cell in top left corner**
m **= number of columns in sample array**
n **= number of rows in sample array**

In addition to $V_l(b)$, $V_r(b)$ has to be calculated since both variances give different results for diagonal stripes, depending on whether they go from top left to bottom right or top right to bottom left (Equation 6-5).

$$V_r(b) = \sum_{i}^{n+1-2b} \sum_{j}^{m+1-2b} \frac{\left[3s_b(i+b,j) - s_b(i,j) - s_b(i,j+b) - s_b(i+b,j+b)\right]^2}{18(n+1-2b)(m+1-2b)b^2} \qquad \text{Equation 6-5}$$

where ***b*** **= block size**
$V_r(b)$ **= variance at block size b with cell in top right corner**
m **= number of columns in sample array**
n **= number of rows in sample array**

The total variance associated with block size b, $V_2(b)$, is calculated as the mean of $V_l(b)$ and $V_r(b)$. Peaks in the variance $V_2(b)$ correspond to the scales of two-dimensional patterns in the vegetation. A measure of how close the pattern is to a perfect pattern of alternating stripes of width b has been suggested by Dale (1990) as:

$$C_2(b) = 27V_2(b)/(2b^2 + 4) \qquad \text{Equation 6-6}$$

where ***b*** **= block size**
$C_2(b)$ **= consistency of pattern**
$V_2(b)$ **= total two-dimensional variance associated with block size *b***

TTLQV can be used to try and connect the detected pattern in the vegetation data with the underlying processes. It is thought that the pattern which can be detected by

these analyses allows inferences on the processes that created these patterns (e.g. Mercer & Hall, 1911; McBratney & Webster, 1981).

C/C^{++} was used to write a program which implements Equations 6-3 to 6-6 for the calculation of the two-dimensional TTLQV (Volume 2).

Geostatistics/Fractal Dimension

The approach of calculating the fractal dimension for data in a plane used in this study has been explained in detail in De Cola (1989) and is based on the linear relationship of perimeter and area of discrete regions. It can be described by the following equation:

$$\ln(p_j) = \ln(c) + D\ln(\sqrt{s_i}) + \varepsilon \qquad \text{Equation 6-7}$$

where p **= perimeter**
c **= index of shape**
D **= fractal dimension**
s **= area**
ε **= error term reflecting the homogeneity of the regions**

The fractal dimension calculated in this way is an estimate of the form or "perimeter complicatedness" (De Cola, 1989: 603) of a region. Regions with smooth perimeters should have a fractal dimension equal to 1 (i.e. close to the dimension of a line) whereas regions with complicated perimeters on the way to filling a plane, will have fractal dimensions close to 2 (the dimension of a plane). Patches in a plane should therefore show a fractal dimension between 1 and 2 ($1 \leq D_{plane} \leq 2$), whereas the fractal dimension of a surface will lie between 2 and 3, giving an indication of the roughness of the surface ($2 \leq D_{surface} \leq 3$). Since the 1996 data were entered into a raster GIS format the calculation of the parameters needed to calculate the fractal dimension of species distributions regions can be easily achieved using a GIS such as IDRISI.

Spatial Indices

Another way of describing and analysing spatial patterns of regions is to assess patch shapes and their arrangement in the study area. Additional to descriptions of area size, perimeter length, number of discrete patches etc., many different indices have been used to this end. Monmonier (1974) suggests a **fragmentation index** (F, Equation 6-8)

in which the neighbourhood of a cell is analysed in terms of how many different classes (e.g. number of species, ranking of species etc.) are present in a specific area around the cell under investigation. In IDRISI the neighbourhood is restricted to a 3 x 3 template. The higher the values for the fragmentation index F, the more different classes are present in the considered area ($0 \leq F \leq 1$). When a presence/absence distribution map of a species is analysed this way the values for F will be restricted to 0 and 0.125 (maximal 2 classes, i.e. present and absent, can be present in the 3 x 3 cell template). The cells containing the value 0.125 after the analysis will have both cells with and without species in their (3 x 3) neighbourhood.

$$F = \frac{(n-1)}{(c-1)} \qquad \text{Equation 6-8}$$

where **n = number of different classes present**
c = number of cells considered (always 9 in IDRISI)

LaGro Jr. (1991) suggests two other indices that seem to be of value. First, the **contiguity index** allows the scientist to assess the amount of straight-sided patch boundaries. It is similar to the fragmentation index in that it uses a 3 x 3 neighbourhood template to calculate the index values (see Figure 6-3). When the values of the products of the template values with the corresponding input image pixel values are summed over the template area this value is the contiguity value of the cell in the centre of the template. The contiguity index for a patch of one class is then calculated according to:

$$C(j) = \frac{\left[\left(\sum_{i=1}^{n} C'(i,j)/n(j)\right) - 1\right]}{(m-1)} + 1 \qquad \text{Equation 6-9}$$

where **$C(j)$ = contiguity index for a patch of class (j)**
$C'(i,j)$ = contiguity value for a pixel (i) of class (j)
$n(j)$ = total number of pixels of class (j)
m = sum of the template values

1	2	1
2	1	2
1	2	1

Figure 6-3: 3 x 3 neighbourhood template with its values used for the calculation of contiguity values.

Second, LaGro Jr. (1991) uses the **clustering index** to reflect any cells proximity to other cells within the same class. It uses the same formula and procedure as the contiguity index the only difference being that the neighbourhood which is considered is increased from a 3 x 3 to a 5 x 5 neighbourhood with slightly different template values (Figure 6-4).

1	2	3	2	1
2	4	5	4	2
3	5	2	5	3
2	4	5	4	2
1	2	3	2	1

Figure 6-4: 5 x 5 neighbourhood template used for the calculation of clustering values.

Spatial Autocorrelation

Griffith (1992) defines spatial autocorrelation as

> ..."the dependencies that exist among observations that are attributable to the relative locations, or underlying two-dimensional ordering, of variable values in geographic space. In turn, these dependencies produce clustering of similar (positive spatial autocorrelation) or dissimilar (negative spatial autocorrelation) values, and hence induce some map pattern."
>
> **(Griffith, 1992: 267)**

A slightly more digestible definition of autocorrelation is given in the help facility of the IDRISI software (1987-1995):

> Autocorrelation is the propensity for data values to be similar to surrounding data values. In a raster image, this describes the degree to which values in any cell will be similar to the cells surrounding it. A common measure of autocorrelation is Moran's I, with a range from -1 to +1. A value close to +1 indicates a smooth surface, with each cell containing a value very similar to the cell next to it. A value close to -1 indicates a very rough or fractured surface, with each cell quite different from its neighbours.

When autocorrelation is measured for the adjacent neighbours of a cell, it is called first lag. Subsequent lags refer to increasingly distant neighbours. One reason why autocorrelation is so important in spatially explicit studies in ecology, is that it influences the selection of available statistics for the analysis of the data. Sub-sampling of data sets where the data exhibit any form of autocorrelation will have to be considered with great care since the selected points for the sub-sample might represent pseudo-replications of the original sample. The other reason why autocorrelation is important in ecological studies is the fact that it very often represents interpretable ecological behaviour of species like clonal growth or dispersal mechanisms. It is therefore an important tool for the exploratory analysis of data sets.

Analytical Methods

Spatial properties of species distributions can be described in their most basic way by the area/perimeter index (area being the number of 0.25m² cells and perimeter the number of 0.5m-long border segments of a given area). The index can be used for different species at the same location to assess dominance. Furthermore, it allows for the direct comparison of the fragmentation of the distribution of a species in a given area. When the values are compared for the same species in blocks of increasing age, any change of these indices during successions can be used to estimate underlying ecological and geophysical processes.

Autocorrelation is brought about by different factors, such as restriction to suitable patchy environments, dispersal mechanisms, clonal growth, etc. This means that the identification of autocorrelation for a certain data set does not necessarily mean that the underlying processes are known, although good guesses usually can be made. The autocorrelation values of the species in this study were calculated using the IDRISI software (Eastman, 1987-1995). The distribution maps were analysed using the King's case (all eight surrounding cells contribute to the calculation of Moran's I). Diagonally neighbouring cells are given a weight of 0.7071, whereas vertically and horizontally adjacent cells are given a weight of 1. Moran's I is the measure to describe the propensity of cells to be surrounded by similar or dissimilar cells. Due to its calculation it can vary from -1 to 1, with values close to -1 describing very rough surfaces where

cells are surrounded by very dissimilar cells and values close to 1 for smooth surfaces on which cells are surrounded by similar cells.

The fractal dimension is yet another tool available to ecologist to evaluate spatial properties of patterns. There have been many different approaches including the use of fractals, mainly in geology and in the geophysical sciences. In its original form, fractals are a measure of self-similarity (Mandelbrot, 1983). Most of the studies using fractals are concerned with characterising a stationary state of a system (e.g. Burrough, 1981; De Cola, 1989; Fitter & Stickland, 1992; Virkkala, 1993). In this study, fractals are being used to investigate the temporal change of distribution patterns, thereby helping to test hypotheses about the importance of particular forms of ecological processes within primary successions. The values for the fractal dimension were calculated using De Cola's (1989) approach ($D_{De\ Cola}$; Equation 6-10). It provides a measure of the perimeter-complicatedness of an area with values for $D_{De\ Cola} \sim 1$ for smooth perimeters and $D_{De\ Cola} > 1$ for complicated perimeters. In this study, the fractal dimension for the distribution of a species within a block was calculated by using the average of the fractal dimensions of all the individual patches within the block.

$$D_{DeCola} = \frac{\ln(p) - \ln(4)}{\ln(\sqrt{s})} - \varepsilon \qquad \text{Equation 6-10}$$

where **p = perimeter**
s = area
ε = error term

Another way to calculate the fractal dimension of a distribution area has been suggested by Virkkala (1993). In his approach, the slope of the regression of the logarithm of the number of area units with the logarithm of the scale is used as D. It represents the amount of squares of a given area occupied by a species and is restricted between 1 and 2 ($D = 2$ means a continuous cover of squares at all scales). Gautestad (1994) suggested improvements to the calculation of D since he shows that Virkkala's calculation of D rests on a misinterpretation of the theoretical relationship between spatial resolution, number of grid cells covered by the species, and the fractal dimension. It is this modified form that is used to calculate D in this study. Due to this transformation, the new range of D_{Gau} is $0 \leq D_{Gau} \leq 2$ ($D_{Gau} = 0$ for widely spaced distributions and $D_{Gau} = 2$ for total cover).

Results

Local maxima of the two-dimensional TTLQV values indicate the scale at which a pattern for a distribution is detected (see Table 6-3).

Table 6-3: Local maxima of the total variance associated with block size ($V_T(b)$) for four animal-dispersed (a) species. Aus refers to Austerdalsbreen, Bod to Bødalsbreen and Nig to Nigardsbreen forelands. The age is estimated maximal time since deglaciation. nm stands for no maximum

Species	Aus3 (91 years)	Aus2 (126 years)	Aus1 (161 years)	Bod3 (65 years)	Bod2 (176 years)	Bod1 (229 years)	Nig7 (149 years)	Nig2 (166 years)	Nig6 (231 years)
Vaccinium uliginosum (a)	nm	nm	15	7,8,13	12	8	5	9,17	3,17
V. myrtillus (a)	nm	nm	19	nm	nm	nm	-	9	15
V. vitis-idaea (a)	-	18	-	9	7,15	nm	5	12	18
Empetrum hermaphroditum (a)	nm	nm	nm	nm	10,17	2,3	nm	nm	13

Almost half of the presented analyses show no maximum at any scale. The analysis was not able to detect any pattern for those distributions. The distribution of *Vaccinium uliginosum* shows varying scales for two-dimensional patterns on 8 of the 9 selected forelands. Smaller scales for the detected patterns are generally restricted to the younger blocks on a specific foreland, although they can sometimes be detected in connection with large-scales on older forelands (e.g. maxima at block size 3 and 17 for *Vaccinium uliginosum* on Nig6). There is, however, a distinct exception to this pattern with the very small pattern size of *Empetrum hermaphroditum* on the oldest of the Bødalsbreen forelands (2-3m).

The mean of the perimeter/area index for animal- and wind-dispersed species shows no distinct trend over successional time for all forelands (see Table 6-4). If these mean values are investigated for the five individual forelands still no conclusive pattern of change over successional time can be shown. It however becomes clear that 81% of blocks on low-altitude forelands show higher values for the wind- than for animal-dispersed species. In contrast 67% of blocks on high-altitude forelands show higher values for the animal- than for wind-dispersed species.

Table 6-4: Mean perimeter/area index values for animal- and wind-dispersed species ordered chronologically. Aus refers to Austerdalsbreen, Bod to Bødalsbreen, Nig to Nigardsbreen, Hog to Høgvaglbreen and Sto to Storbreen forelands. Aus, Bod and Nig are low-altitude (l) and Hog and Sto are high-altitude (h) forelands

Foreland block name	Estimated age at time of investigation	Mean of animal-dispersed species	Mean of wind-dispersed species
Sto8 (h)	45	2.09	2.50
Bod3 (l)	65	1.70	2.07
Aus3 (l)	91	2.31	1.91
Hog5 (h)	119	-	0.98
Aus2 (l)	126	1.50	2.07
Sto6 (h)	144	2.88	2.58
Nig4 (l)	149	1.59	2.15
Nig7 (l)	149	2.15	2.26
Nig5 (l)	155	1.80	1.89
Hog4 (h)	156	2.00	1.59
Hog6 (h)	160	-	0.66
Aus1 (l)	161	2.11	2.01
Hog3 (h)	165	2.80	1.65
Nig2 (l)	166	1.73	2.25
Nig8 (l)	166	1.92	1.68
Nig1 (l)	172	1.69	2.19
Bod2 (l)	176	1.34	2.09
Nig9 (l)	182	1.45	1.83
Sto3 (h)	186	2.08	2.15
Sto4 (h)	186	1.96	2.02
Hog2 (h)	186	4.00	1.89
Sto1 (h)	216	2.35	1.96
Sto2 (h)	216	2.68	1.65
Sto5 (h)	216	2.59	1.91
Bod1 (l)	229	1.42	1.79
Nig3 (l)	231	1.88	2.13
Nig6 (l)	231	1.69	2.20
Hog1 (h)	9996	4.00	2.27
Nig10 (l)	9996	1.84	2.23
Sto7 (h)	9996	1.53	2.34

Since the mean is strongly influenced by extreme outliers investigation of the behaviour of individual species was expected to reveal more about the pattern change over successional time. The four dominant animal-dispersed species, *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *V. myrtillus* and *V. vitis-idaea* show a rather constant development of indices from higher values on young ground within the low-altitude forelands to lower numbers on older ground (Table 6-5).

For the dominant wind-dispersed species there doesn't seem to be any common trend across the forelands, nor does there seem to be a general pattern for the change of the index across the species. The only consistent feature is that the values for *Salix phyllicifolia* are consistently higher (i.e. it is present in many small, highly fragmented

patches) than for the other species. Visual comparison of the distribution maps confirms that this species is far less abundant and only present in small patches in the surveyed blocks.

Table 6-5: Perimeter/area indices for four animal-dispersed (a) species. Aus refers to Austerdalsbreen, Bod to Bødalsbreen and Nig to Nigardsbreen forelands. The age is estimated maximal time since deglaciation

Species	Aus3 (91 years)	Aus2 (126 years)	Aus1 (161 years)	Bod3 (65 years)	Bod2 (176 years)	Bod1 (229 years)	Nig7 (149 years)	Nig2 (166 years)	Nig6 (231 years)
Vaccinium uliginosum (a)	2.34	1.13	0.61	1.67	1.56	1.20	2.48	2.26	1.97
V. myrtillus (a)	1.32	0.60	0.96	1.91	1.25	0.98	3.18	2.37	2.19
V. vitis-idaea (a)	3.56	0.64	-	1.81	1.57	0.69	1.55	1.21	1.67
Empetrum hermaphroditum (a)	0.41	0.08	0.40	0.99	0.17	0.12	1.38	1.08	0.94

As for the perimeter/area index the mean Moran's I values for the two dispersal groups for all the forelands show no distinguishable trend through successional time (Table 6-6). Temporal patterns discernible on the individual forelands are an increase of the values for the wind-dispersed species on the Austerdalsbreen foreland with age. On the Bødalsbreen foreland the values for the animal-dispersed species decrease with age. When the values for the animal- and wind-dispersed species on low-altitude forelands are compared 75% of the blocks show consistently higher values for animal than wind-dispersed species in the same blocks. On the high-altitude forelands however no such trend can be distinguished.

For three of the dominant animal-dispersed species (*Vaccinium uliginosum*, *V. myrtillus* and *V. vitis-idaea*) Moran's I increases consistently with time since deglaciation on Austerdalsbreen and Bødalsbreen (see Table 6-7). The development of autocorrelation of *Empetrum hermaphroditum*, another dominant animal-dispersed species, however, is not as consistent.

Table 6-6: Mean autocorrelation values (Moran's I; King's case) for animal- and wind-dispersed species ordered chronologically

Foreland block name	Estimated age at time of investigation	Mean of animal-dispersed species	Mean of wind-dispersed species
Sto8	45	0.31	0.21
Bod3	65	0.49	0.41
Aus3	91	0.28	0.33
Hog5	119	-	0.35
Aus2	126	0.43	0.39
Sto6	144	0.17	0.21
Nig4	149	0.52	0.37
Nig7	149	0.38	0.28
Nig5	155	0.41	0.42
Hog4	156	0.44	0.18
Hog6	160	-	0.33
Aus1	161	0.37	0.48
Hog3	165	0.22	0.25
Nig2	166	0.47	0.38
Nig8	166	0.30	0.31
Nig1	172	0.49	0.36
Bod2	176	0.47	0.31
Nig9	182	0.58	0.45
Sto3	186	0.00	0.27
Sto4	186	0.41	0.32
Hog2	186	0.37	0.33
Sto1	216	0.20	0.30
Sto2	216	0.24	0.41
Sto5	216	0.30	0.35
Bod1	229	0.45	0.36
Nig3	231	0.46	0.38
Nig6	231	0.47	0.33
Hog1	9996	0.00	0.16
Nig10	9996	0.38	0.30
Sto7	9996	0.35	0.06

Table 6-7: Autocorrelation values (King's case) for four animal-dispersed species. Aus refers to Austerdalsbreen and Bod to Bødalsbreen. The age is estimated maximal time since deglaciation

Species	Aus3 (91 years)	Aus2 (126 years)	Aus1 (161 years)	Bod3 (65 years)	Bod2 (176 years)	Bod1 (229 years)
Vaccinium uliginosum	0.28	0.63	0.83	0.51	0.57	0.65
V. myrtillus	0.33	0.47	0.62	0.44	0.56	0.59
V. vitis-idaea	0.09	0.82	-	0.47	0.57	0.81
Empetrum hermaphroditum	0.59	0.34	0.57	0.54	0.23	0.09

For neither of the fractal dimension values (D_{Gau} or $D_{De\ Cola}$) any distinct trend over time for all the forelands can be shown to exist (Table 6-8). On the Bødalsbreen foreland on its own an increase could be detected for the D_{Gau} values for both animal- and wind-dispersed species. On the Høgvaglbreen foreland the D_{Gau} values show a decrease for

animal-dispersed species (in this special case only one species, *Empetrum hermaphroditum* was present in the blocks). $D_{De\ Cola}$ values on the other hand increase for animal-dispersed species on the Austerdalsbreen foreland.

One consistent pattern of the D_{Gau} values is that on 69% of the blocks on low-altitude forelands the values for animal-dispersed species are higher than the ones for wind-dispersed species. On the high-altitude forelands 91% of blocks show higher D_{Gau} values for wind than for animal-dispersed species (see Table 6-8). In comparison to that, the $D_{De\ Cola}$ values show no pattern on the low-altitude forelands, but in 83% of the blocks on high-altitude forelands the $D_{De\ Cola}$ values for wind-dispersed species are higher than for animal-dispersed species.

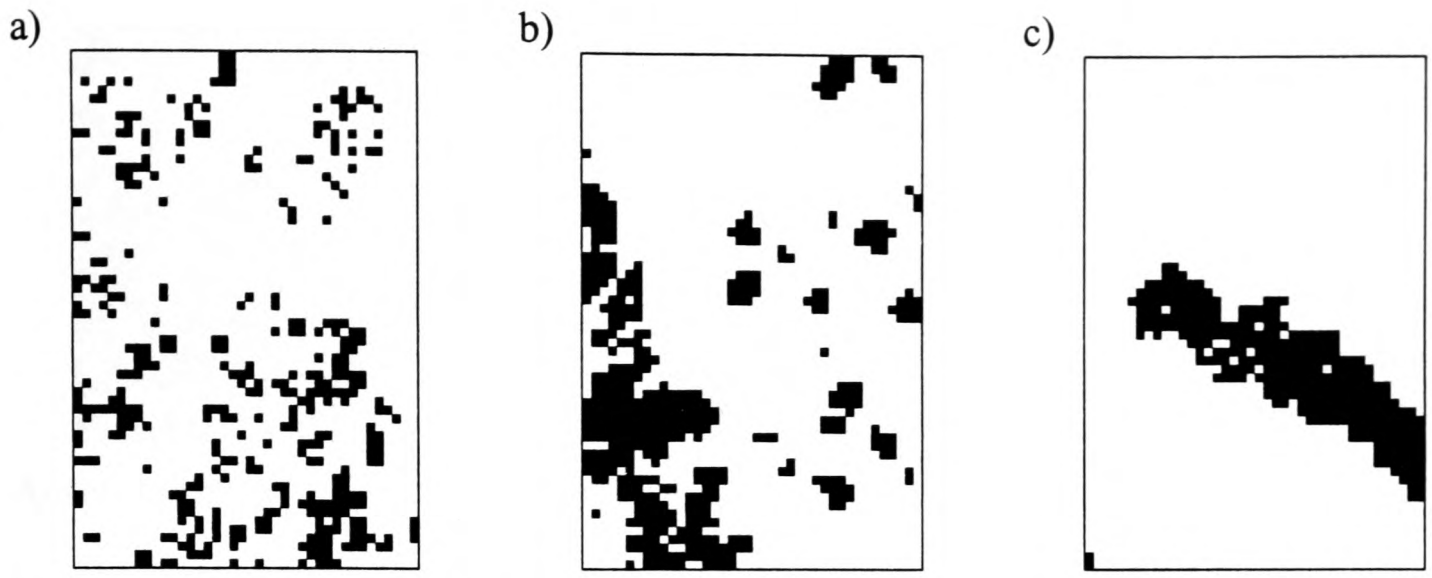
Table 6-8: Fractal dimension values ($D_{De\ Cola}$, after De Cola, 1989 and D_{Gau}, after Gautestad, 1994) for animal-dispersed and wind-dispersed species. Aus refers to Austerdalsbreen, Bod to Bødalsbreen and Nig to Nigardsbreen forelands

Foreland block name	Estimated age at time of investigation	$D_{De\ Cola}$ animal-dispersed	$D_{De\ Cola}$ wind-dispersed	D_{Gau} animal-dispersed	D_{Gau} wind-dispersed
Sto8	45	1.15	1.16	1.05	1.55
Bod3	65	1.13	1.19	0.93	0.64
Aus3	91	1.15	1.21	0.97	1.03
Hog5	119	-	1.19	-	1.80
Aus2	126	1.16	1.19	1.21	0.81
Sto6	144	1.10	1.14	0.49	1.17
Nig4	149	1.17	1.12	1.06	0.63
Nig7	149	1.18	1.05	0.88	0.26
Nig5	155	1.20	1.09	1.46	0.58
Hog4	156	1.11	1.19	0.86	1.25
Hog6	160	-	1.42	-	1.92
Aus1	161	1.17	1.20	1.12	1.01
Hog3	165	1.22	1.26	0.68	1.37
Nig2	166	1.24	1.24	1.14	0.68
Nig8	166	1.19	1.25	1.18	1.15
Nig1	172	1.17	1.12	0.95	0.85
Bod2	176	1.18	1.12	1.16	0.77
Nig9	182	1.19	1.11	1.09	0.76
Sto3	186	1.27	1.20	1.12	1.39
Sto4	186	1.19	1.25	1.09	1.33
Hog2	186	1.00	1.14	-	1.16
Sto1	216	1.17	1.15	1.18	1.21
Sto2	216	1.16	1.18	0.70	1.39
Sto5	216	1.15	1.19	1.02	1.33
Bod1	229	1.15	1.18	1.34	1.04
Nig3	231	1.15	1.13	1.19	0.61
Nig6	231	1.15	1.18	1.04	0.41
Hog1	9996	1.00	1.02	0.29	2.00
Nig10	9996	1.23	1.10	1.09	0.59
Sto7	9996	1.21	1.10	1.39	1.87

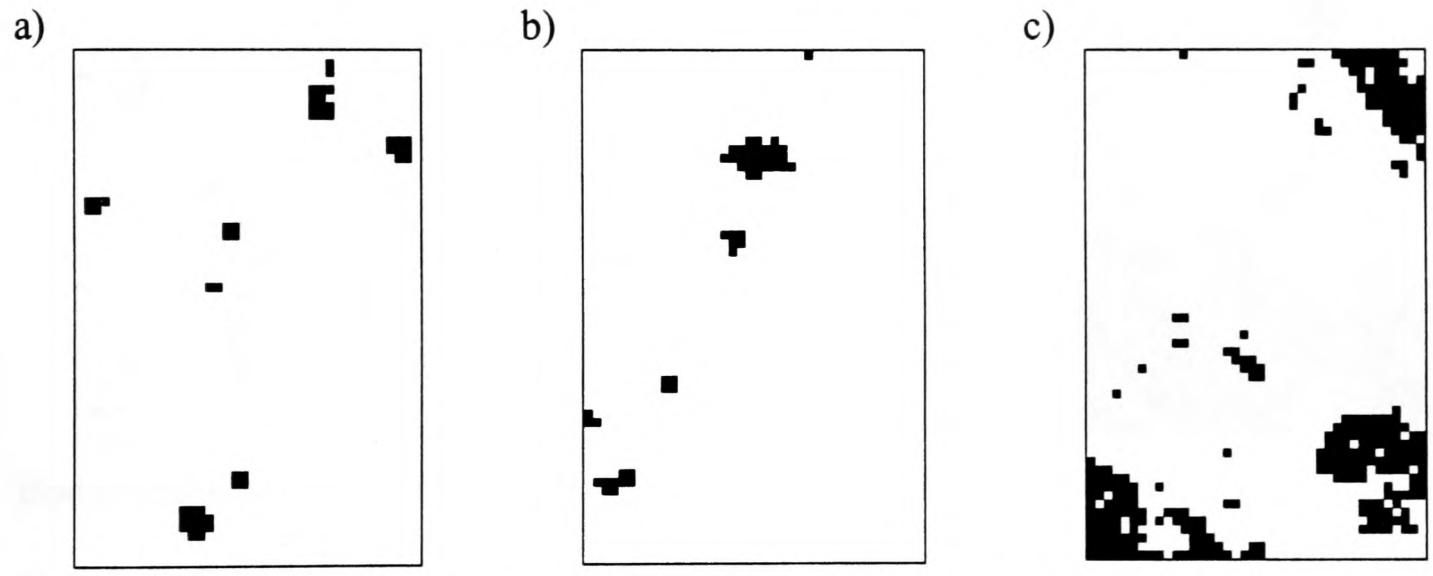
For better visualisation some of the distribution maps on which the values are based are presented on the following pages.

Low altitude forelands (Austerdalsbreen, Bødalsbreen and Nigardsbreen; see Figure 3-13 for location of blocks on the forelands).

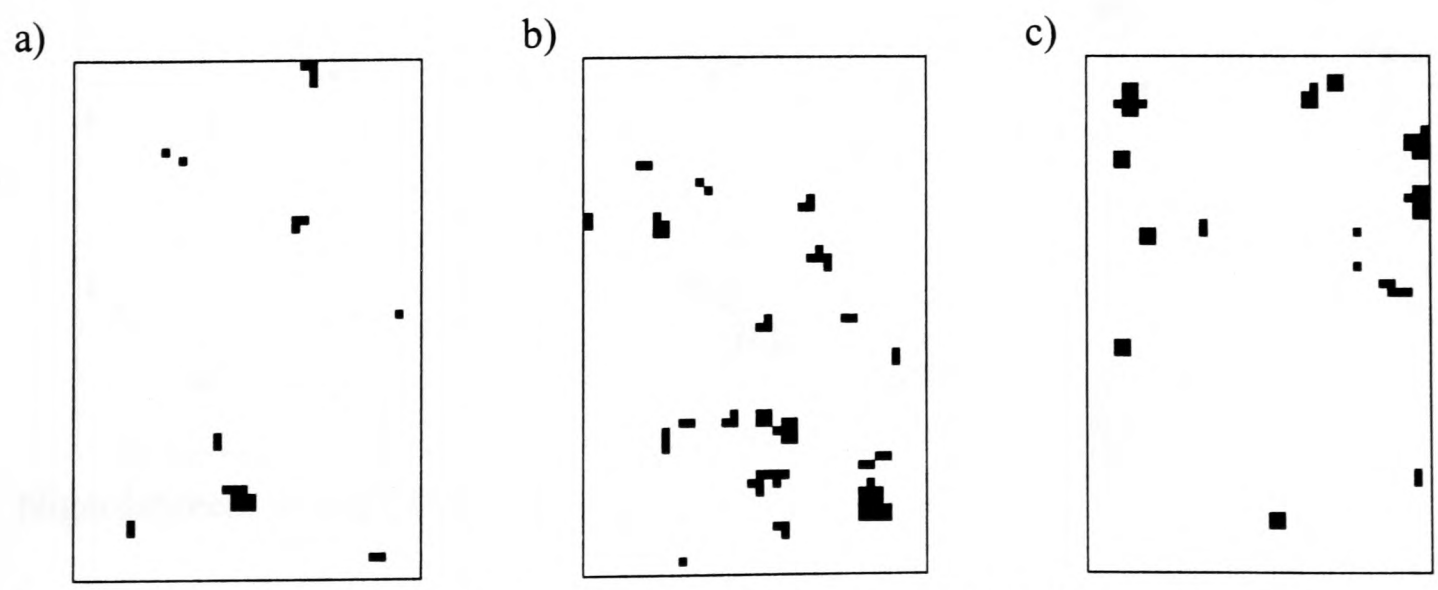
Vaccinium uliginosum (animal dispersed)



Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)



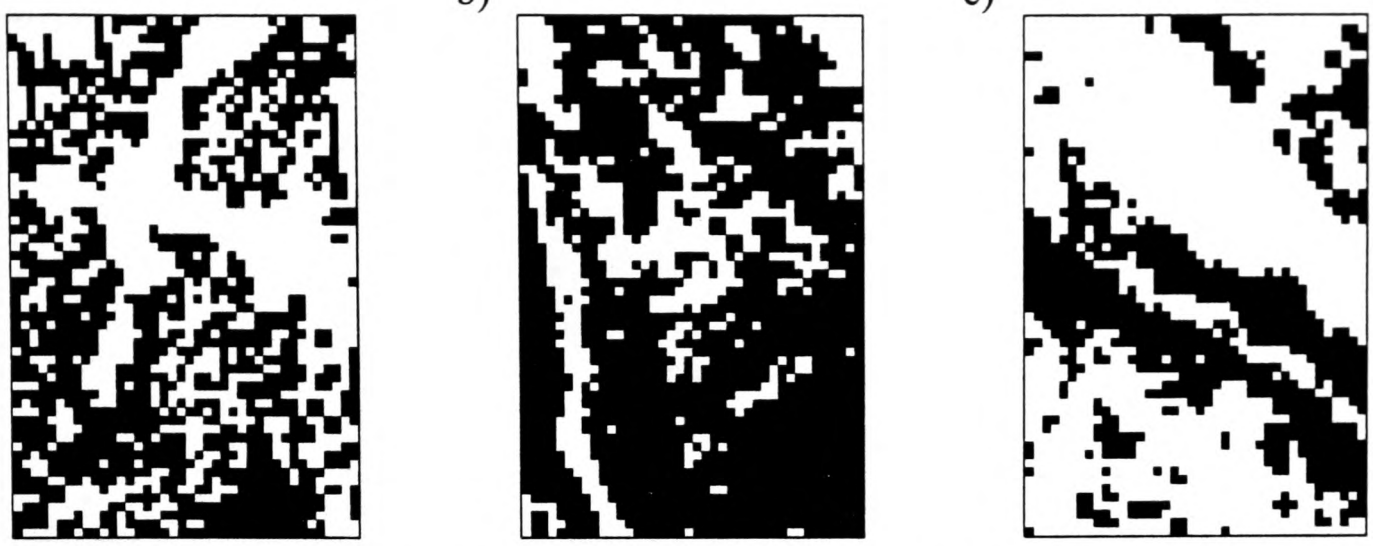
Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)



Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

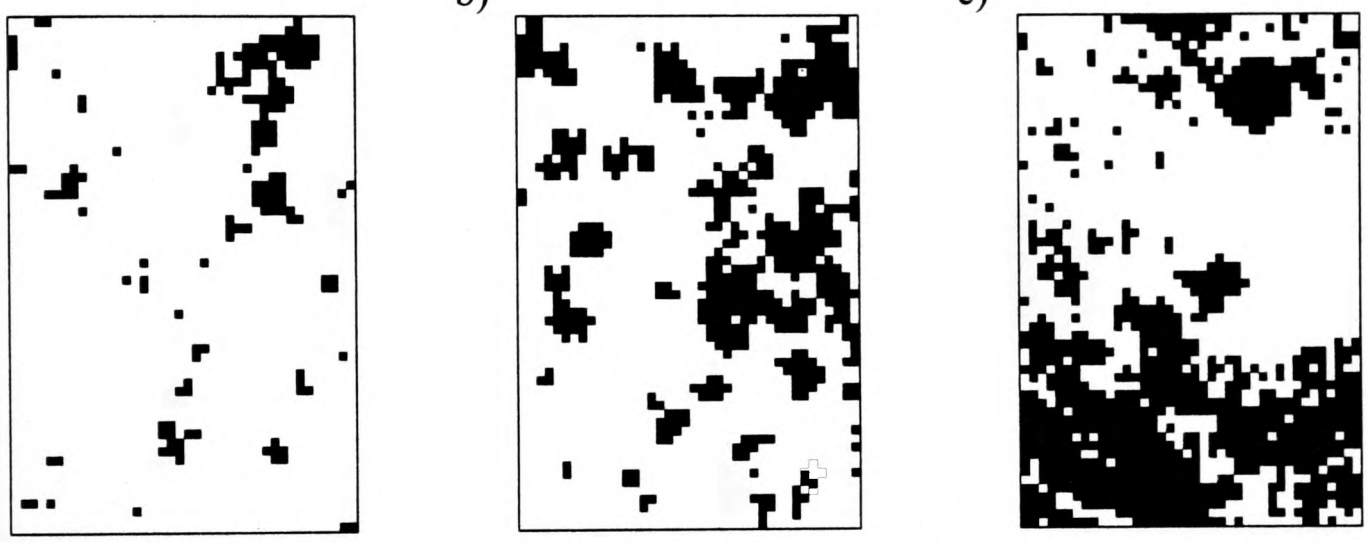
Vaccinium myrtillus (animal dispersed)

a) b) c)



Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)

a) b) c)



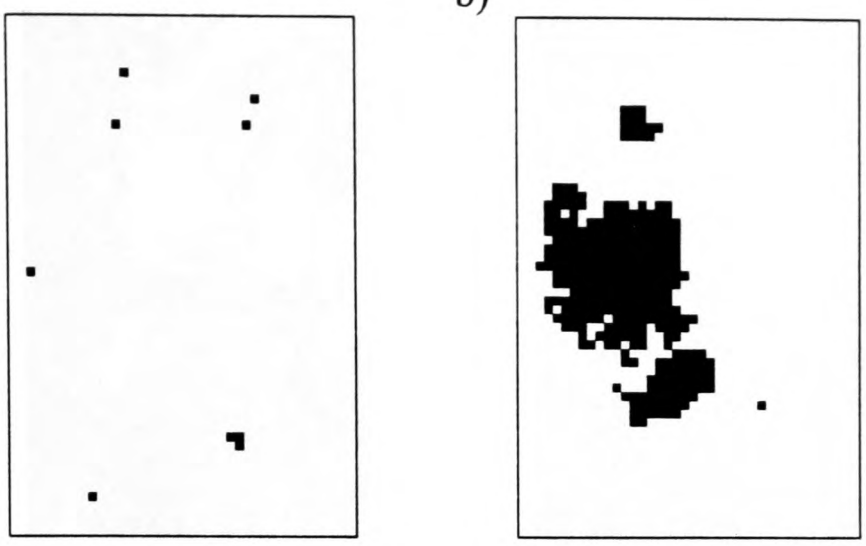
Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)

a) b) c)

Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

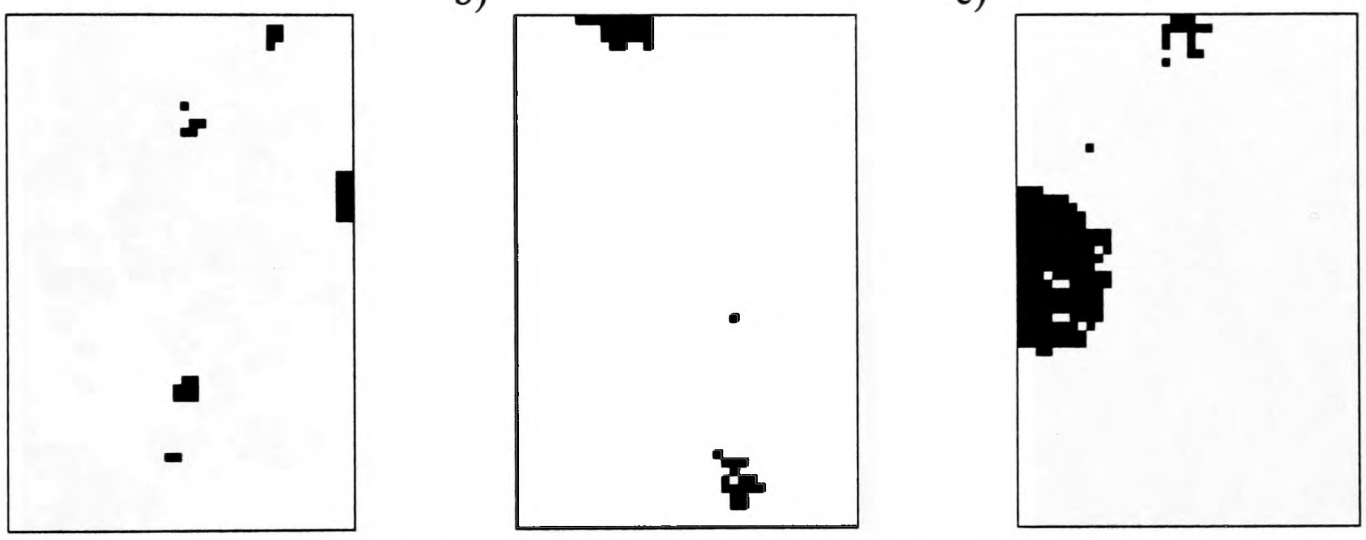
Vaccinium vitis-idaea (animal dispersed)

a) b) c)



Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)

a) b) c)



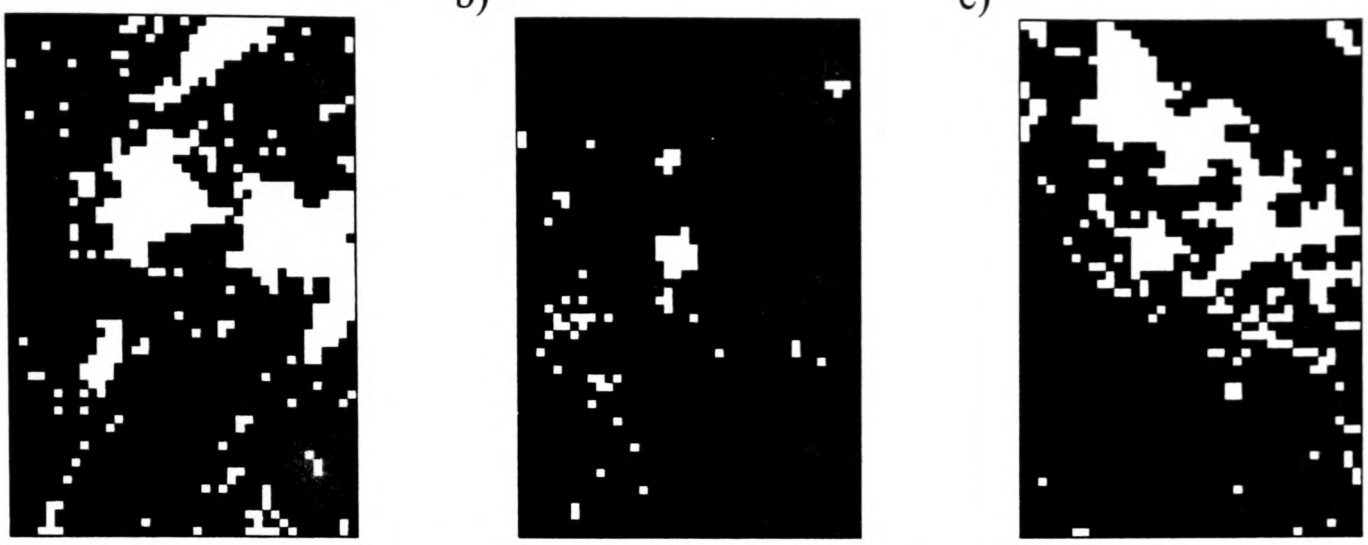
Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)

a) b) c)

Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

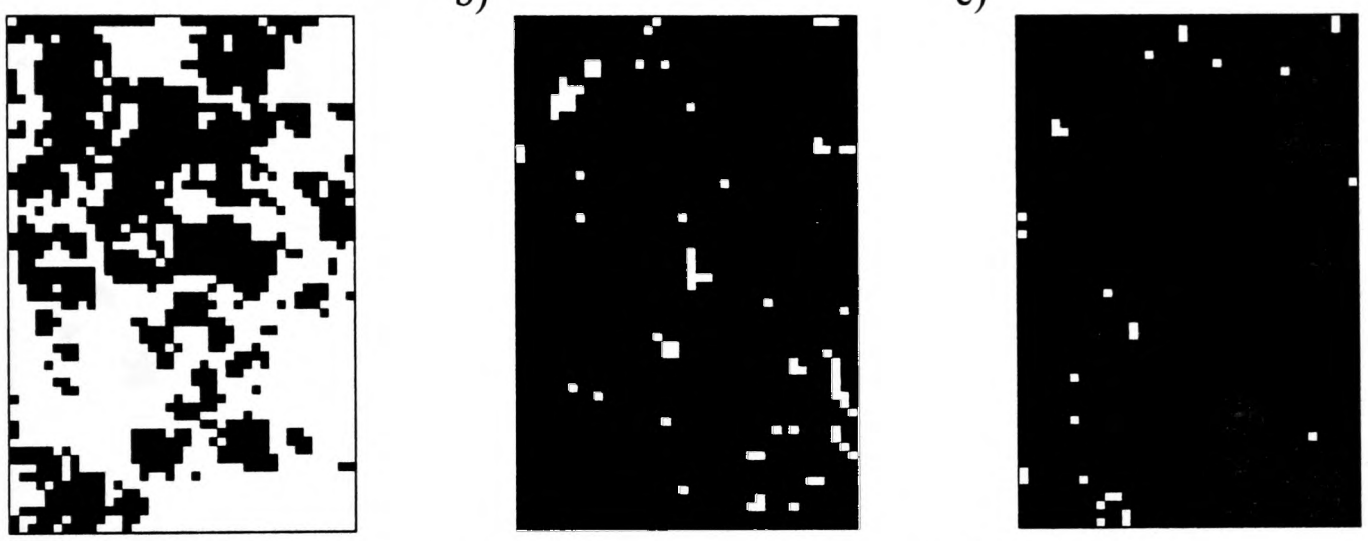
Empetrum hermaphroditum (animal dispersed)

a) b) c)



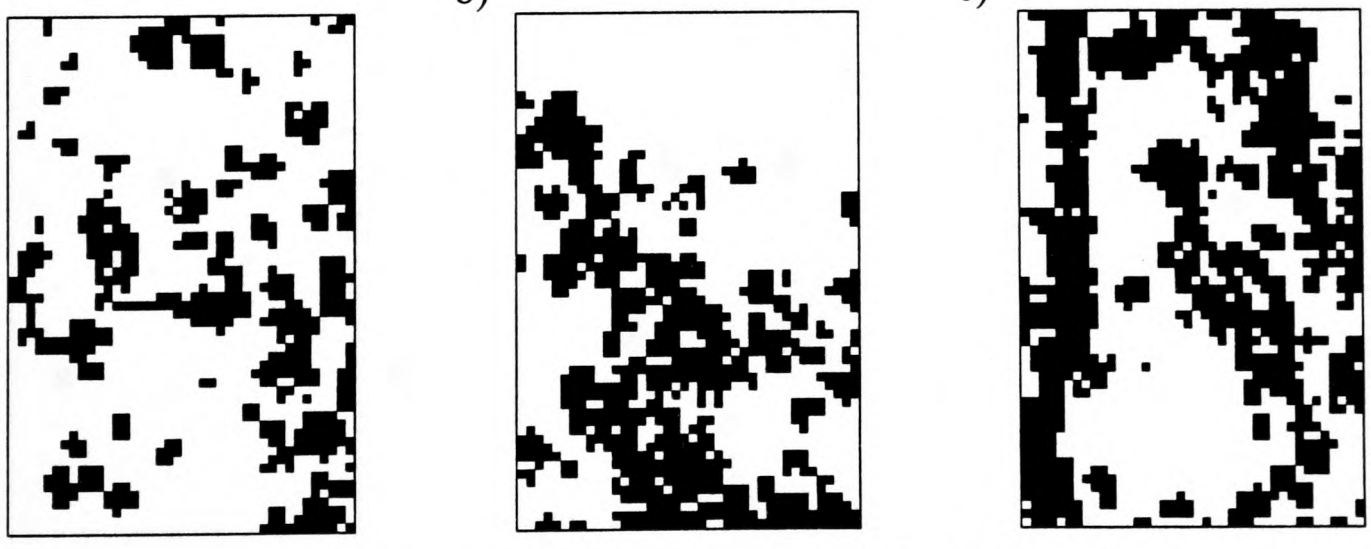
Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)

a) b) c)



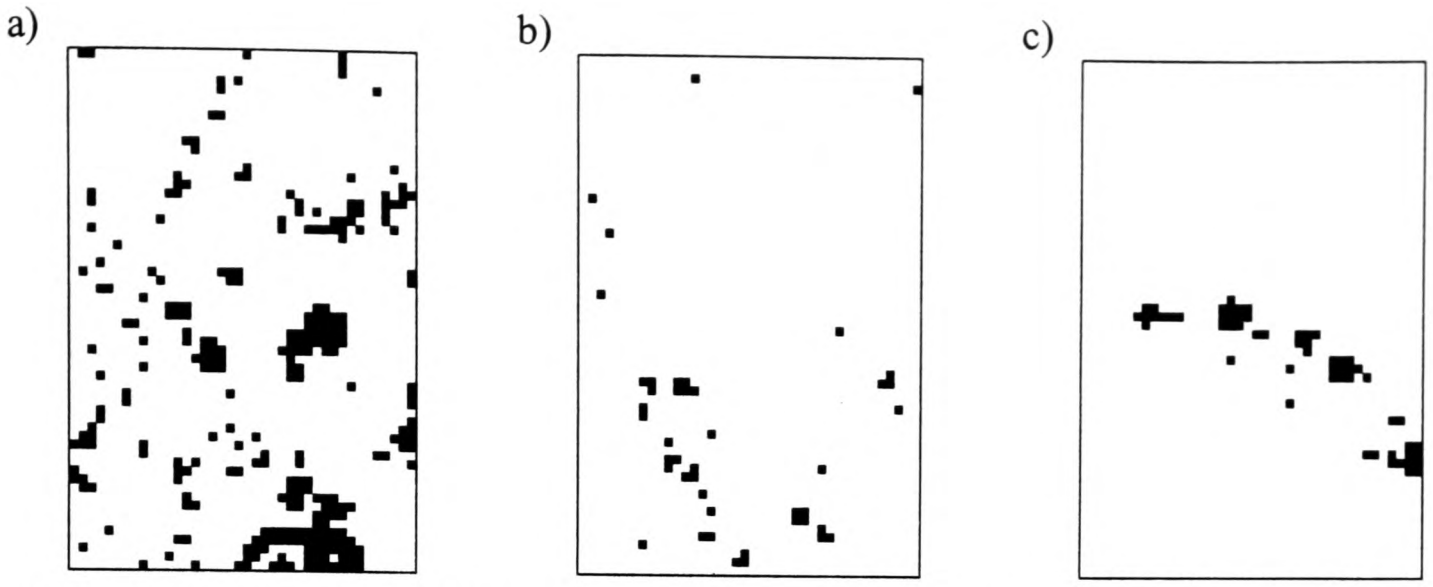
Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)

a) b) c)

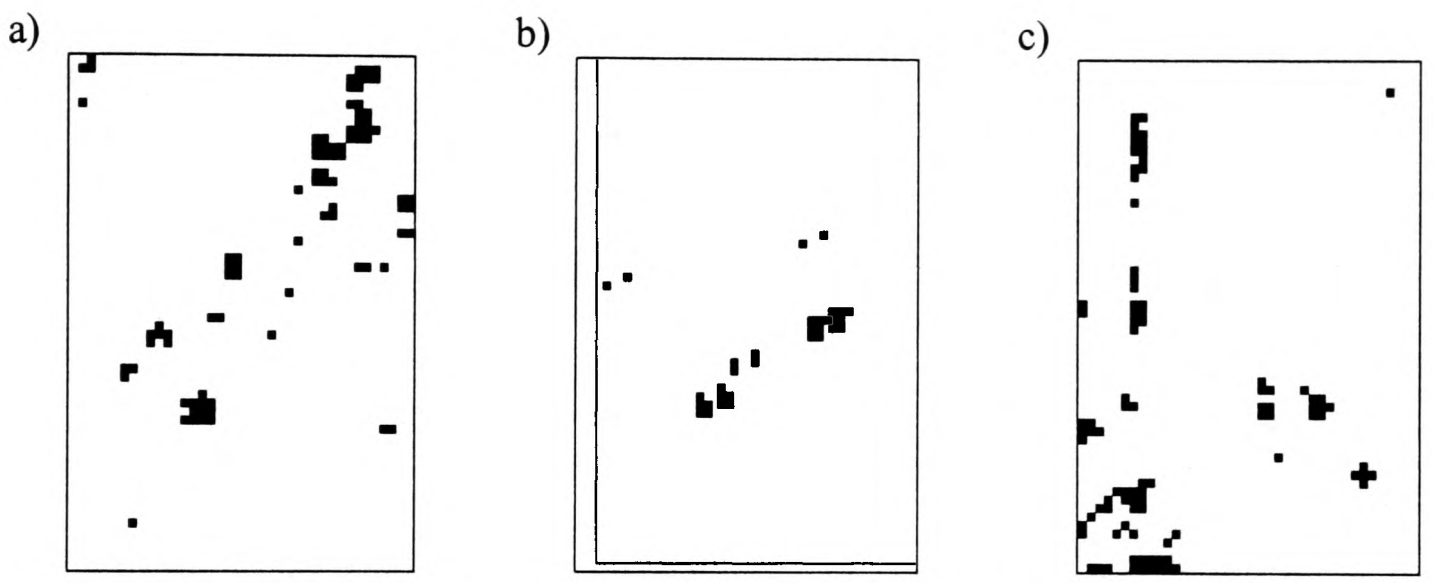


Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

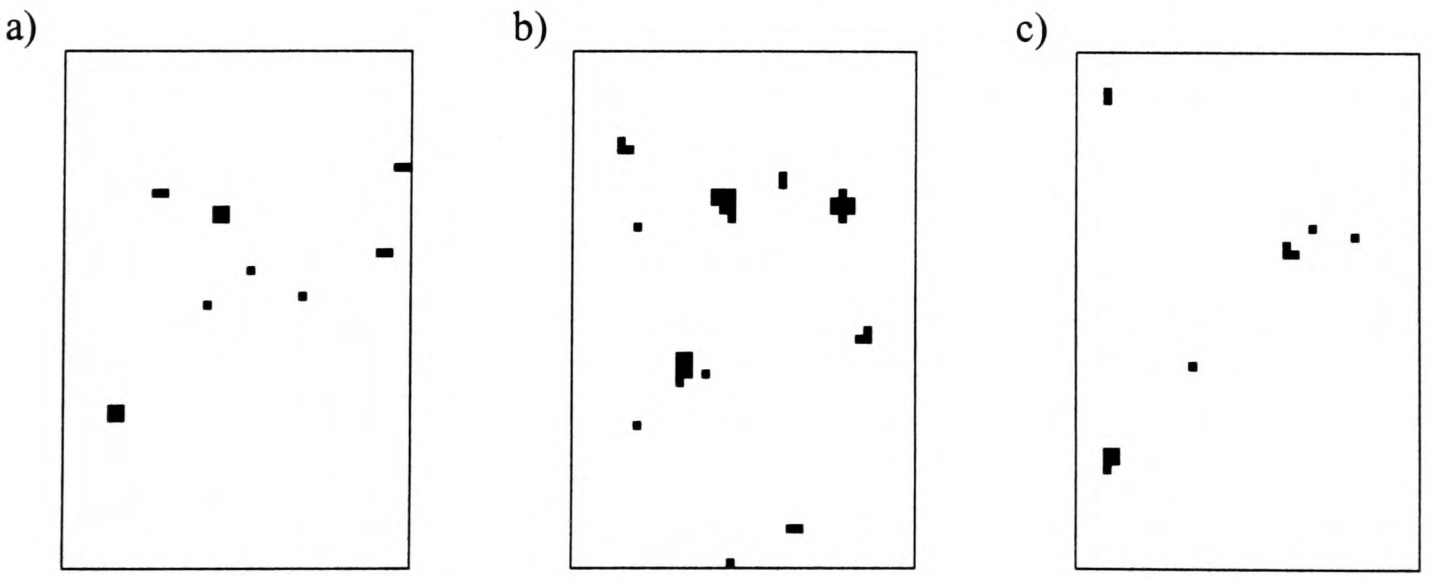
Salix phyllicifolia (wind dispersed)



Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)



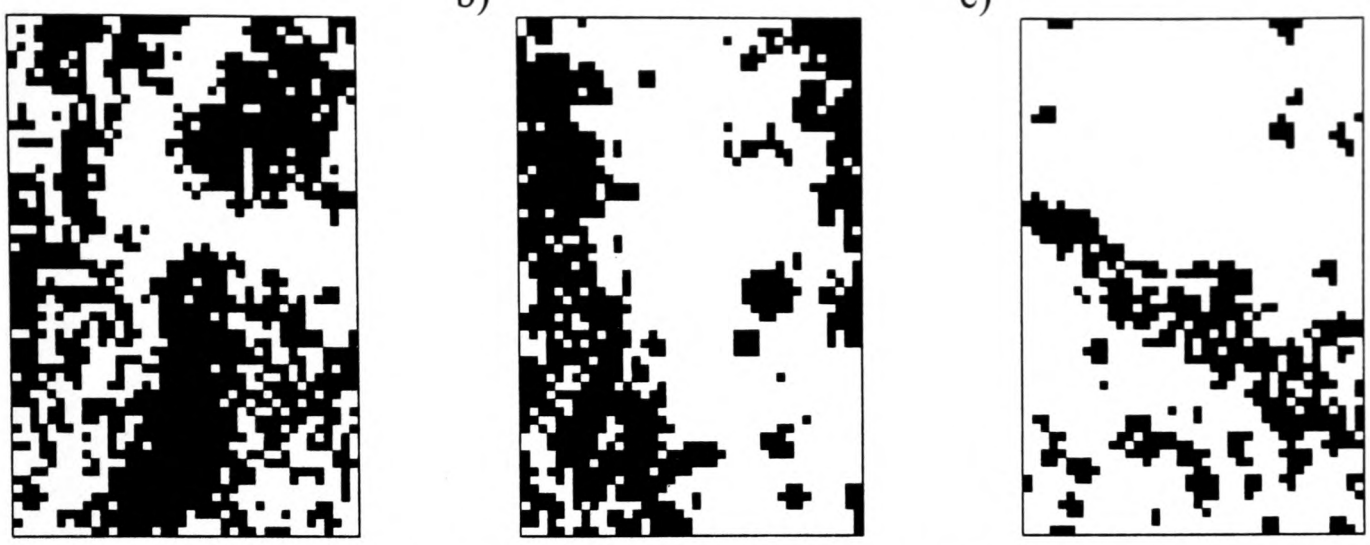
Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)



Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

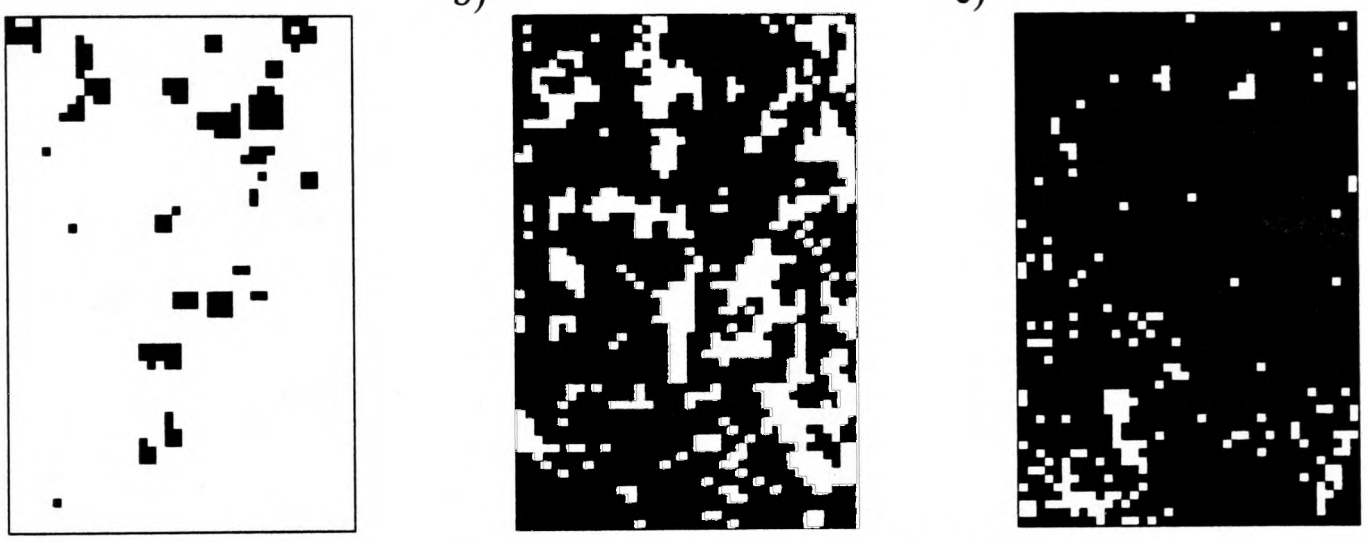
Calluna vulgaris (wind dispersed)

a) b) c)



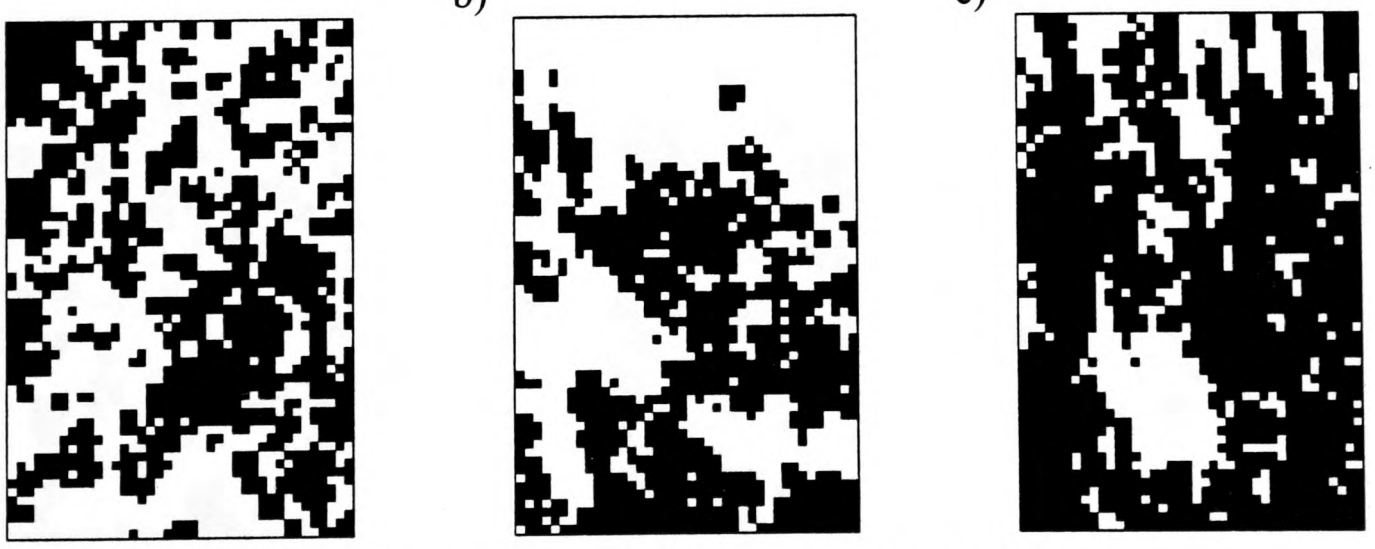
Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)

a) b) c)



Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)

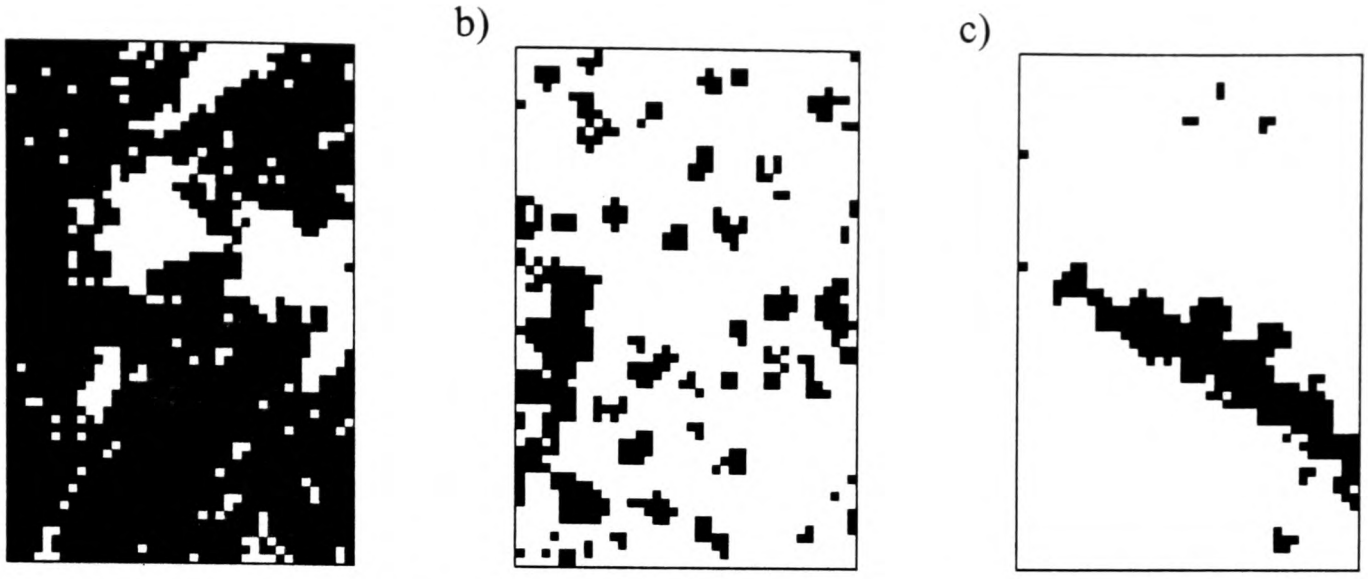
a) b) c)



Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

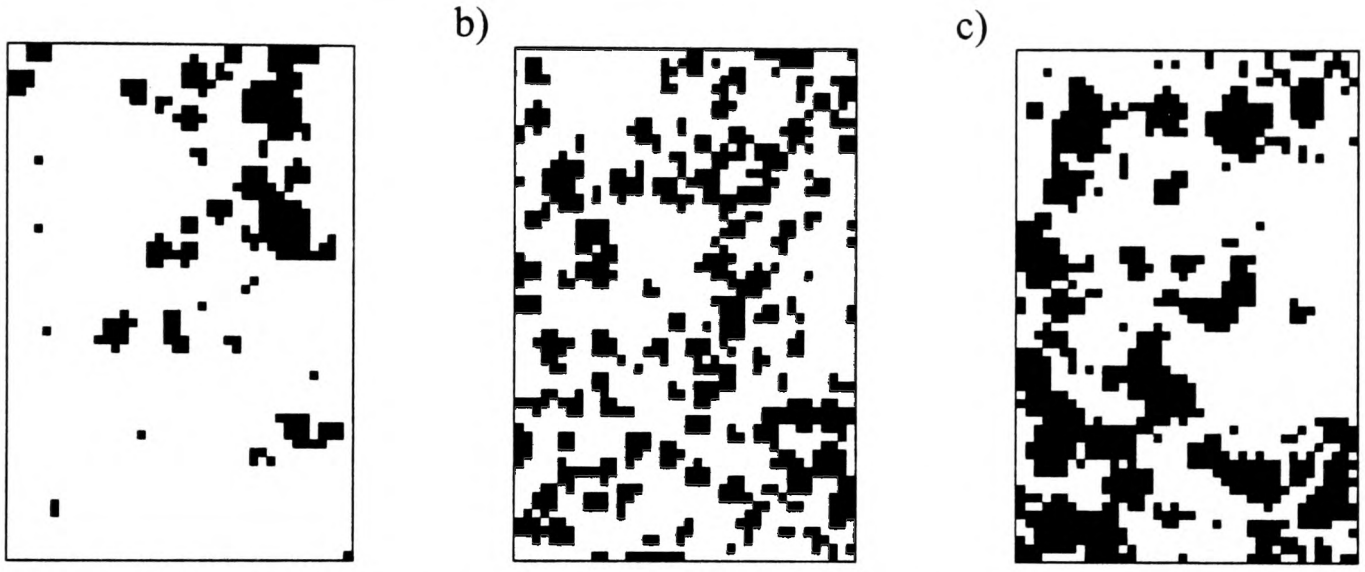
Betula pubescens (wind dispersed)

a) b) c)



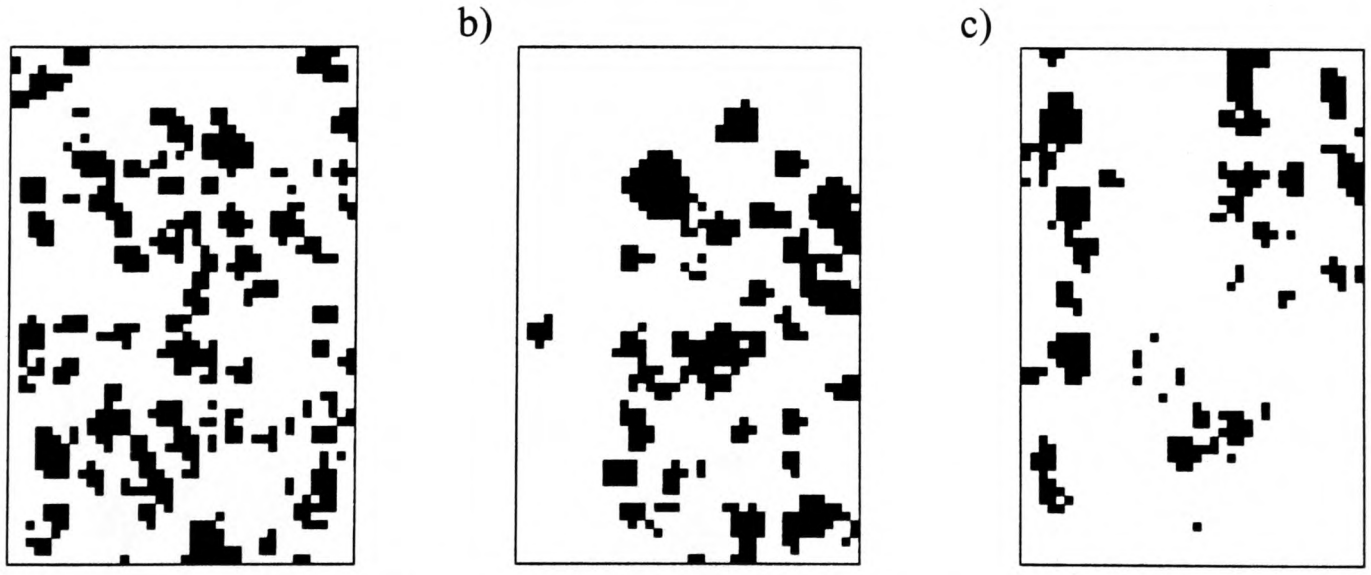
Austerdalsbreen: a) Aus3 (91 yrs); b) Aus2 (126 yrs); c) Aus1 (161 yrs)

a) b) c)



Bødalsbreen: a) Bod3 (65 yrs); b) Bod2 (176 yrs); c) Bod1 (229 yrs)

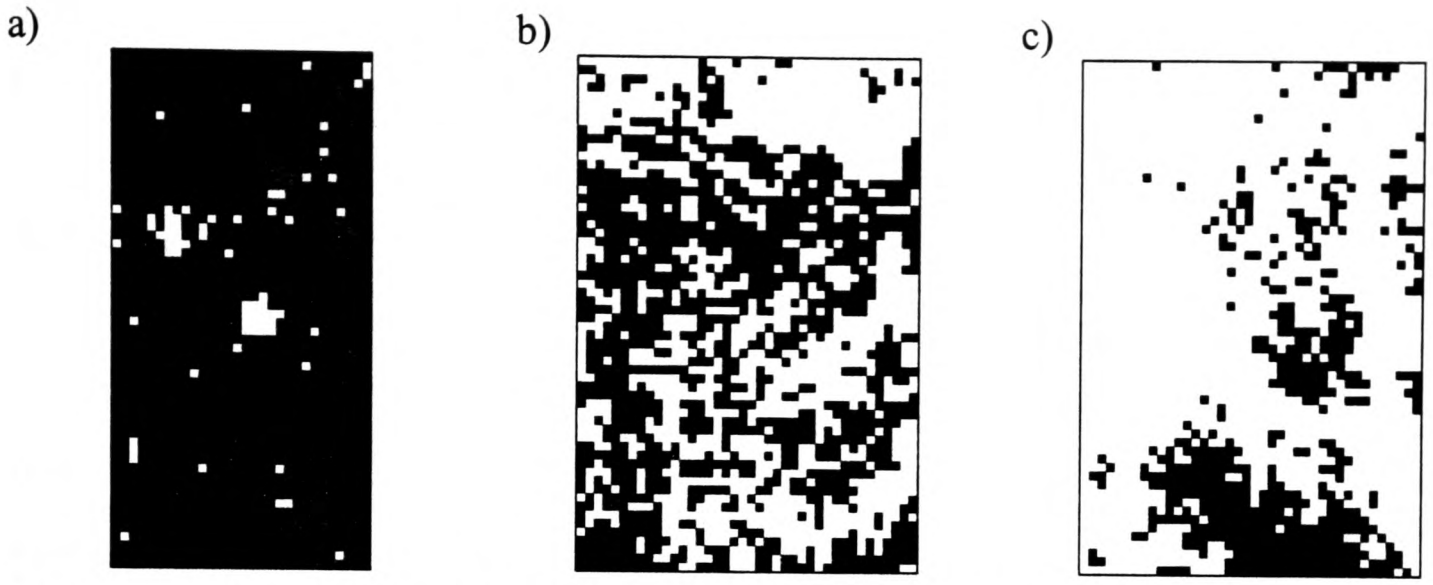
a) b) c)



Nigardsbreen: a) Nig7 (149 yrs); b) Nig2 (166 yrs); c) Nig6 (231 yrs)

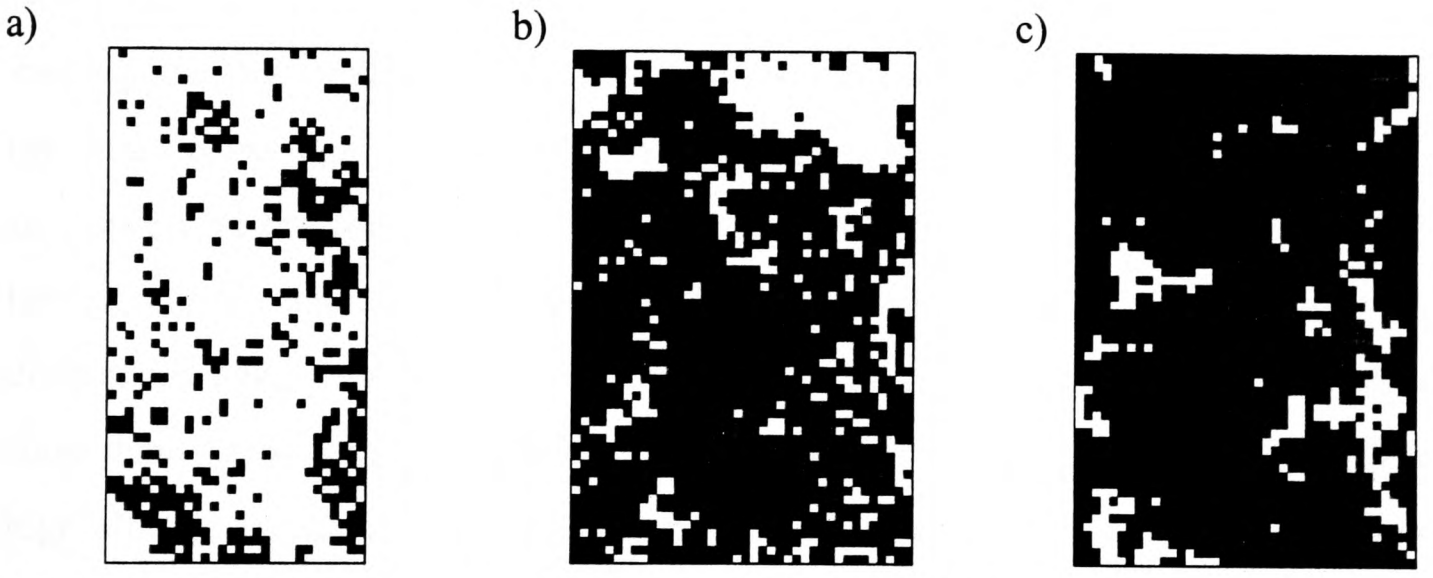
High altitude forelands (Storbreen and Høgvaglbreen; see Figure 3-13 for location of blocks on the forelands).

Empetrum hermaphroditum (animal dispersed)

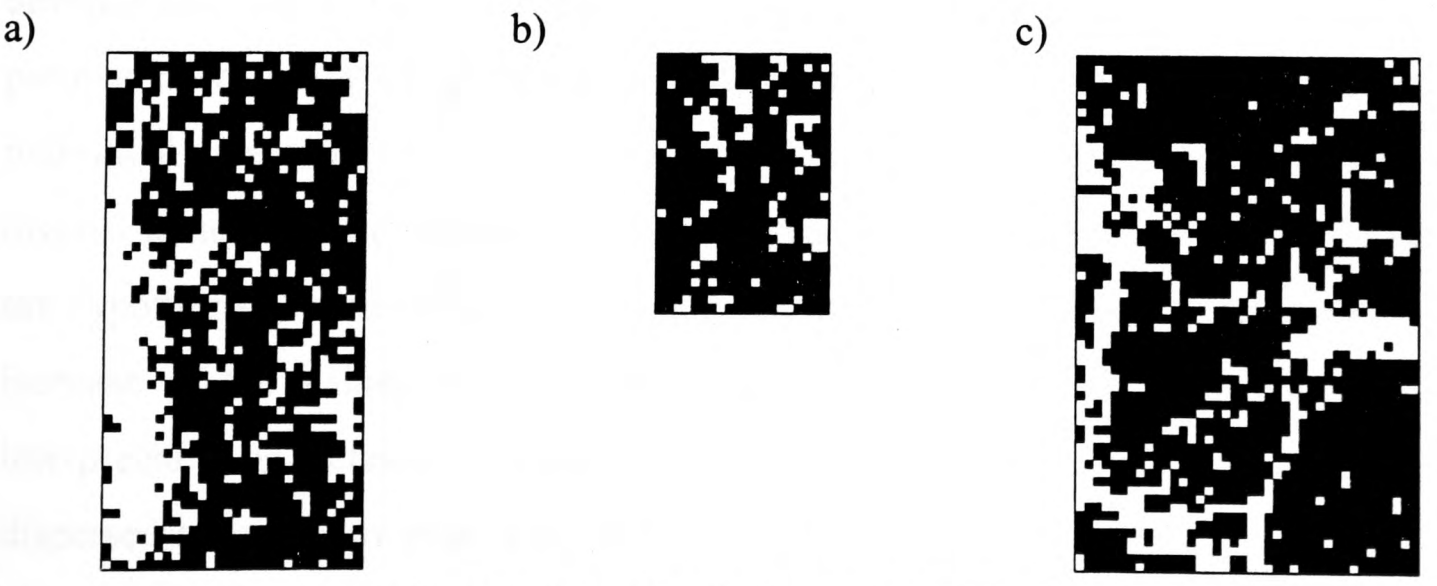


Storbreen: a) Sto8 (45 yrs); b) Sto6 (144 yrs); c) Sto5 (216 yrs)

Salix herbacea (wind dispersed)



Storbreen: a) Sto8 (45 yrs); b) Sto6 (144 yrs); c) Sto5 (216 yrs)



Høgvaglbreen: a) Hog5 (119 yrs); b) Hog3 (165 yrs); c) Hog2 (186 yrs)

Discussion and Conclusion

The frame for this study is set by the hypothesis that the difference in the dispersal mechanisms of animal- and wind-dispersed species may be detected in the spatial pattern that the respective species exhibit during primary succession on glacier forelands, hereafter referred to as hypothesis of differential colonisation.

Primary succession on glacier forelands is produced by a complex network of interwoven processes. Simple chronological ordering of the blocks from all forelands could not be expected to produce clear trends for the four spatial pattern descriptors (perimeter/area index, Moran's I and two fractal dimension measures). The results presented in Tables 1,3,and 5 demonstrate that indeed none of the descriptors shows a simple trend when analysed in this general way. There are a number of problems associated with chronosequence approaches that could explain this lack of temporal correlation. The chronological ordering of the blocks in itself can be affected by difficulties in the accurate dating of recently deglaciated terrain (Matthews, 1992: 11). Other factors like disturbances, which have been known to reset successional seres, varying starting conditions and diverging or parallel pathways of succession, also play important roles (e.g. Fastie, 1995). It also has to be noted that the earliest stages of the succession on the forelands were not sampled, which reduces the overall length of the time gradient, making the detection of temporal developments harder. Since regional differences have been known to exist for primary successions on glacier forelands for some time (summarised in Matthews, 1992: 220), the mixture of data from low- and high-altitude forelands might also contribute to the difficulty in finding an explicit trend.

The next step in the analysis of the data was therefore to investigate the pattern development for the three low- and two high-altitude forelands separately. For the mean perimeter/area index of all animal- and all wind-dispersed species no time trend for the individual forelands could be found. Some of the other descriptors, however, show distinct trends. On the Bødalsbreen foreland the pattern descriptor that directly supports the hypothesis of differential colonisation for wind- and animal-dispersed species, is the increase of the values of D_{Gau} for animal-dispersed species. This increase can be interpreted as an increase of overall cover of the species with time. D_{Gau} values for wind-dispersed species, however, also increase over time. This result might be an indication that the wind-dispersed species on this foreland have not yet reached the cover levels

which produce the competitive pressures that cause the distribution to break up into more fragmented areas. The temporal decrease of Moran's I values for animal-dispersed species on the Bødalsbreen foreland also does not directly support the hypothesis of differential colonisation. It is, however, conceivable that by being dominated in its earlier successional stages by mainly two species (i.e. *Calluna vulgaris* and *Empetrum hermaphroditum*) both wind- and animal-dispersed species have to compete for space to establish themselves in the dominant groundcover. This would subsequently lead to the observed trends of the formation of more continuous, less fragmented areas for the investigated species. Confirmation of this hypothesis can be found in the decreasing Moran's I values for the two dominant species. They are also the only species that show an increase in the number of unconnected patches over time indicating a fragmentation of their distribution with a parallel decrease in their average patch size from larger than 550m² to less than 10m².

On the Austerdalsbreen foreland there is an increase of the Moran's I values for wind-dispersed species as well as an increase in $D_{De\ Cola}$ values for animal-dispersed species. Both trends are opposing the expected trends of the hypothesis of differential colonisation. They suggest that wind-dispersed species develop from more patchy to more continuous distributions whereas the perimeter of distribution areas of animal-dispersed species becomes more complicated (convoluted) with time. On this foreland, similar to the Bødalsbreen foreland discussed before, one species (*Empetrum hermaphroditum*) dominates the three blocks (average area for each block is 235, 581.25 and 159.9m²). With one dominant species, all other species will be restricted in their potential to develop their distributions. It is only through time that they can enlarge their distributions competitively against the dominant species, which would explain the trend in the pattern descriptors.

On the Høgvaglbreen foreland D_{Gau} values for animal-dispersed species decrease over time. These values are, in this specific case, just the values of one animal-dispersed species, namely *Empetrum hermaphroditum*. Since this species is only present in a few cells in the surveyed blocks scarcity of distribution values probably pose a serious problem for the fractal dimension to produce meaningful results. Caution is therefore advised for the use of these descriptors for very sparse distributions.

None of the other forelands shows any signs of discernible trends for the average spatial descriptors of animal- and wind-dispersed species over time. Blocks on the

individual forelands contain a great variety of different environments, whose ratio alters for the series of blocks surveyed. This and the fact that due to time constraints only a few blocks of a particular age zone could be surveyed on each foreland leads to a situation in which real replicate samples for a sound statistical analysis could not be collected. The data is therefore likely to be influenced by unusual effects making a detection of temporal trends difficult.

To investigate the hypothesis of differential colonisation further, the pattern development of four animal-dispersed species (*Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea* and *Empetrum hermaphroditum*) was examined individually. Despite no trend in the index for the mean of all animal-dispersed species, the four selected species exhibit a general decrease of the perimeter/area index on the low-altitude forelands (Table 6-5). This is in keeping with a development from many smaller patches to fewer, larger patches. It seems that the mean value was unduly influenced by some rare species like *Sorbus aucuparia* and *Juniperus communis*. The Moran's I values for the three *Vaccinium* species on the low-altitude forelands also show the expected increase, with *Empetrum hermaphroditum* showing no trend. As with the D_{Gau} values for this species on the Høgvaglbreen foreland discussed earlier, the Moran's I values for very dense distributions might be influenced by the prevalence of the species in these areas and should be used with the appropriate care. When the average values of the pattern descriptors for animal- and wind-dispersed species within each block are compared, a consistent pattern emerges with either wind or animal-dispersed species showing higher values on low- and high-altitude forelands (Table 6-9)

Table 6-9: Relation of mean descriptor values for animal (Animal) and wind (Wind) dispersed species on low- and high-altitude glacier forelands

	Perimeter/area index	Autocorrelation (Moran's I, Kings case)	Fractal dimension D_{Gau}	Fractal dimension $D_{De\ Cola}$
Low-altitude forelands	Wind > Animal	Animal > Wind	Animal > Wind	No trend
High-altitude forelands	Animal > Wind	No trend	Wind > Animal	Wind > Animal

As can be seen from Table 6-9 there are major differences between the patterns on low- and high-altitude forelands. The descriptors strongly suggest that in the same blocks on low-altitude glacier forelands wind-dispersed species are present in smaller, more patchy and more widely spaced areas than animal-dispersed species. In contrast to this,

wind-dispersed species on high-altitude glacier forelands tend to exist in larger, more continuous patches with rather more convoluted perimeters. This observation lends credibility to the previously mentioned supposition that primary succession on low- and high-altitude glacier forelands are fundamentally different (e.g. Matthews, 1992: 221). Lying below the treeline, general ground cover on low-altitude forelands is relatively high. Most of the cover is provided by the three *Vaccinium* species, *Empetrum hermaphroditum* and *Calluna vulgaris*. Assuming that the wind-dispersed species (*Betula* and *Salix spec.*) can potentially reach all "suitable" sites for colonisation in an area, they rely on a gap in the dense ground cover and are probably constrained by moisture for germination (Vetaas, 1994). This might explain why the majority of the wind-dispersed species show the observed patchy spatial pattern on low-altitude forelands.

In contrast, the environment on high-altitude forelands is generally more severe and, other than in sheltered areas, no full ground cover develops. This situation provides more empty "safe" sites for colonisation for wind-dispersed species and combined with strong winds that provide an effective way of distributing the seeds this can lead to the more continuous, less patchy distribution pattern of wind-dispersed species on high-altitude forelands. It is in these hostile environments that the biotic vectors of animal-dispersed species instigate the nuclei of distributions for animal-dispersed species, which form small highly fragmented and more widely spaced patterns. Unfortunately no prediction can be made about the processes in the pioneer zone on these glaciers, since the youngest terrains have not been sampled.

The use of the TTLQV procedure was hampered by a problem in determining the maxima for the various block sizes. This could only be done visually by eyeballing the variance graph and reading off the horizontal axis the block size for which the variance was thought to form a local maximum. Nevertheless, for some of the species an increase in the pattern size with age could be demonstrated (e.g. *Vaccinium vitis-idaea*, *V. myrtillus* and *V. uliginosum* on Nigardsbreen and *V. vitis-idaea* on Bødalsbreen). This would be in keeping with the development of larger vegetation patches as succession progresses. The detected pattern sizes for *V. uliginosum* and *Empetrum hermaphroditum* on the Bødalsbreen foreland show, however, the reverse or an inconclusive trend. The fact that for many of the analysed distributions TTLQV did not detect any pattern, while

other pattern descriptors still provide interpretable results, stresses the point that pattern analysis should never be restricted to one tool only.

The results of this study show that the use of a suite of spatial analytical methods provides an appropriate way to analyse the development of distribution pattern of woody species on glacier forelands. Using different indices and spatial statistics not merely duplicates information, but adds to the elucidation of different processes important for the development of the patterns under investigation. Careful interpretation of the results allows us to gain more information about primary succession on glacier forelands.

However, some of the pattern descriptors used in this study seem to have problems with very dense or very sparse distribution patterns. Thus, caution is urged in the use of those indices in those cases. A better understanding of the theoretical background for the use of these indices is needed.

For some of the indices a relation between area and perimeter enters the equation. In the case of this study the surveyed blocks were quite small in comparison to the sort of Landsat scenes, which have previously been analysed with these methodologies. The problem of boundary effect is therefore expected to be quite prominent within the analysis of the data. This will influence all the calculations which depend on an accurate estimation or measurement of the length of the real distribution boundary.

This study shows that pattern development can, in many cases, be explained by the dispersal mechanism of the plants involved. On low-altitude forelands, with a lack of empty, suitable sites for colonisation wind-dispersed species tend to show a pattern of smaller, more patchy distributions, whereas on high-altitude forelands the more homogeneously advancing wind-dispersed species show more contiguous, less fragmented distribution patterns than animal-dispersed species.

To add further to the understanding of primary succession in these areas, extension of the investigation of the pattern development into the pioneer zones of the relevant glacier forelands could provide us with even more insight into the processes involved in those successions.

7. Spatially Explicit Models of Succession on Glacier Forelands

"Nature! We are surrounded by her and locked in her clasp: powerless to leave her, and powerless to come closer to her. Without asking us or warning us she takes us up into the whirl of her dance, and hurries on with us until we are weary and fall from her arms."

- GOETHE, *Maxims and Reflections,* early 19th century

Preface

In the previous chapter the geo-statistical properties of spatial distribution patterns of selected species on five glacier forelands were investigated. The results indicate that there is a difference in distribution patterns between animal- and wind-dispersed species as well as low- and high-altitude forelands.

To investigate the spatial aspects of succession on glacier forelands further, in this final data analysis chapter I develop models of the distribution of dominant woody species. In addition to the use of an ecological environmental favourability index and the species richness of an area, variables representing the spatial arrangement of the data and a form of autocorrelation measure are used in logit-regression modelling to estimate their influence on the distribution of the species.

The modelling approach also allows the use of varying proportions of the original data set, sub-sampled in different spatial layouts, to calibrate the models. This gives an indication of the effects of sampling effort and design on the performance of the models.

Introduction

Maps and atlases form an important part of the documentation and analysis of distributions of organisms in regional large-scale as well as local small-scale investigations (e.g. Perring & Walters, 1962; Haeupler & Schönfelder, 1989; Meinunger, 1992; Smith, 1994; Ostendorf, Mayr & Tappeiner, 1998). The data from these atlases, when analysed with appropriate statistical methods provide important insights into the factors controlling the distribution of the organisms (e.g. O'Brien, 1998). For ecologists there are a number of modelling approaches. They include mathematical models based

on regression, cellular automata and other geostatistical approaches (e.g. Hobbs & Legg, 1983; Davis & Goetz, 1990; Baker, Egbert & Frazier, 1991; Silvertown *et al.*, 1992; Brown & Rothery, 1993; Ostendorf & Reynolds, 1993; van Hees, 1994; Augustin, Mugglestone & Buckland, 1996). For presence/absence data, logistic regression analysis provides an established way to analyse the relationship between the response probability and the explanatory variables. It is, however, only in recent years that aspects like spatial autocorrelation and the spatial arrangement of the data have been considered explicitly in certain studies (e.g. Smith, 1994).

It is the aim of this study to establish the use of spatial variables as an important part of logit-regression modelling and to demonstrate the usefulness of this approach in the modelling of the dynamic systems of succession on glacier forelands.

The model most often used is the binary response model. The result of mathematical models is a representation of one variable (in this case the presence or absence of a dominant woody species) by an equation of other variables. Because ecological studies are often very time consuming, this approach can be used to evaluate if, for example, geomorphological features of an area can be translated into an environmental favourability index, which then can be used as an explanatory variable for the distribution of dominant woody species.

Four basic models were produced in the present analysis. The variables used in the logit models were easting, northing, their interaction (easting*northing), the richness of the rest of the woody species within a cell, an environmental favourability index derived from geomorphological sketch maps and an autocorrelation measure. It already has been shown by Ostendorf (1998) that topography can be used successfully to predict the distribution of arctic tundra vegetation. The main interest in the present study lay therefore in the performance of the environmental favourability index in connection with the geographical variables (easting, northing and their interaction) for the prediction of the presence/absence of woody species. Geomorphological sketch maps necessary for the calculation of the environmental favourability index are very easy to produce. This would mean that equipped with these maps and a limited number of sub-samples of the presence/absence of species within an area, predictions for the distribution of the species over a wider range should be possible.

For the development of a model, it is common practice to use parts of the original data sets for the calibration of the model. The rest of the data set, which was not used in

the production of the model, can then be used to evaluate the performance of the model, by comparing predicted values of occurrence with observed values of the original data set. This approach provides the possibility of examining the sampling effort necessary to gain an adequate representation of the distribution pattern of a certain region.

By selecting different proportions of the original data set as the sub-sample size for the calibration of the model, and varying the sub-sampling designs, I explore the amount of data necessary to be sampled and the sampling strategy most likely to produce a reasonably accurate model. The development of the model includes the identification of the variables which are both relatively easily obtainable in the field, and contribute significantly to the performance of the model.

Methods

A General Linear Model (GLM) with a logit link function was used for the predictive modelling of the species distributions. In this study the SAS package (SAS Institute, 1989-1996) was used to calculate the logistic regressions for the model. It uses the maximum likelihood method for this purpose, but it can be shown that for the logistic-binomial model, fitting by maximum likelihood is equivalent to iterative weighted least squares (Brown & Rothery, 1993).

The GLM in its original form has three components:

1) A linear predictor function constructed from explanatory variables. Suppose the data set has response variable Y, which takes on two values: 1 indicating presence; and 0 indicating absence, and three possible explanatory variables: x_1, x_2, and x_3. For this example the function is:

$$\theta(i) = \beta_0 + \beta_1 * x_1(i) + \beta_2 * x_2(i) + \beta_3 * x_3(i) \qquad \text{Equation 7-1}$$

where β_0 to β_3 are the coefficients (parameters) for linear predictor variables $x_1(i)$, $x_2(i)$, and $x_3(i)$ are the values of the explanatory variables.

2) A distribution or probability function for the response variable which depends on the mean μ and sometimes other parameters as well. For this example, the probability function is binomial.

3) A link function, g(.), which relates the mean to the linear predictor function. For logistic regression the link function is the logit:

$$g(p(i)) = \text{logit}(p(i)) = \log(p(i)/(1 - p(i))) = \theta(i) \qquad \text{Equation 7-2}$$

where **p(i) = Pr(Y = 1 | x(i)): response probability to be modelled**
x(i): set of explanatory variables for the ith observation.

The equation for the logistic-binomial model can be given as

$$p_i = \frac{e^{\alpha+\beta x_i}}{1+e^{\alpha+\beta x_i}} \qquad \text{Equation 7-3}$$

where p_i=probability of the *i*th subject
x_i value of the explanatory variable

The properties of the logistic response curve are illustrated in Figure 7-1.

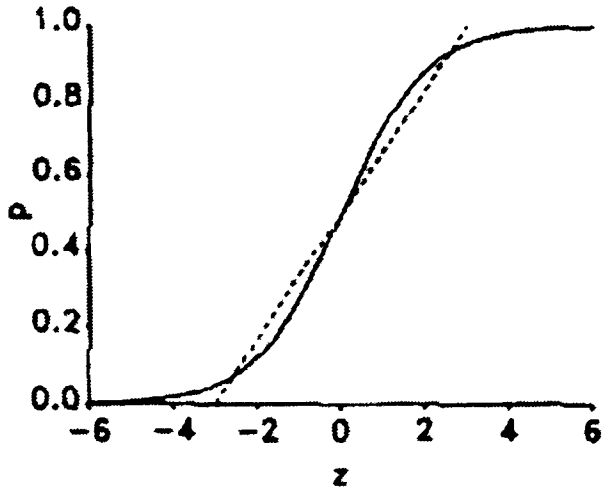


Figure 7-1: Properties of the logistic response curve relating the probability *p* of an event to the value of a standardised explanatory variable $z=\alpha+\beta x$.

Only dominant woody species, which were present in at least 10% of the original cells were included in the analyses. For the training of the model three proportions of the original data sets were sub-sampled (10%, 20% and 50%). Each proportion was sub-sampled in sets of squares of three different sizes (3*3, 4*4 and 5*5). These squares were systematically arranged across the original data set to give the sampling design shown in Figure 7-2.

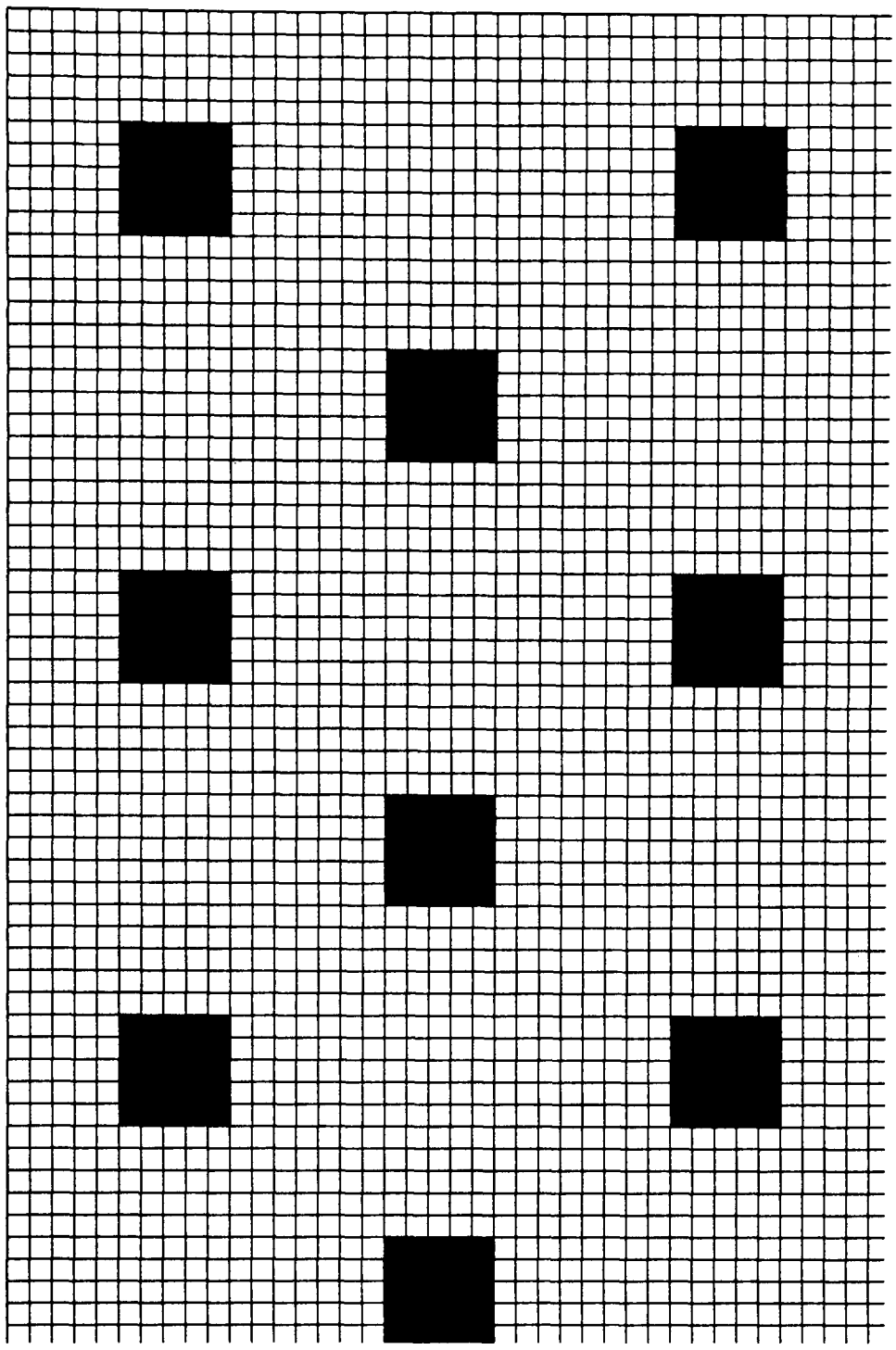


Figure 7-2: One example of a sub-sampling matrix for proportion 9.4% and square size 5*5.

The environmental variability of the blocks entered the logistic model, as the environmental favourability index. The index was derived from geomorphological sketch maps, depending on the amount of disturbance, the water regime and the soil properties associated with the corresponding geomorphological feature (Table 7-1). The calculation of this index was subjective and was based on the experience gained during three field seasons. The calculated values were ordered and transformed into an ordinal scale ranging from 1 to 9 (least suitable to most suitable).

Table 7-1: Environmental favourability index of geomorphological features in the 1996 blocks. Variables for *d*, *w* and *s* range from 1 to 5 (from least to most). The environmental favourability index is calculated as $(1/d + w + s) / 3$

feature	level of disturbance *d*	water regime *w*	soil properties *s*	environmental favourability index (calculated)	Ordinal environmental favourability index
Path	5	1	1	0.73	1
Fluted ridge	5	1	2	1.06	2
Ridge	4	1	2	1.08	3
Boulders	3	3	1	1.44	4
Snowbed	4	4	1	1.75	5
Slope	4	2	3	1.75	5
Plane	3	3	3	2.11	6
Cryoturbation	5	4	3	2.40	7
Low ditch	2	4	3	2.50	8
Mud flat	2	3	4	2.50	8
Channel	3	4	4	2.78	9
Depression	3	4	4	2.78	9

Summary of the model specifications is presented in Table 7-2. Models 1-3 forced the use of the specified variables in the model. Because of the potential of colinearity between the factors entering the models a fourth model was created using stepwise selection of the variables. This allows variables to be entered or removed at each selection step until no improvement of the model performance can be achieved by entering or removing any other variables.

Table 7-2: Parameters entering the 3 basic models. Easting, northing and easting*northing are geographical location variables, rest is a measure of species richness and ac is an autocorrelation measure

Model number	Parameters entering the model
Model 1	Easting+ northing + easting*northing + rest + env
Model 2	Easting+ northing + easting*northing + rest + env + ac
Model 3	Easting+ northing + easting*northing + env + ac
Model 4	Stepwise selection of variables

By using the optional output information on tolerance provided by the SAS-software, an estimation of the multicollinearity of the variables in the model could be attempted. The tolerance is computed by regressing each variable on all the other explanatory variables, calculating the R^2, then subtracting that from 1. Low tolerance values below 0.4 suggest high levels of multicollinearity (Allison, 1999, p.50).

An example for the naming convention of the 9 subsets of one model are given in Table 7-3.

Table 7-3: Naming convention for species calvul (*Calluna vulgaris*) using model 1 and the 9 possible subsets of calibration data. The first digit of the model name corresponds to the model number, the second to the layout and the third to the proportion

		Sub-sampling plot size		
Model 1		3*3 (layout1)	4*4 (layout2)	5*5 (layout3)
Sub-sampling proportion	10% (proportion1)	calvul131	calvul141	calvul151
	20% (proportion2)	calvul132	calvul142	calvul152
	50% (proportion3)	calvul135	calvul145	calvul155

Logit regressions were calculated for each of the 9 subsets for each species and the four models (i.e. 36 models per species). The logit model contained the presence and absence values of the selected plant species as the dependent variable. The sum of the number of other woody species in the cells of the investigation block (a measure of richness), easting and northing variables as representations of spatial orientation, an autocorrelation measure, and an ordinal environmental favourability index, derived from the geomorphological sketch map of the block entered the model as factors. The autocorrelation measure for the calibration of the models was the number of adjoining cells, within the sub-sampled square, in the same state (presence or absence). Since, for the prediction, autocorrelation values for all cells were not obtainable, the means of all autocorrelation values from the calibration data set were used in the predicted cells. The parameters obtained from the models were used to predict probabilities of presence/absence of the species for the whole sample block. The resulting distribution map of the species was then compared to the observed distribution map of the species and a confusion matrix (Figure 7-3) was calculated for all models. This matrix allows for the calculation of various error measures.

		Observed	
		+	-
Predicted	+	a	b
	-	c	d

Figure 7-3: A confusion matrix, b = false positives, c = false negatives, a and d = correctly predicted positives and negatives, respectively.

Fielding & Bell (1997) in their review of various prediction errors in presence/absence models point out, that the misclassification rate and some other error measures (such as positive and negative predictive power), are influenced by the proportion of the sum of rightly and wrongly predicted presences of the total number of observations (prevalence). Other measures of error which can be easily obtained from the confusion matrix and which are ecologically interpretable and meaningful are sensitivity, specificity, odds-ratio, Kappa statistic and NMI (Table 7-4).

Table 7-4: Confusion matrix derived measures of classification accuracy

Measure	Calculation
Prevalence	(a+c)/N
Sensitivity	a/(a+c)
Specificity	d/(b+d)
Misclassification rate	(b+c)/N
Odds-ratio	(a*d)/(c*b)
Kappa statistic	[(a+d)-(((a+c)(a+b)+(b+d)(c+d))/N)]/[N-(((a+c)(a+b)+(b+d)(c+d))/N)]
NMI	[-a.ln(a)-b.ln(b)-c.ln(c)-d.ln(d)+(a+b).ln(a+b)+(c+d).ln(c+d)]/[N.lnN-((a+c).ln(a+c)+(b+d).ln(b+d))]

All the above mentioned error measures are dependent on the cut-level (threshold), which is the value of the calculated probability above which a presence is assumed. A threshold independent error assessment is also available. It is the so-called ROC plot (receiver operating characteristic plot), which was developed in signal processing (Deleo, 1993). It can be obtained by plotting all sensitivity values (true positive fraction, the probability that the model predicts a presence for an observed location) on the y-axis against the false positive values (1- specificity, the probability that the model predicts a presence in an empty location) for all available thresholds on the x-axis. The area under

the ROC curve (AUC), a single value, describes the threshold independent overall accuracy of the model. The value for the AUC ranges from 0.5 to 1; 0.5 indicates randomness while 1 indicates perfect predictions by the model. For example, an AUC-value of 0.6 means that in six out of ten instances random selection of a point from the group of known presences will be associated with a predicted probability that is greater than the predicted probability of a randomly selected point from the group of known absences.

Data preparation and the calculation of the autocorrelation measure were carried out using EXCEL and SPSS. SAS was used for the calculation of the logit regression because of its flexibility to program repeated calculations on different data sets. A C/C^{++} program was written to calculate the error measures based on the confusion matrix and an estimate of the AUC-values for each model (code in Volume 2). Because of the different nature of the stepwise selection model its results will be presented separate from the initial three models.

Results

For the overall comparison of model performance, AUC of the ROC-plots lends itself as a good estimator (e.g. Fielding & Bell, 1997). The average performance of the three initial models across all forelands is 0.68 This means that in roughly 68 cases of a selection of 100 from the group of known presences the calculated probability is higher than from a selection of known absences. The average performance of the stepwise selection model across all forelands is 0.84. The average performance of all models is therefore 0.76.

The mean performance of the various models for the individual species across the forelands is summarised in Table 7-5. It ranges from 0.61 to 0.95.

Table 7-5: Average of the AUC of ROC-plots for each species (mean over all model configurations and all blocks on all forelands where the species is present). * denotes mean AUC larger than total mean model performance.

Species	Average AUC models 1-3	Average AUC model 4
Arctostaphylos uva-ursi (arcuva)	0.9137*	0.7962
Betula nana (betnan)	0.6813*	0.8211
Betula pubescens (betpub)	0.6551	0.8336
Calluna vulgaris (calvul)	0.6967*	0.8358
Empetrum hermaphroditum (empher)	0.6799	0.8446*
Loiseleuria procumbens (loipro)	0.6698	0.8529*
Phyllodoce caerulaea (phycae)	0.6685	0.8103
Salix herbacea (salher)	0.6408	0.8638*
Salix lanata (sallan)	0.6145	0.8830*
Salix phyllicifolia (salphy)	0.6571	0.7853
Salix reticulata (salret)	0.6522	0.9474*
Vaccinium myrtillus (vacmyr)	0.6756	0.8407*
Vaccinium uliginosum (vaculi)	0.6815*	0.8097
Vaccinium vitis-idaea (vacvit)	0.6731	0.8248

It can be seen in Table 7-6 that for all forelands the mean performance of model 4 for each foreland is significantly higher than the combined mean of the other three models and with the exception of two forelands the AUC values of model 4 are higher than the overall mean of 0.76.

Table 7-6: Average AUC of ROC-plots for all species present in the relevant blocks. For the location of the blocks see Figure 3-13

Foreland block name	Average AUC models 1-3	Average AUC model 4
Aus1	0.787	0.877
Aus2	0.690	0.840
Aus3	0.689	0.846
Bod1	0.691	0.853
Bod2	0.617	0.821
Bod3	0.721	0.818
Hog1	0.722	0.916
Hog2	0.648	0.804
Hog3	0.555	0.868
Hog4	0.567	0.975
Hog5	0.670	0.741
Hog6	0.672	0.894
Nig1	0.624	0.777
Nig2	0.702	0.812
Nig3	0.725	0.796
Nig4	0.798	0.837
Nig5	0.704	0.874
Nig6	0.639	0.791
Nig7	0.577	0.736
Nig8	0.666	0.842
Nig9	0.626	0.796
Nig10	0.605	0.834
Sto1	0.614	0.823
Sto2	0.728	0.871
Sto3	0.663	0.854
Sto4	0.688	0.815
Sto5	0.745	0.885
Sto6	0.651	0.807
Sto7	0.620	0.817
Sto8	0.648	0.838

Kruskal-Wallis analysis of the different model configurations for each species indicates, that the average AUC show highly significant differences between the four models, with model 4 consistently producing the highest AUC values. Similarly there is a significant difference between the three proportions used for the calibration of the models. The 50% sub-sampling proportion is the proportion, which tends to perform better than the two other proportions. The layout of the sub-sampling squares shows no significant variation between the three square sizes (Table 7-7;Kruskal-Wallis ANOVA $p<<0.01$ for models and proportions and $p = 0.326$ for the layout).

Table 7-7: Average AUC values for different model configurations. Significant differences exist between the four models and between the three proportions (p<<0.01; Kruskal-Wallis) with no significant differences between the three layouts (p=0.326)

Species	model1	model2	model3	model4	layout1	layout2	layout3	proportion1	proportion2	proportion3
Arcuva	0.9116	0.9129	0.9166	0.7962	0.9112	0.9143	0.9155	0.9063	0.9052	0.9296
Betnan	0.6899	0.6840	0.6701	0.8211	0.6827	0.6934	0.6679	0.6678	0.6763	0.6999
Betpub	0.6668	0.6634	0.6352	0.8336	0.6593	0.6548	0.6513	0.6330	0.6567	0.6757
Calvul	0.7137	0.6960	0.6803	0.8358	0.6960	0.7042	0.6899	0.6677	0.7026	0.7197
Empher	0.7189	0.6804	0.6404	0.8446	0.6839	0.6756	0.6802	0.6602	0.6775	0.7020
loipro	0.6796	0.6640	0.6658	0.8529	0.6730	0.6629	0.6735	0.6380	0.6750	0.6964
phycae	0.6827	0.6728	0.6501	0.8103	0.6754	0.6671	0.6631	0.6447	0.6686	0.6923
salher	0.6610	0.6419	0.6195	0.8638	0.6491	0.6443	0.6290	0.6129	0.6415	0.6680
sallan	0.6445	0.6058	0.5932	0.8830	0.6332	0.6025	0.6078	0.6094	0.6146	0.6194
salphy	0.6650	0.6594	0.6467	0.7853	0.6650	0.6577	0.6484	0.6413	0.6518	0.6780
salret	0.7318	0.6122	0.6124	0.9474	0.6727	0.6623	0.6215	0.6592	0.6452	0.6520
vacmyr	0.6952	0.6776	0.6541	0.8407	0.6835	0.6729	0.6705	0.6490	0.6765	0.7013
vaculi	0.6973	0.6851	0.6621	0.8097	0.6945	0.6797	0.6704	0.6587	0.6810	0.7048
vacvit	0.6913	0.6747	0.6532	0.8248	0.6767	0.6620	0.6807	0.6471	0.6754	0.6968

The tolerance values for the variables included into model 4 indicate that for certain variables there seems to be an issue with multicollinearity. Using the 0.4 cutoff level for the tolerance values as suggested by Allison (1999), Figure 7-4 demonstrates that for the variables easting, northing and their interaction term (en) the tolerance levels fall below this value, therefore indicating multicollinearity for those variables.

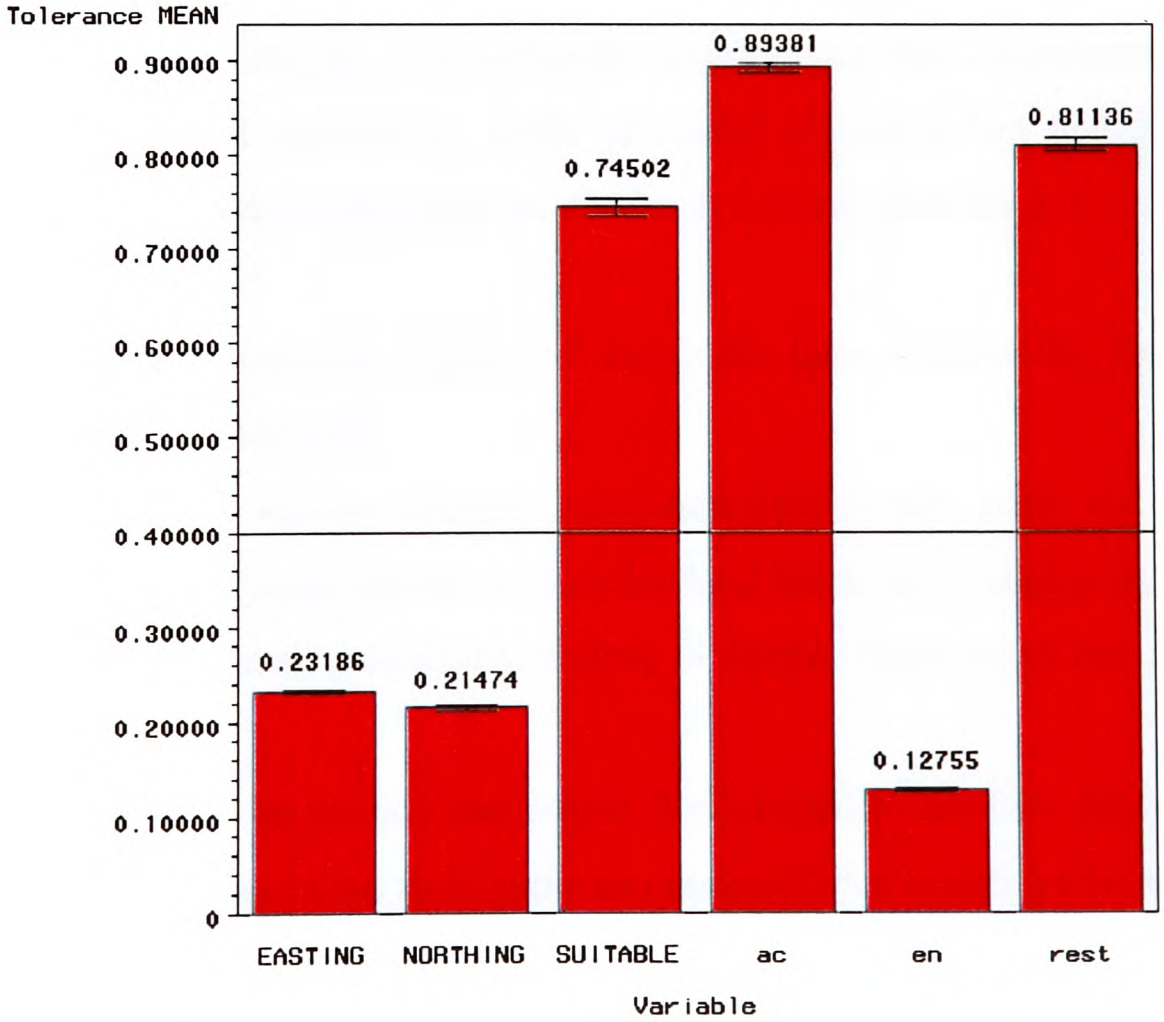


Figure 7-4: Average tolerance values of variables entering model 4 using stepwise selection (calculated from 1143 models).

A look at the number of times the available variables actually entered model 4 shows that the stepwise selection method added ac, rest and suitable (the autocorrelation value, the number of other woody species within the same sampling quadrat and the suitability index, respectively) significantly more often to the model than the location variables. They are the variables, which should be treated with care as shown in the previous paragraph, since they may suffer from multicollinearity (see Table 7-8). The stepwise selection method seems to be therefore a good way of avoiding problems with multicollinearity.

Table 7-8:Actual number of times variables have entered model 4 using the stepwise selection option

Intercept	Easting	Northing	EN	Rest	Suitable	Ac
1143	442	378	316	571	499	955
100%	38.7%	33.1%	27.6%	50%	43.7%	83.6%

The behaviour of *Empetrum hermaphroditum* on the Austerdalsbreen foreland was found to be representative of the dominating species with high levels of model performance. It was therefore decided to include its distribution maps, the model parameters, the model errors and the predicted distribution maps in this part of the thesis (Figure 7-5). The first figure displays the surveyed distributions, the environmental sketch-maps and the predicted probability levels of model 1, layout 3x3 and 50% proportion, for the three Austerdalsbreen foreland blocks. It also contains the ROC-plots for the relevant blocks.

As a comparison to the previous, Figure 7-6 shows the same features for *Betula pubescens* for the same foreland blocks.

Distribution maps of all species analysed, environmental sketch maps and the predictions of all 27 models for each species in each foreland block are available on the enclosed CD. A graphics program specifically written to display those maps has also been included.

The foreland directories also contain two output files created by the C++ program used to calculate the AUC-values of the ROC-plots and the confusion matrix based error measures of the models. **Auc2.out** files contain two columns with the model name in the first column and the AUC-value in the second column. **Modcros2.out** files contain for each model 99 cut-levels in steps of 0.01 units of probability, and the following error measures prevalence, sensitivity, specificity, 1-specificity, false positive , false negative,

misclassification error, correct classification, oddsratio, Kappa statistic and NMI (abbreviated as: Prev, Sens, Spec,1-Spec, FP, FN, Miscl, Corcl, Oddr, Kappa and NMI). These files are best opened with a spreadsheet program such as Excel (tab delimited text files).

Volume 2 of this thesis contains printed versions of the environmental sketch maps and species distribution maps for quick reference. Only the predicted distribution maps using the model with the highest AUC-value are included in the printed version.

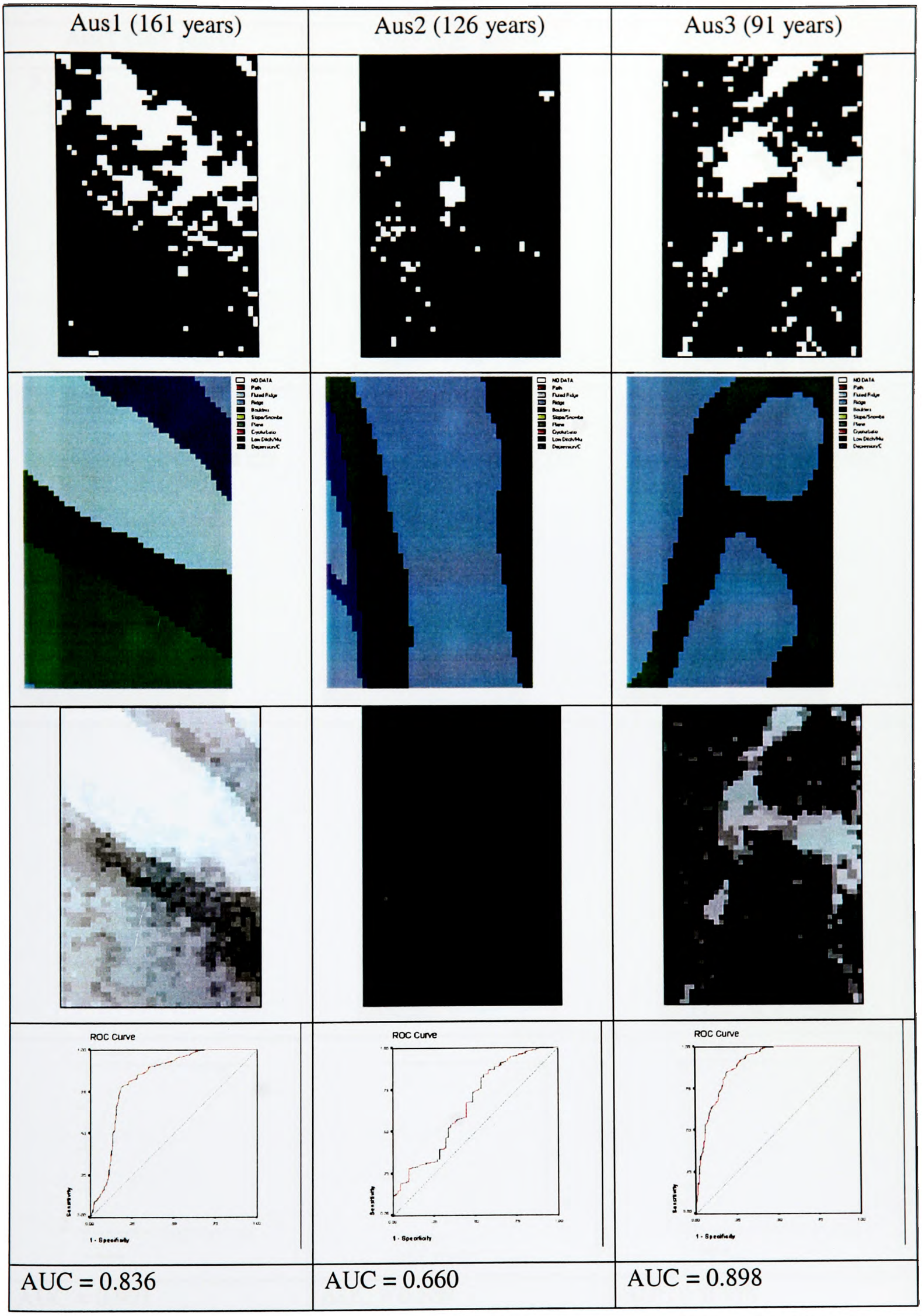


Figure 7-5: Distribution maps, environmental sketch-maps, predicted probabilities from model1, layout 3*3 and 50 sub-sampling proportion, ROC curves and AUC values for *Empetrum hermaphroditum* in three Austerdalsbreen foreland blocks.

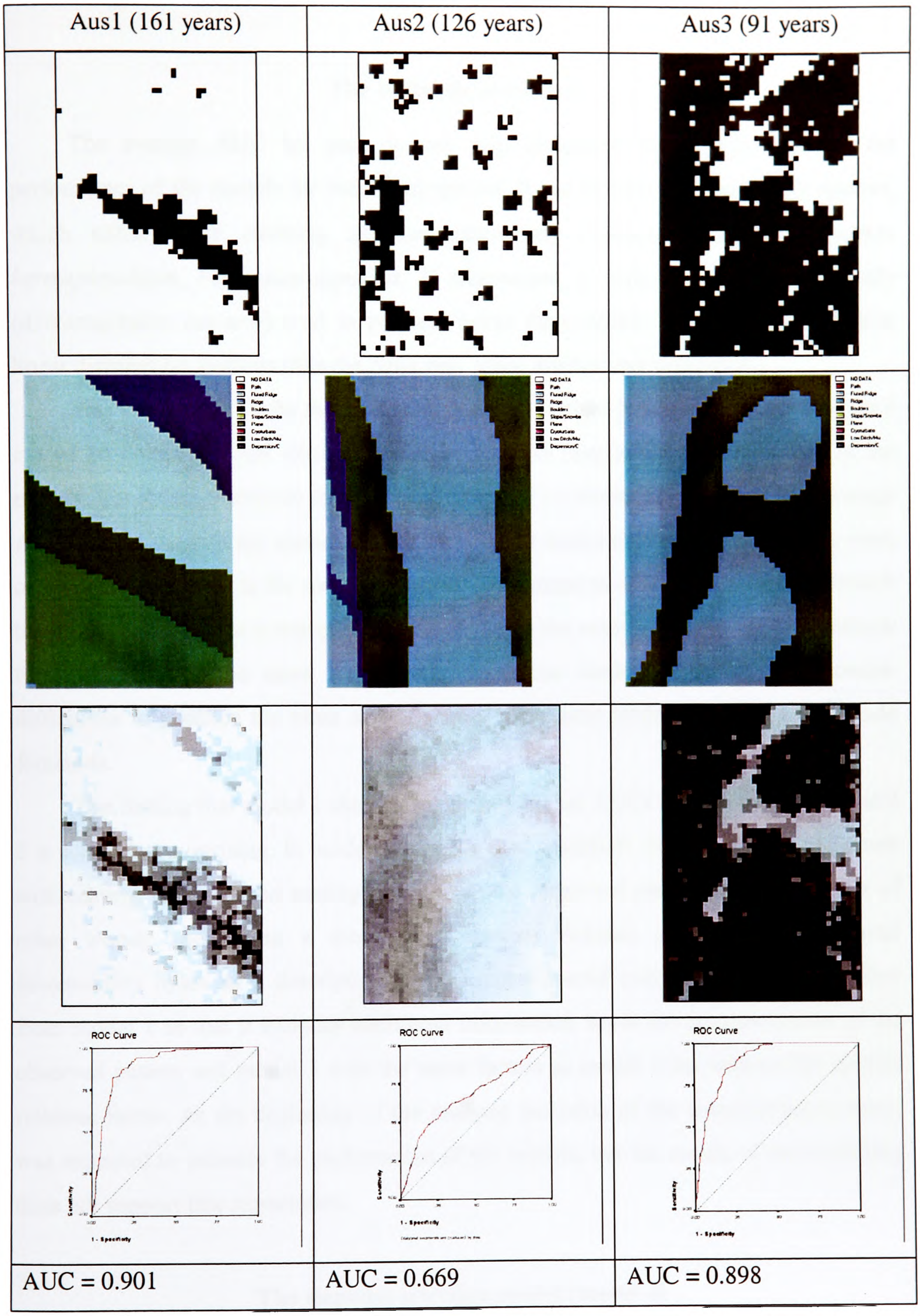


Figure 7-6: Distribution maps, environmental sketch-maps, predicted probabilities from model1, layout 3*3 and 50 sub-sampling proportion, ROC curves and AUC values for *Betula pubsecens* in three Austerdalsbreen foreland blocks.

Discussion

The initial three models

The average AUC for each species was calculated as an indication for the performance of the models for individual species. It can be seen that models for species, which either occur covering an area extensively (*Calluna vulgaris, Empetrum hermaphroditum, Vaccinium myrtillus, V. uliginosum, V. vitis-idaea*) or very sparsely (*Arctostaphylos uva-ursi*) tend to perform better than models for species that follow linear distribution features (like the *Salix* spp. along ditches and waterways).

The average AUCs for the models from the individual forelands demonstrates for 9 out of 16 blocks on low altitude forelands a higher than average performance of the models. For the high altitude forelands only 5 out of 14 blocks show higher than average AUC-values. As with the species, which show better model performance if they are more or less area covering, in the more favourable environments of the low altitude forelands the model performance is better than average. Since the environment of the high altitude forelands tends to be more fragmented, regression modelling seems to encounter difficulties to produce the same sort of high performance levels as on the low altitude forelands.

The finding that model 1 shows consistently higher AUCs than model 2 and model 3 is somewhat surprising. In model 1 only the bare essentials enter the model as factors with easting, northing and easting*northing as the locational parameters, the number of other woody species as a measure of species richness and the environmental favourability index as a description of the environmental conditions. Model 2 differs from model 1 in that it includes additional information about the autocorrelation of the observed pattern and model 3 with the same factors as model 3 but without the species richness factor. At the beginning of the analysis inclusion of the autocorrelation factor was expected to increase the performance of the models, but the results of the modelling does not support this expectation.

The stepwise selection model (model 4)

The AUC values for each species are generally higher than the mean values for the other three models (with the exception for *Arctostaphylos uva-ursi*). The reason for the

better performance of model 4 is presumed to be the way the selection method for this model seems to pre-empt problems with multicollinearity between variables. It was shown in Table 7-8 and Figure 7-4 that by using the stepwise selection of variables, the variables entering the model were primarily variables, which were not expected to suffer from multicollinearity. Comparison of the AUC values for species with different dominance shows that very abundant species like *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea* show high levels of accurate predictions. *Arctostaphylos uva-ursi* and *Salix phyllicifolia* on the other hand are represented very sparsely and show comparably low AUC values. This is in contrast to the finding using the other three models and could be due to the fact that for these sparse species, with very localised distributions within the sampling quadrats, the location variables become more important. Because they only entered about one third of the models with stepwise selection, the loss of the location information might account for the poorer performance of the model.

General considerations

The possible multicollinearity between the factors entering the models may help to explain the apparent unusual finding that out of the three initial models the one with the least number of variables produces consistently higher AUCs than the other models (Table 7-7). By limiting the number of variables entering the model, possible collinearity is reduced, producing better predictive models. Table 7-7 also shows that model 4, using the stepwise selection of variables entering the model produces very much higher AUC values than any of the other models. This finding makes a point for using this method as the default selection method. It is however still necessary to check the relevant tolerance values for specific models to get a better idea about if the variables selected for the model may suffer from multicollinearity.

The results of this chapter show that modelling the distribution of species even with a very limited number of factors is a valid approach and that it helps to further our knowledge about succession on glacier forelands. It becomes however clear that certain patterns, like the dominant area covering patterns of some species in this study produce better model performances than the linear distribution patterns of some environmentally restricted species (willows growing along waterways). Another observation is that

species which form dense mats of ground cover tend to produce models with better performance parameters than higher shrubs and plants with tree like phenology.

It is not surprising that the highest sub-sample proportion produces the best model performance (see discussion of data selection in methods). This result adds strength to the well know fact that model performance is increased with the amount of data available for the calibration of the model. It is therefore advisable for any modelling study to obtain separate data sets for the calibration and testing of the model.

In this study no indication about the importance of the sampling design on the performance of the models could be found. In the environments studied here there does not seem to be any discernible influence of the patch size within the training data set on the performance of the model.

It is, for example, conceivable that if the false positive prediction rate of the model is high, this might mean that the environment is not saturated, leading the model to falsely predict presence of organisms in suitable environments and conditions, where it is presently not found.

In this thesis it was tried to use the bootstrapping method to estimate means and standard errors of the parameters of the logistic regression models. During the course of this thesis it however became clear that no commercially available forms of implementing this approach for ecological research is available yet. Attempts to overcome this shortcoming by programming the procedures in S-Plus with the help of a statistician from Oxford University ran into severe problems. This approach had subsequently to be abandoned. It is nevertheless my conviction, that bootstrapping will be of great value for ecological modelling in the future.

By including the distribution maps and the environmental sketch maps in Volume 2 an attempt was made to make this information from three hard field seasons available to other researchers and to facilitate exchange of relevant data in the area of succession theory.

8. Summary and Conclusions

The formulation and testing of hypotheses forms the process through which science progresses. Being specific in their aims, hypotheses have to be discussed and related to a broader conceptual framework to contribute properly to progress within a discipline. It is the placement of the results of this research into the context of succession theory and the methods available to scientists, which forms the content of this chapter. The findings are summarised and their wider relevance for succession research on glacier forelands is discussed.

The first hypotheses tested in chapter 4 of this thesis have been formulated in previous work (see Matthews, 1992: 168). Support for the hypothesis of progressive increase of vegetation cover could be demonstrated for the Storbreen foreland. Both on a small- and large-scale, longer time since deglaciation leads to the development of higher plant cover values. This is attributable to the growth of individual plants as well as the demonstrated increase in the number of species and the observed change in life-forms. An increased importance of hemicryptophytes and woody chamaephytes in later stages of the succession supports the idea of a development towards a more layered vegetation. Despite the limitations of the sampling design and the lack of data on the youngest foreland terrains on the second foreland (Nigardsbreen), analysis of the available data does not contradict the previously stated hypotheses.

Chapter 4 also reports the results of a new approach using Ellenberg indicator values to estimate environmental conditions at a specific location from the average requirements of plant species found in this location. Ellenberg indicator values have previously been used by Persson (1981) to aid the interpretation of ordination diagrams. Here the average value of the Ellenberg indicator value for reaction (an estimator for the pH conditions of the soil) for a specific location could subsequently be shown to correlate strongly with estimated values for soil-pH based on work by Messer (1988). This demonstrates the usefulness of these values for research in which time and money constraints may require the scientist to estimate average conditions of certain environmental variables from readily available vegetation data.

In chapter 5 it was shown that well established analytical procedures, such as ordination and classification are still valuable tools for investigation of vegetation

variation on glacier forelands (e.g. Hallgren, Palmer & Milberg, 1999). The use of a different sampling regime to improve on the subjective placement of the sampling quadrats was investigated and it was shown that, although the significance of the results and the strength of the correlation of environmental factors with the vegetation variation was reduced when compared to traditional studies, such as those that follow the Braun-Blanquet sampling regime, they were nevertheless ecologically interpretable, especially when different methods were used to complement each other (e.g. ordination and classification). Similar to Persson's (1981) use of Ellenberg indicator values they were successfully used in this part of the thesis to help in the interpretation of ordination diagrams.

Comparison of the low-altitude glacier foreland of Nigardsbreen with the high-altitude glacier foreland of Storbreen shows that both forelands are similarly influenced by time-dependent factors. However, this study also confirms and quantifies the importance of geographical factors and shows that these factors exert a relatively greater influence at a fine spatial scale than at the historically important scale of landscape units. It was especially in the small-scale investigation that micro- and meso-topography were found to be the most important factors for the determination of the variation in the vegetation. There has been some recent research examining the importance of allogenic factors on the primary succession on glacier forelands (e.g. Jumpponen *et al.*, 1999) and the results from this thesis should encourage researchers to spend even more time and effort to quantify the importance of these factors.

Having demonstrated the importance of geographical arrangement and patchiness in these environments this thesis went on to explore new ground in the application of geographical analytical tools to vegetation pattern during succession on glacier forelands. A combination of a perimeter/area index, fractal dimensions and an autocorrelation measure was used for the first time in a study on primary succession on glacier forelands. The value of these pattern descriptors has been shown in other studies in ecology and geography (e.g. Palmer, 1990; Virkkala, 1993; Xu, Moore & Gallant, 1993; Gautestad & Mysterud, 1994). Using spatial indices for the analysis of distribution pattern in a successional environment, it is possible to investigate the temporal change of these indices (and related patterns) for specific plant species. This then can be used to test hypotheses about the influence of e.g. dispersal mechanisms on primary succession in those areas.

With the use of this new analytical approach it was demonstrated that animal-dispersed species tend to invade the forelands by means of relatively long distance or jump-dispersal events, which lead to the establishment of small patches. These later grow in size and coalesce to form larger and more contiguous areas of distribution. The behaviour of wind-dispersed species showed a more stochastic pattern, in correspondence with the hypothesised advance in a wider front. This might be thought of as an extension of the work of Stöcklin and Bäumler (1996), on the influence of life-forms in plant succession on recently deglaciated terrain. Their work, however, focussed on the pioneer zone, whereas the present study concentrates on the later stages of the succession. It could be shown that some of the pattern descriptors used in this study seem to have problems with very dense or very sparse distribution patterns. More investigations into the theoretical background and behaviour of these indices in ecological studies are therefore needed. Large parts of chapter 6 were presented at the "Spatial Analysis in Biogeography and Ecology" Session of the British Ecological Society conference in 1999 in Leicester, and are about to be published in the proceedings of this conference (Grimm, 2000).

To further our understanding of spatial aspects of succession on glacier forelands logit-regression modelling was used in chapter 7. This approach has been successfully used for the analysis of the influence of certain environmental and ecological factors on the distributions of organisms (e.g. Smith, 1994). This is however its first application on data from a successional environment and it was performed to analyse the temporal development of species-environment relations. Despite the existence of other modelling approaches (see chapter 2) it was felt that logit-regression presented a readily implemented way of analysing large amounts of geo-referenced data. Error measures, which can easily calculated by comparing the predicted probabilities of the modelled distributions with the observed distribution of a species give us some idea about the performance of the models (see chapter 7). This can be used as an estimate for the importance of certain parameters entering the model. In the context of dynamic successional environments, temporal change of the error measures also permits to formulate hypotheses about the ecological mechanisms involved.

One focus in this part of the thesis lay on the importance of autocorrelation. It could be shown in chapter 6 that many species on glacier forelands exhibit high levels of autocorrelation. This is a reflection of the clumped distribution patterns, which are

thought to be a manifestation of the ways plants invade and spread on glacier forelands. With the arrival of new propagules new centres of growth are established from which radial growth will lead to patches of contiguous distributions.

Results in chapter 7 demonstrated that the autocorrelation factor devised for the model did not increase the performance of the three initial models. A basic model with location variables easting, northing, easting*northing, the number of other woody species as a measure of species richness, and the environmental favourability index as a description of the environmental conditions, produced consistently better performance than models that included an estimate of the autocorrelation of the distribution data (with and without the species richness variable). This is an interesting finding and it could be due to the way the autocorrelation value had to be calculated and used for the prediction in the models (see chapter 7, Methods).

The additional approach of using stepwise selection of variables to enter the logistic regression model made it possible to investigate another aspect of regression modelling. This is the potential problem of multicollinearity between the variables. This feature of the data can adversely affect the result of the modelling exercise. It could however be shown that by using stepwise selection of the variables mainly variables, which do not seem to suffer from multicollinearity entered the model. In situations where large numbers of models are created and multicollinearity of the variables is suspected it is not always possible to follow the preferred route of checking tolerance and variance inflation values for the variables of each model. In these cases the stepwise selection method seems to provide a relatively robust way of using the most appropriate variables in the models. It is therefore recommended as one quick and effective way for the creation of statistically sound logistic regression models.

Another finding of the modelling was that predictions from models for species with extensive areal coverage as well as very sparse species tend to perform better than models for species that follow linear distribution features (like *Salix* spp. along watercourses). The use of varying proportions of the original data for the calibration of the models supports the well known fact that, by using a larger amount of the available data for calibration the model, its performance increases (Fielding & Bell, 1997). As was laid out in the methods section of chapter 7 (pp. 155) different sizes of sub-sample blocks were used to select the data for the model calibration. This was done to test the hypothesis that fewer larger blocks rather than more smaller blocks are able to capture

the properties of distribution patterns better. But no indication about the influence of the size of the sub-sampling blocks could be demonstrated.

The experience of researching this thesis, at the limits of statistical analysis of geographically referenced vegetation data, also demonstrate the need for further work in this area. Many different analytical strategies with potentially promising results had to be abandoned because of practical problems with the implementation of the statistical analysis. I am convinced that, for example, bootstrapping will play a much greater role in the future of modelling ecological data. There is certainly a need for the implementation of those methods in ecological analytical computer programs, to make them more widely available.

The large amount of field data collected also posed a problem, not least because of the potentially large number of models that can be speedily produced and modified. New methods of evaluating large numbers of slightly differing models are needed in the future. But this also stresses the point that simple "data diving" will always pose a problem: the formulation of clear hypotheses, should always help with the selection, testing and application of models.

It has been shown in this study that scale influences the results of many of the analyses. With the environment in the arctic/alpine areas of the study sites being dominated by periglacial processes, small-scale disturbances influence the distribution of suitable sites for the colonisation of plant species. They also reset successional seres thereby hampering the basic chronosequence approach. To improve our knowledge of primary successions on glacier forelands an even more accurate way of dating localities is necessary. Attempts have already been made by Maizels & Petch (1985) and Petch & Whittaker (1997) and it is thought that this is a step into the right direction.

After having summarised the results of this work it is important to put this research into a theoretical context. For a long time ecological theories did not consider the heterogeneity of ecological systems. This was in part due to methodological problems, but also to the prejudice that ecological systems are organised and well defined homogeneous entities (see McIntosh, 1991). Both the notion of temporal as well as spatial homogeneity was, however, contested early on (e.g. Gleason, 1926). On the basis of these realisations, non-equilibrium theories for the understanding of ecological concepts developed over the last 25 years. In this study temporal and spatial heterogeneity of the environment and the vegetation could be demonstrated. The driving

force for both forms of heterogeneity is disturbance, which has been identified as a major influence in determining successional pathways on glacier forelands. Patch-dynamics (see Jax, 1994) is a concept, which caters for the absence of an equilibrium and this heterogeneity on glacier forelands.

Since the heterogeneity of the vegetation is largely based on the patchiness of the environment (see chapter 7), it is thought that the geoecological component (the interaction of biological and physical factors; Matthews, 1992), is another important component, which has to be present in the theoretical framework for succession in these areas.

One area in which this thesis contributes significantly to vegetation science is the new analyses of spatial distribution patterns of individual plant species on glacier forelands. It became evident from the results in this study that certain groups of species show similar patterns. Animal- and wind-dispersed species, for example, form two groups when the descriptors of their spatial patterns are investigated. The groups are distinct through both the manifestation of the spatial patterns at a given time as well as the temporal change of those patterns during succession (see chapter 6). This can be seen as indirect evidence for the existence of assembly rules on glacier forelands. These assembly rules can be defined as restrictions on the presence and abundance of species based on the presence and abundance of other species and have been shown to exist in other plant communities (e.g. Drake, 1990; Wilson & Whittaker, 1995). Very little is known about how commonly assembly rules operate and the supporting evidence for their existence on glacier forelands adds to the sparse knowledge base available.

One main interest in this thesis was the description and analysis of spatial vegetation patterns created by succession. It has to be the aim of conceptual frameworks to relate those patterns to the mechanisms, which produced these patterns. It is through the understanding of the mechanisms of succession, that we increase our knowledge about succession and vegetation dynamics.

The process-oriented model of Pickett *et al.* (1987a; 1987b) provides a sound basis for the mechanistic explanation of primary succession on glacier forelands (as indeed for other primary successions; e.g. Schmitt, 1997 and Schmitt & Whittaker, 1998; see Table 2-1). It is the large scale disturbance of the glacier retreat that produces the environment where we observe primary successions. The hierarchical systems provides all the causes and processes identified in this thesis as being important for primary succession on

glacier forelands. Some of the processes and mechanisms related to Pickett *et al.*'s hierarchical model which were identified as being important in this thesis are:

- Disturbances that are working locally to alter the micro-topography (e.g. cryoturbation, sedimentation, etc.) and exert pressure on already established plants (e.g. grazing).
- Dispersal and the nature of the propagule pool. This is influenced by the geography of the foreland (tumbling of propagules onto the foreland from steep valley sides, the type of surrounding vegetation and the dispersal agents).
- Differential species performance due to resource availability (e.g. soil depth and soil pH), topography (aspect), life history strategies and presence of competitors.

Since the study sites of this thesis all lie in highly dynamic environments, it is important to remember that the strength of various influences on the vegetation can change during the succession (Walker & Chapin III, 1987; see Figure 2-2). This is important when one decides on a conceptual framework like the mechanistic model proposed by Pickett *et al.*. All the various mechanisms and processes will be of different importance at various stages of a succession and in different locations. This stresses the point that, despite the undoubted usefulness of models for the formulation of new hypotheses and experimental design, analysis of patterns and description of observed successional seres are still important to add to our understanding of successions.

9. References

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VEGETATION SUCCESSION ON GLACIER FORELANDS IN THE JOSTEDALSBREEN REGION AND JOTUNHEIMEN, SOUTH-CENTRAL NORWAY

VOLUME 2

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Table of Contents

1. DISTRIBUTION MAPS OF WOODY SPECIES 2

Austerdalsbreen foreland block I (Aus1) 2
Austerdalsbreen foreland block II (Aus2) 5
Austerdalsbreen foreland block III (Aus3) 8
Bødalsbreen foreland block I (Bod1) 11
Bødalsbreen foreland block II (Bod2) 14
Bødalsbreen foreland block III (Bod3) 17
Høgvaglbreen foreland block I (Hog1) 19
Høgvaglbreen foreland block II (Hog2) 20
Høgvaglbreen foreland block III (Hog3) 21
Høgvaglbreen foreland block IV (Hog4) 22
Høgvaglbreen foreland block V (Hog5) 23
Høgvaglbreen foreland block VI (Hog6) 24
Nigardsbreen foreland block I (Nig1) 25
Nigardsbreen foreland block II (Nig2) 27
Nigardsbreen foreland block III (Nig3) 30
Nigardsbreen foreland block IV (Nig4) 32
Nigardsbreen foreland block V (Nig5) 34
Nigardsbreen foreland block VI (Nig6) 37
Nigardsbreen foreland block VII (Nig7) 39
Nigardsbreen foreland block VIII (Nig8) 41
Nigardsbreen foreland block IX (Nig9) 44
Nigardsbreen foreland block X (Nig10) 46
Storbreen foreland block I (Sto1) 49
Storbreen foreland block II (Sto2) 54
Storbreen foreland block III (Sto3) 57
Storbreen foreland block IV (Sto4) 60
Storbreen foreland block V (Sto5) 63
Storbreen foreland block VI (Sto6) 65
Storbreen foreland block VII (Sto7) 68
Storbreen foreland block VIII (Sto8) 70

2. C/C^{++} CODE 73

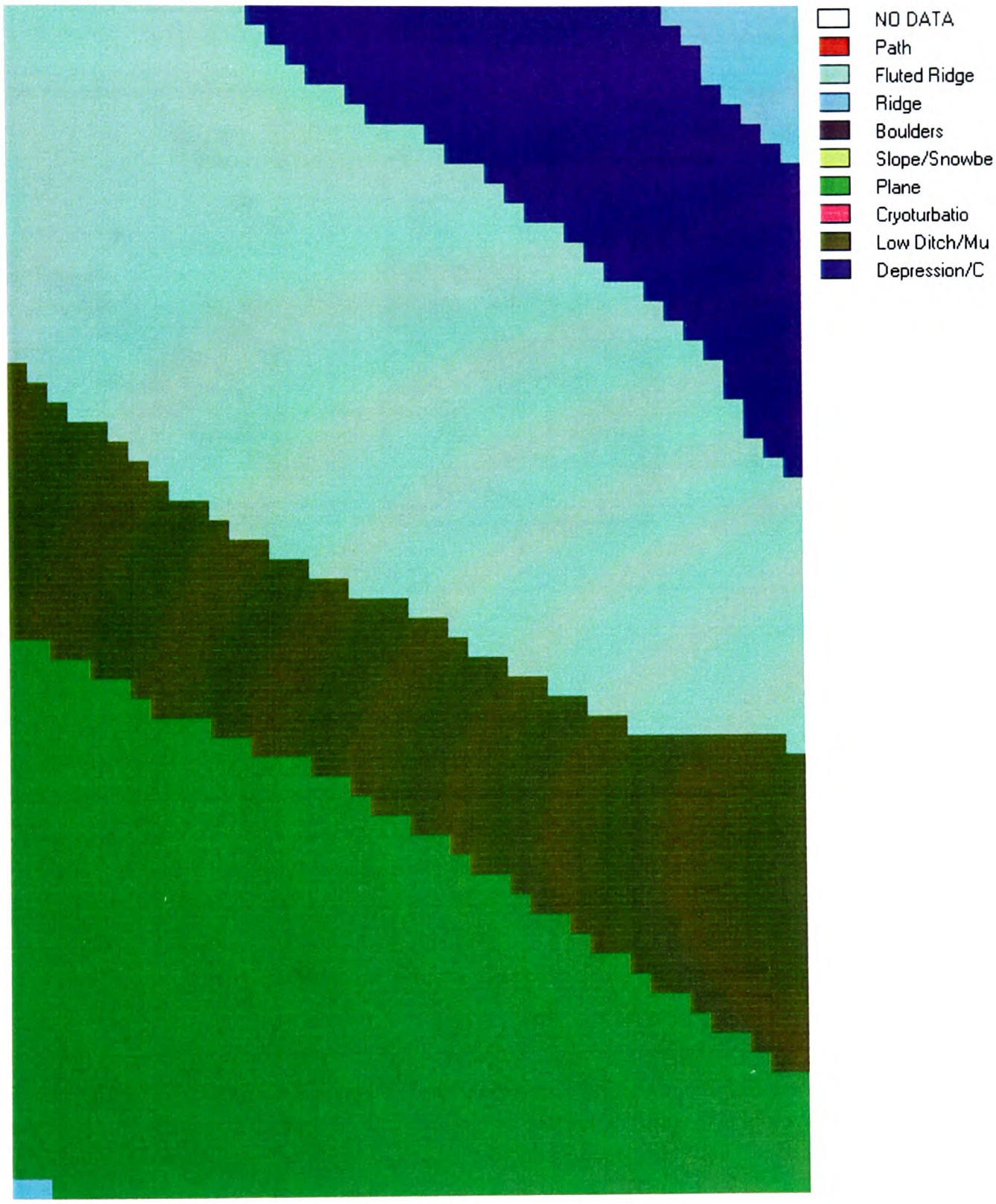
TTLQV program 73
Model error and AUC program 78

1. Distribution Maps of Woody Species

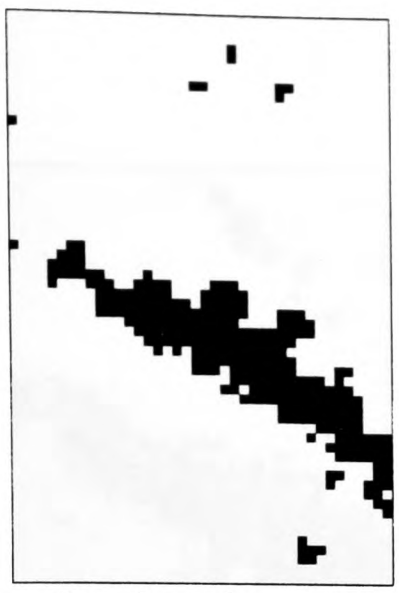
Austerdalsbreen foreland block I (Aus1)

For the location of the blocks on the forelands see Volume 1 Figure 3-13.

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



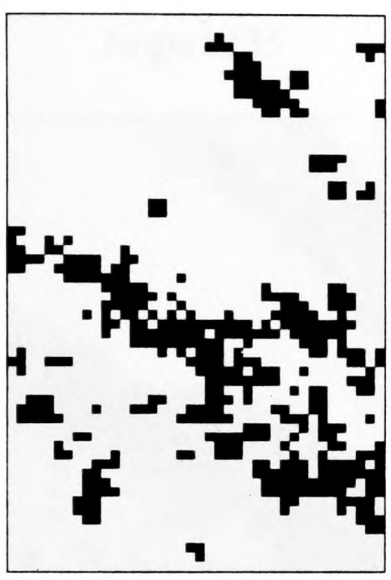
Environmental sketch-map



Betula pubescens

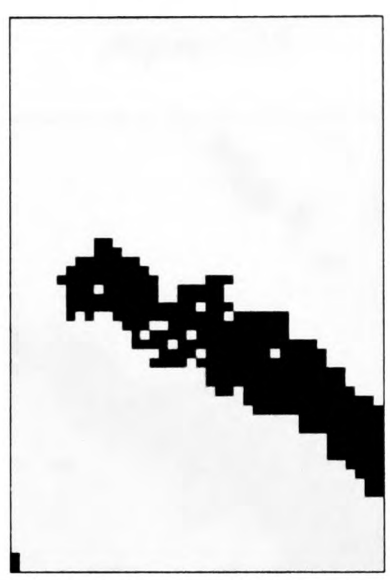
Calluna vulgaris

Empetrum hermaphroditum

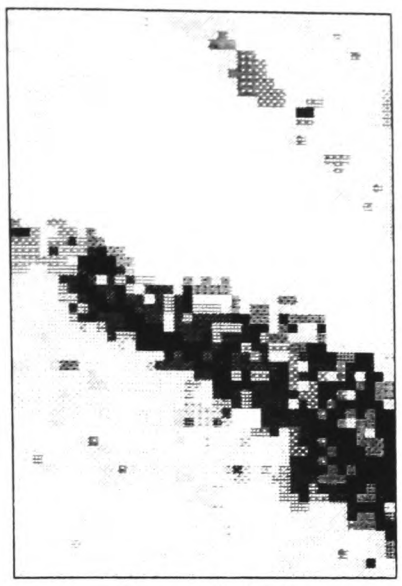


Phyllodoce caerulea

Vaccinium myrtillus



Vaccinium uliginosum



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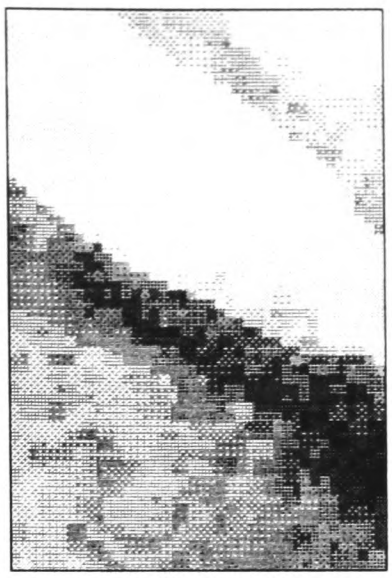

calvul245

empher135

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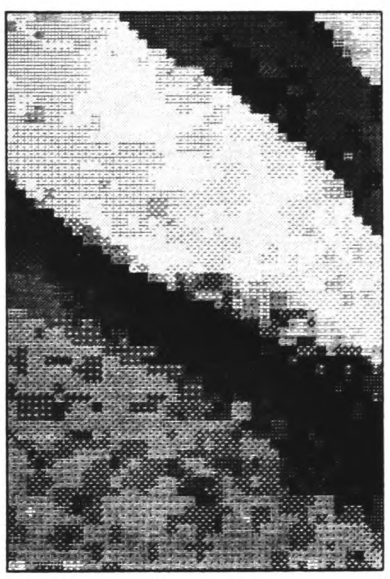

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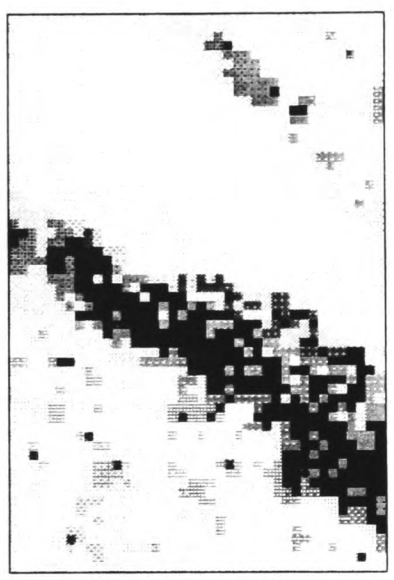
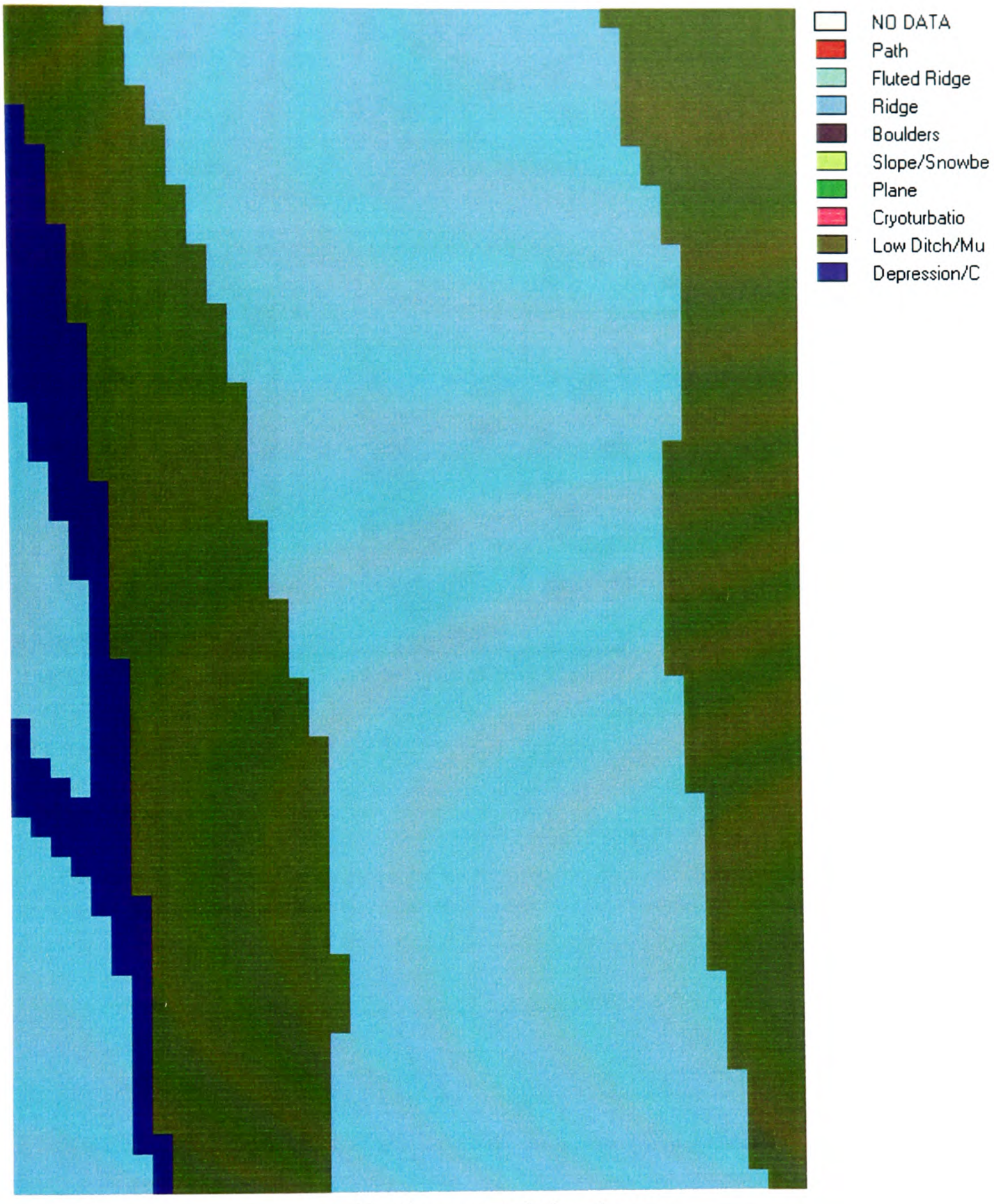


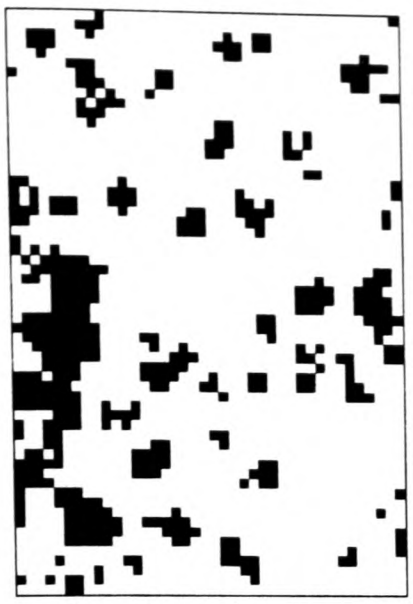
vaculi145

Austerdalsbreen foreland block II (Aus2)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

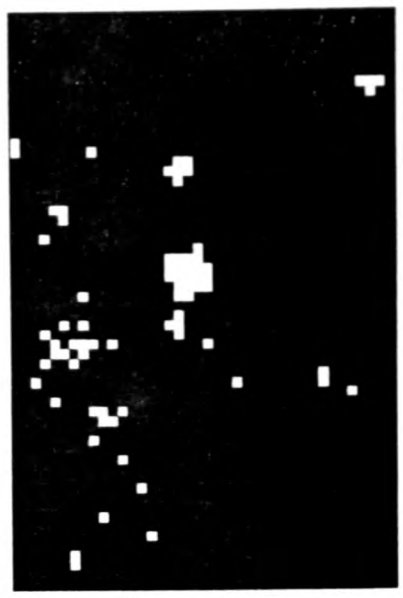


Environmental sketch-map



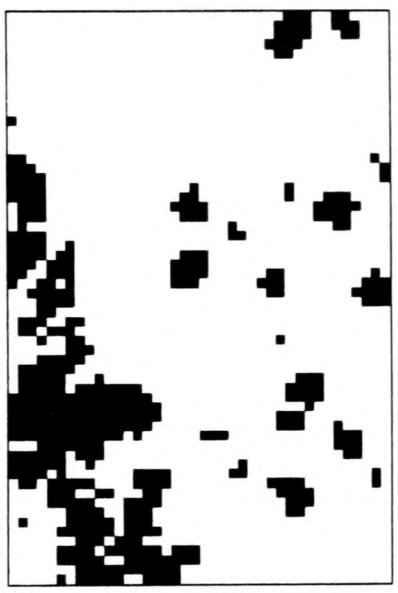
Betula pubescens

Calluna vulgaris

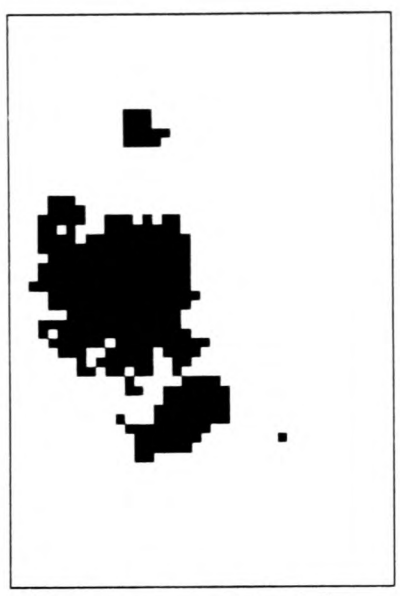


Empetrum hermaphroditum

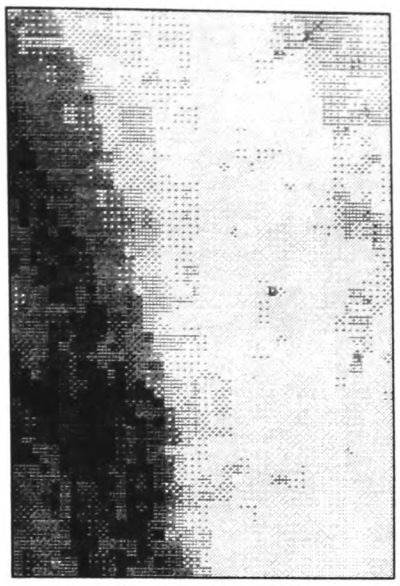
Vaccinium myrtillus



Vaccinium uliginosum



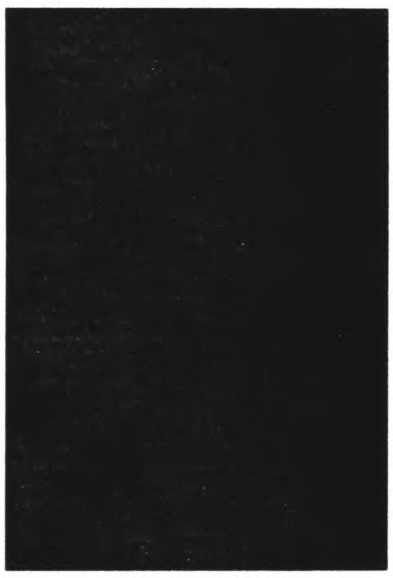
Vaccinium vitis-idaea



betpub145

calvul252

empher142



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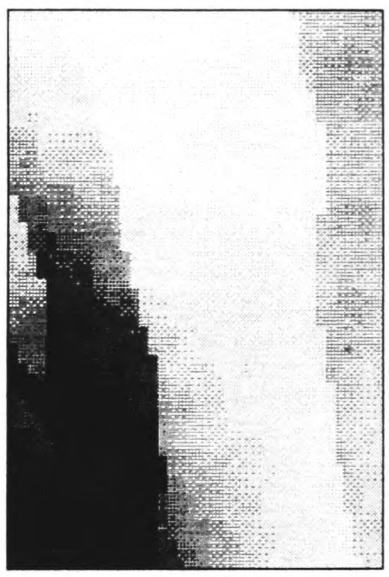

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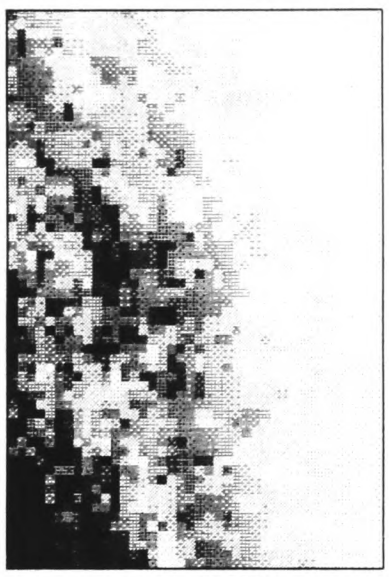
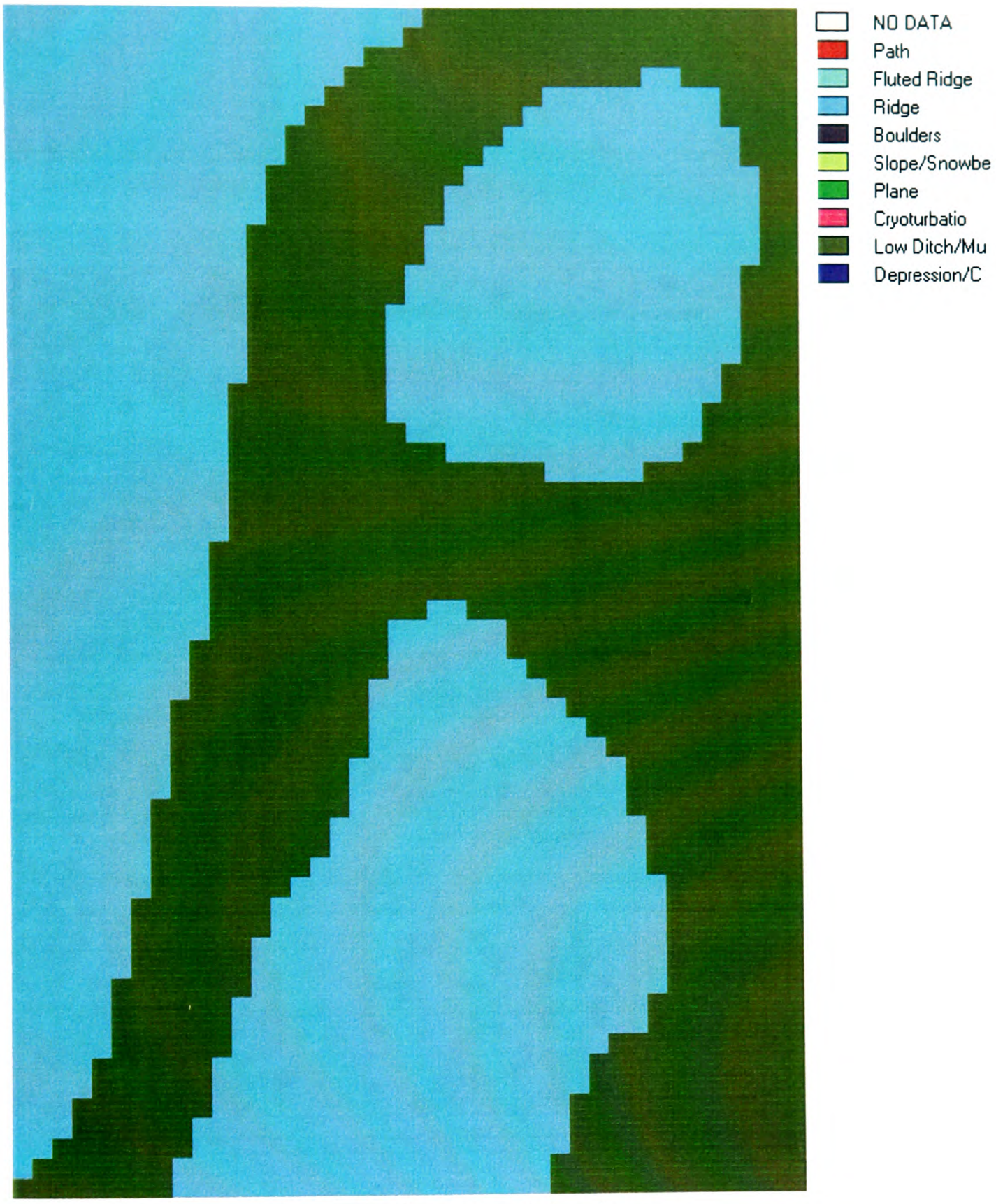


vacvit152

Austerdalsbreen foreland block III (Aus3)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

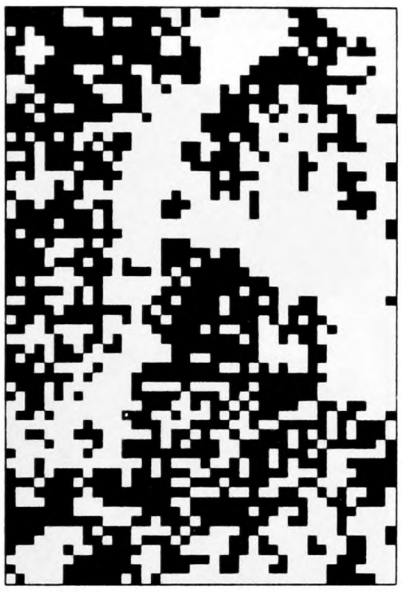


Environmental sketch-map

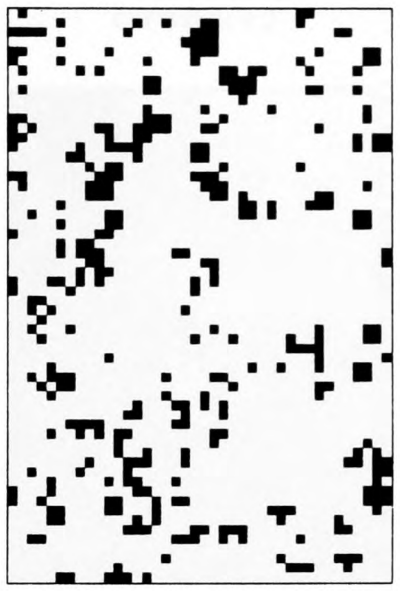
Betula pubescens

Calluna vulgaris

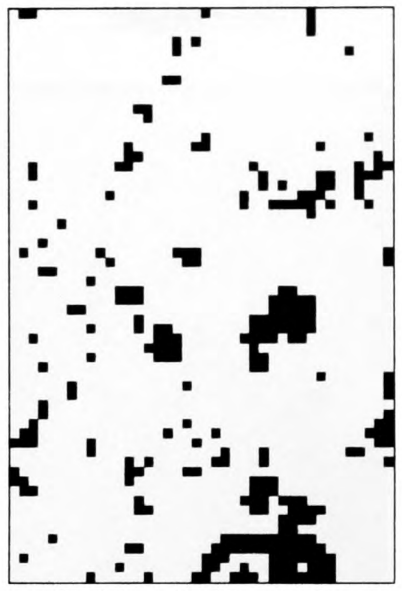
Empetrum hermaphroditum



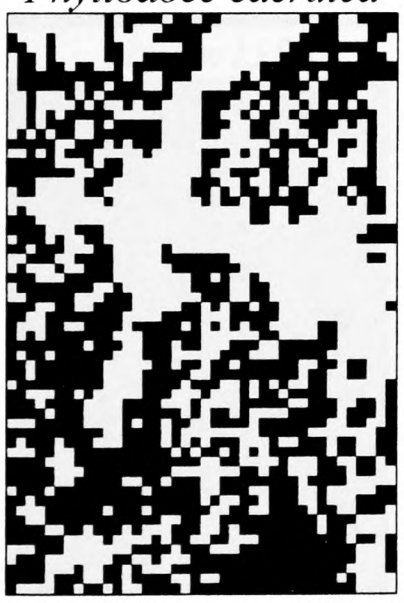
Phyllodoce caerulea



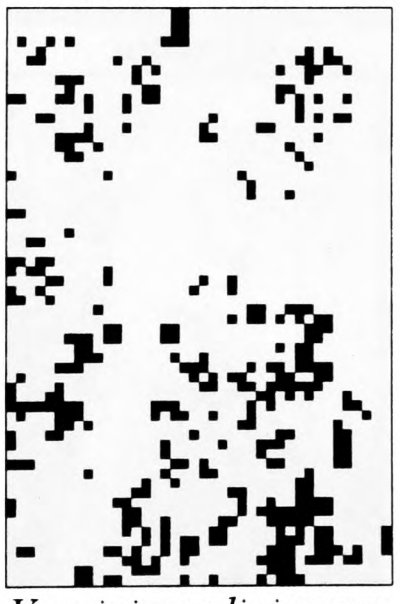
Salix herbacea



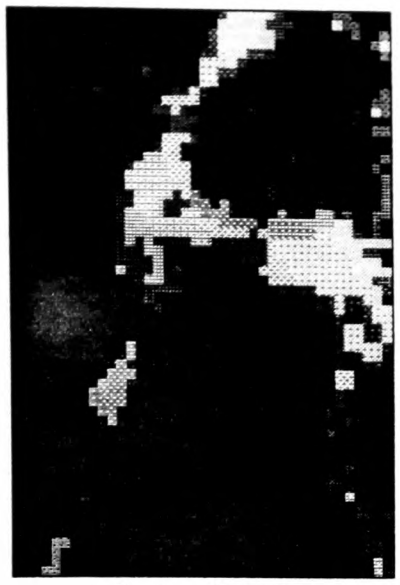
Salix phyllicifolia



Vaccinium myrtillus



Vaccinium uliginosum



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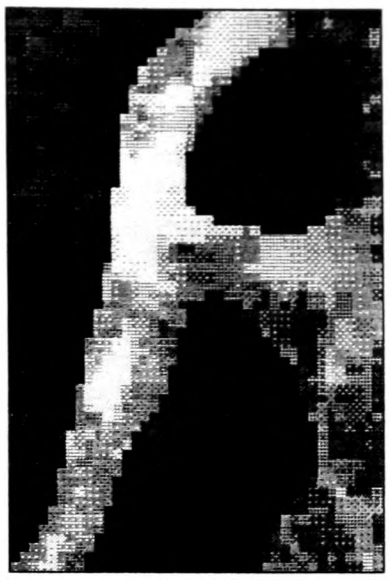
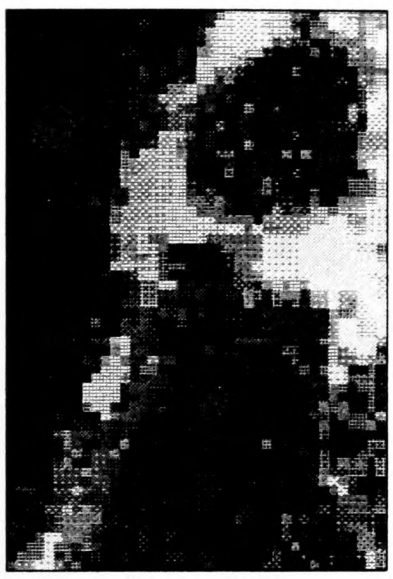
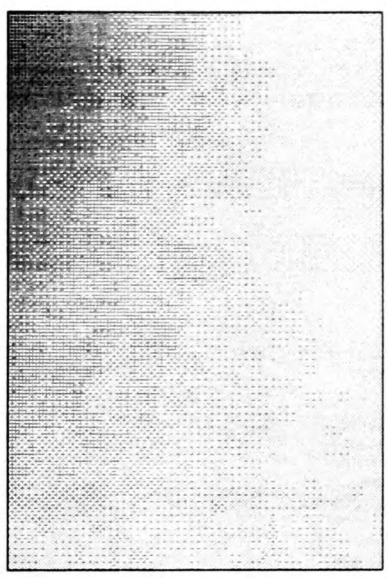


calvul245

empher135



phycae155



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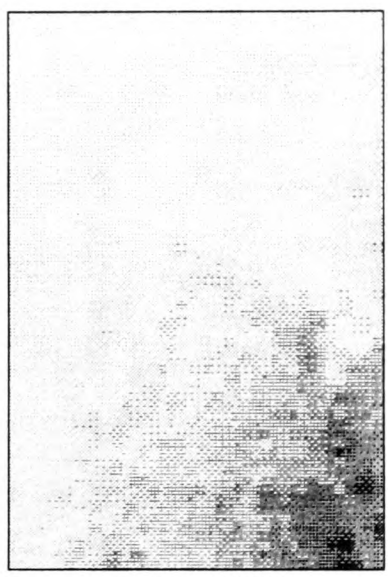

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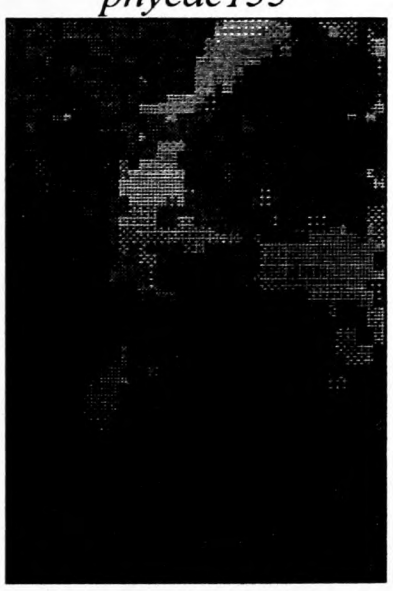
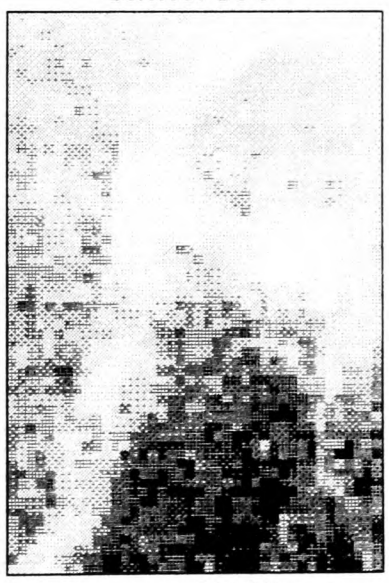


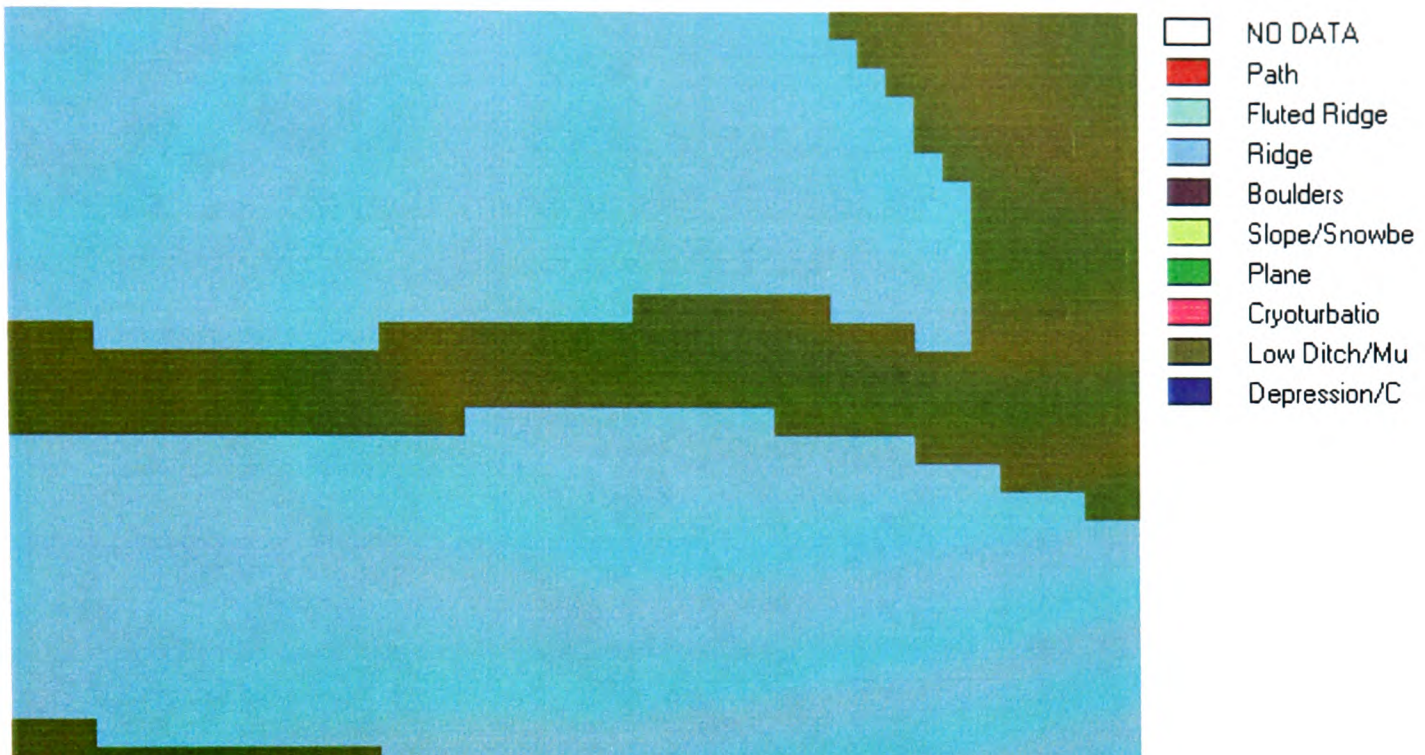
vacmyr241



vaculi155

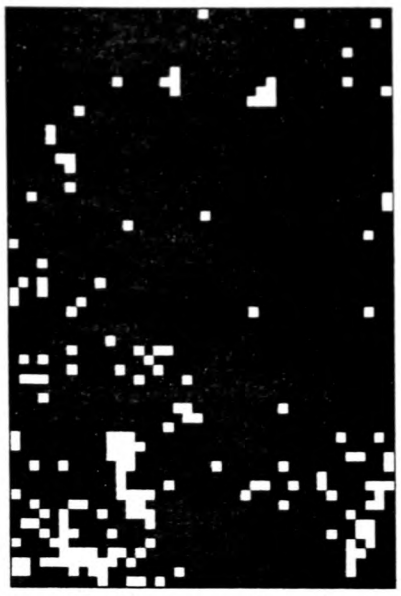
Bødalsbreen foreland block I (Bod1)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

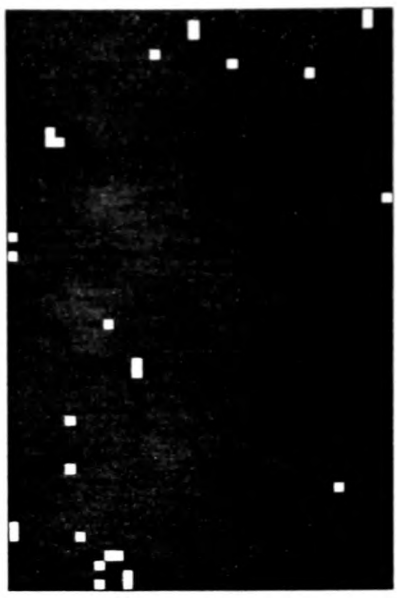


Environmental sketch-map

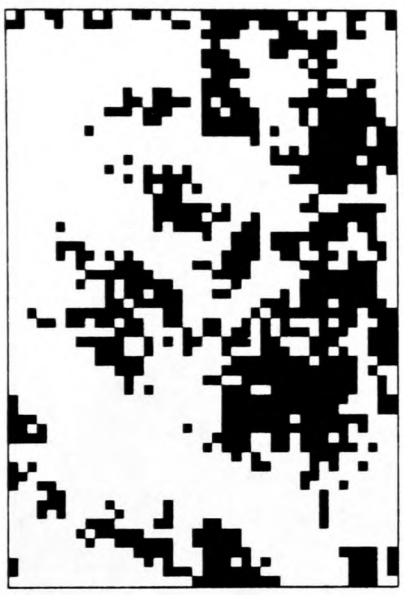
Betula pubescens



Calluna vulgaris

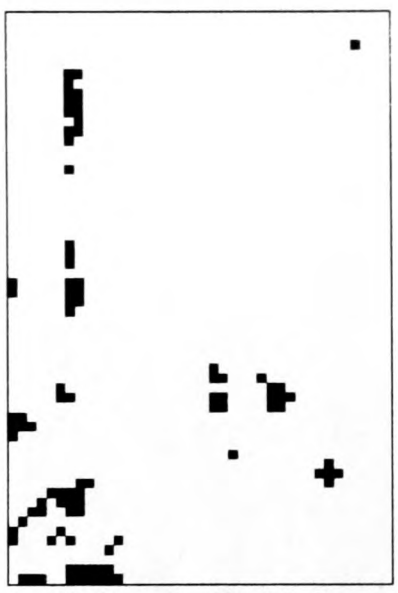


Empetrum hermaphroditum



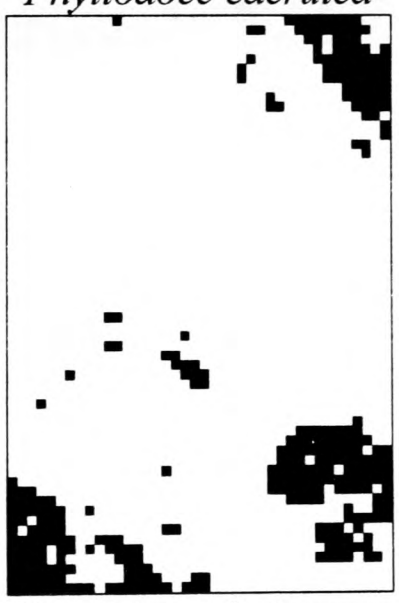
Loiseleuria procumbens

Phyllodoce caerulea



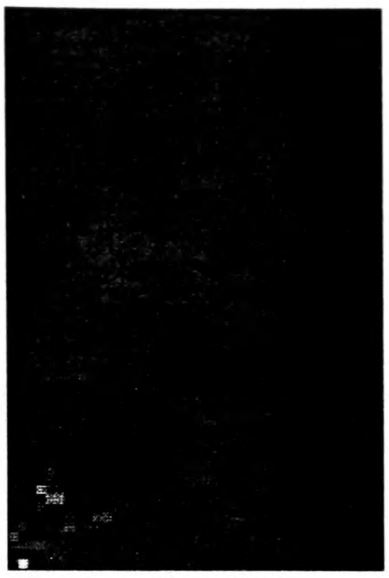
Salix phyllicifolia

Vaccinium myrtillus



Vaccinium uliginosum

betpub142



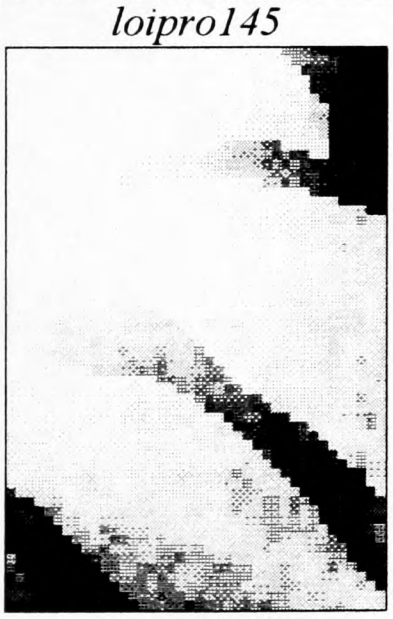
calvul155

empher145

loipro145

phycae145

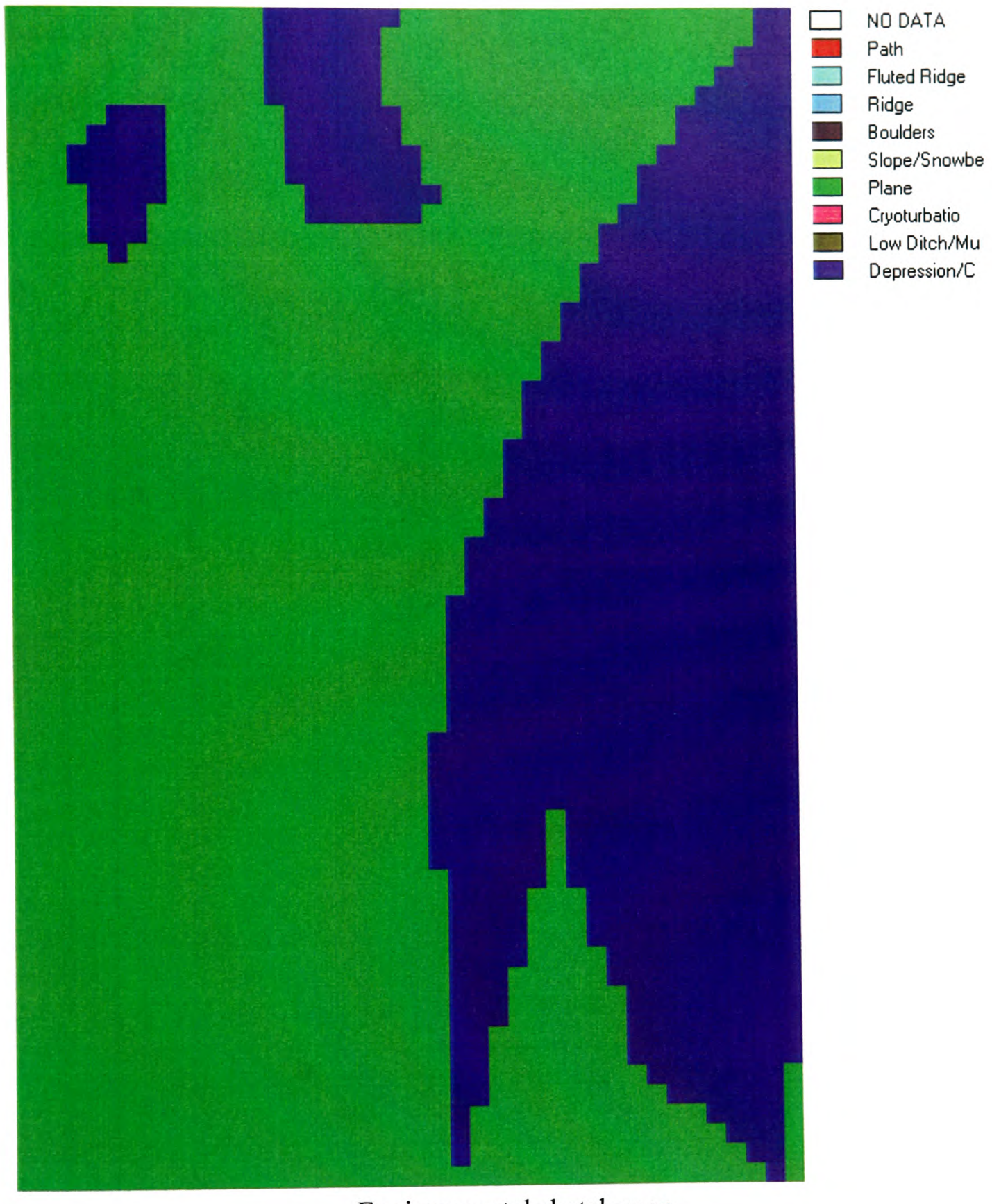
vacmyr132



vaculi135

Bødalsbreen foreland block II (Bod2)

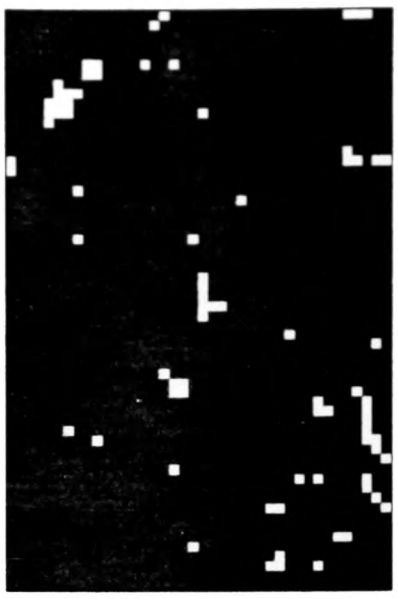
Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



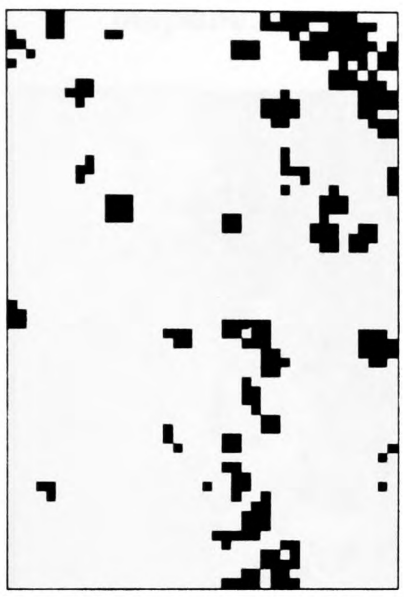
Environmental sketch-map

Betula pubescens

Calluna vulgaris

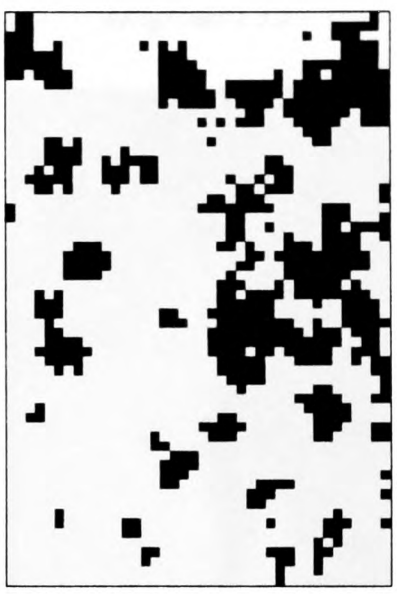


Empetrum hermaphroditum

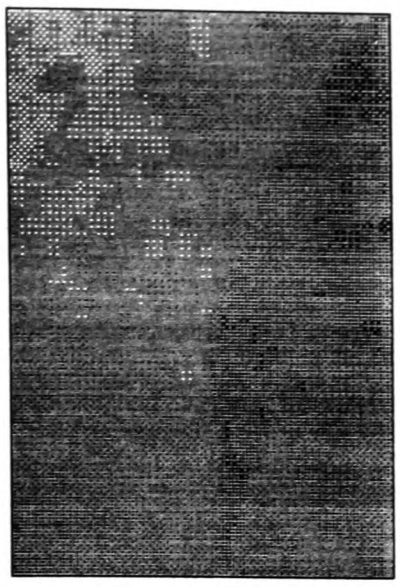


Loiseleuria procumbens

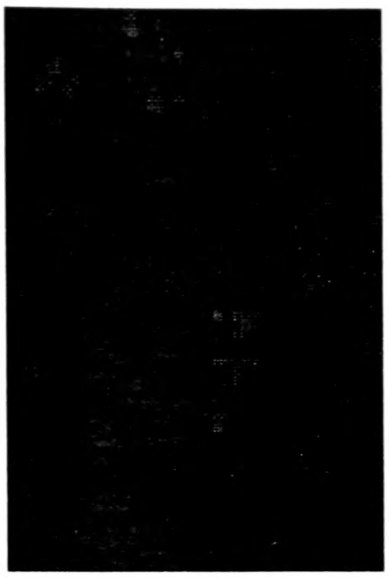
Phyllodoce caerulea



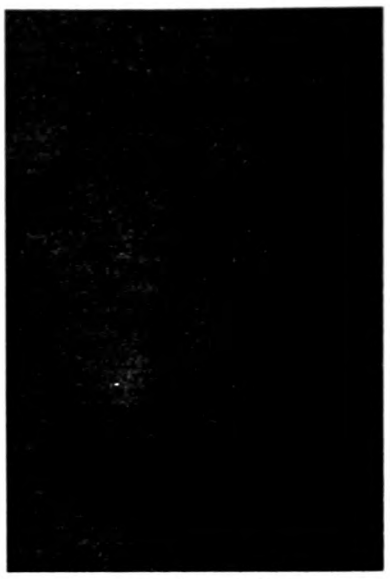
Vaccinium myrtillus



betpub255



calvul155



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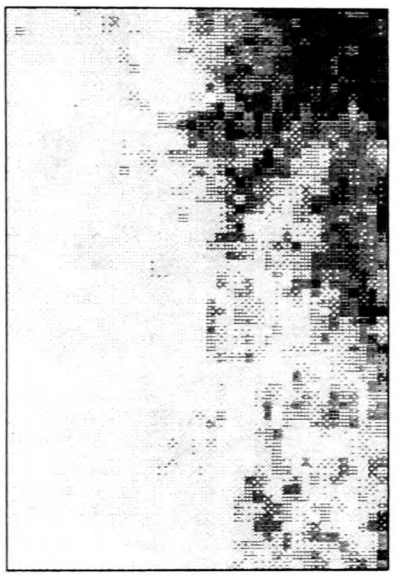


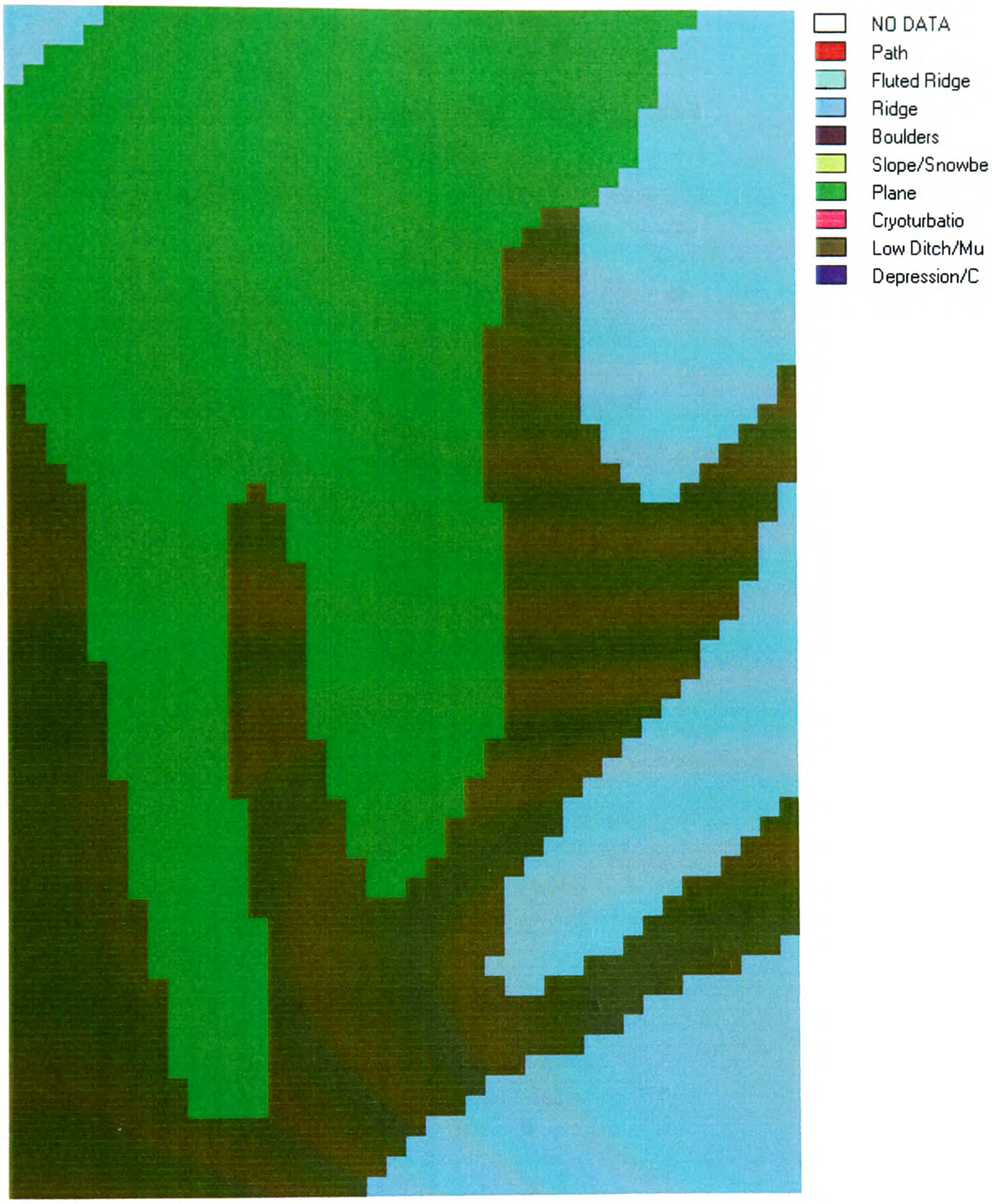
loipro152

phycae135

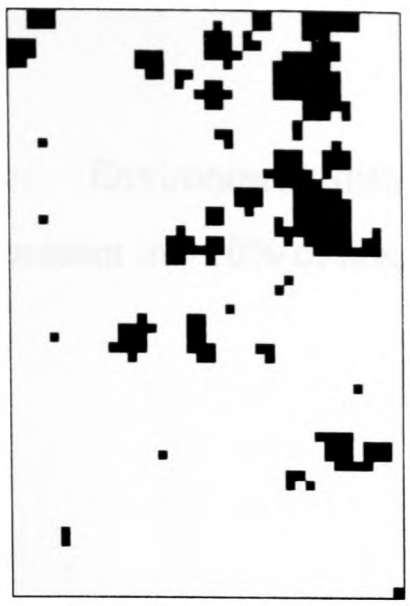
vacmyr235

Bødalsbreen foreland block III (Bod3)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

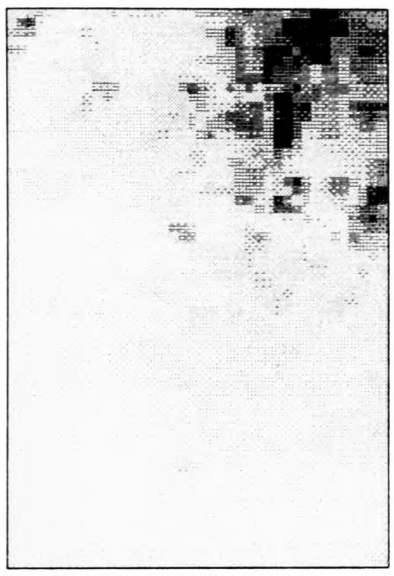


Environmental sketch-map



Betula pubescens

Empetrum hermaphroditum

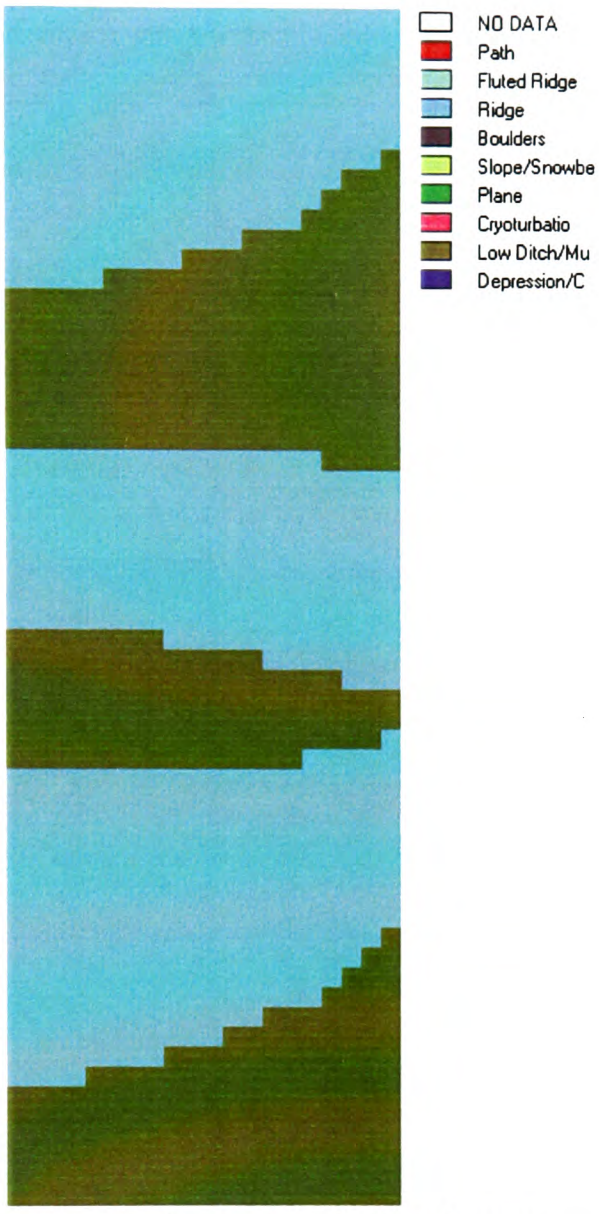


betpub245

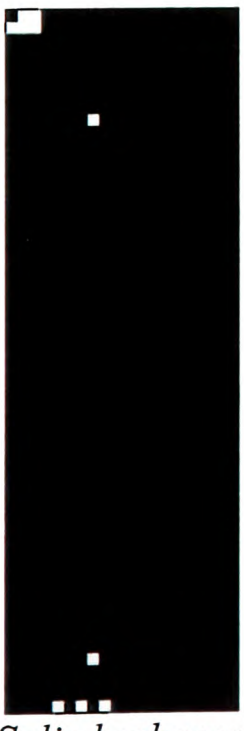
empher145

Høgvaglbreen foreland block I (Hog1)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 30m.



Environmental sketch-map

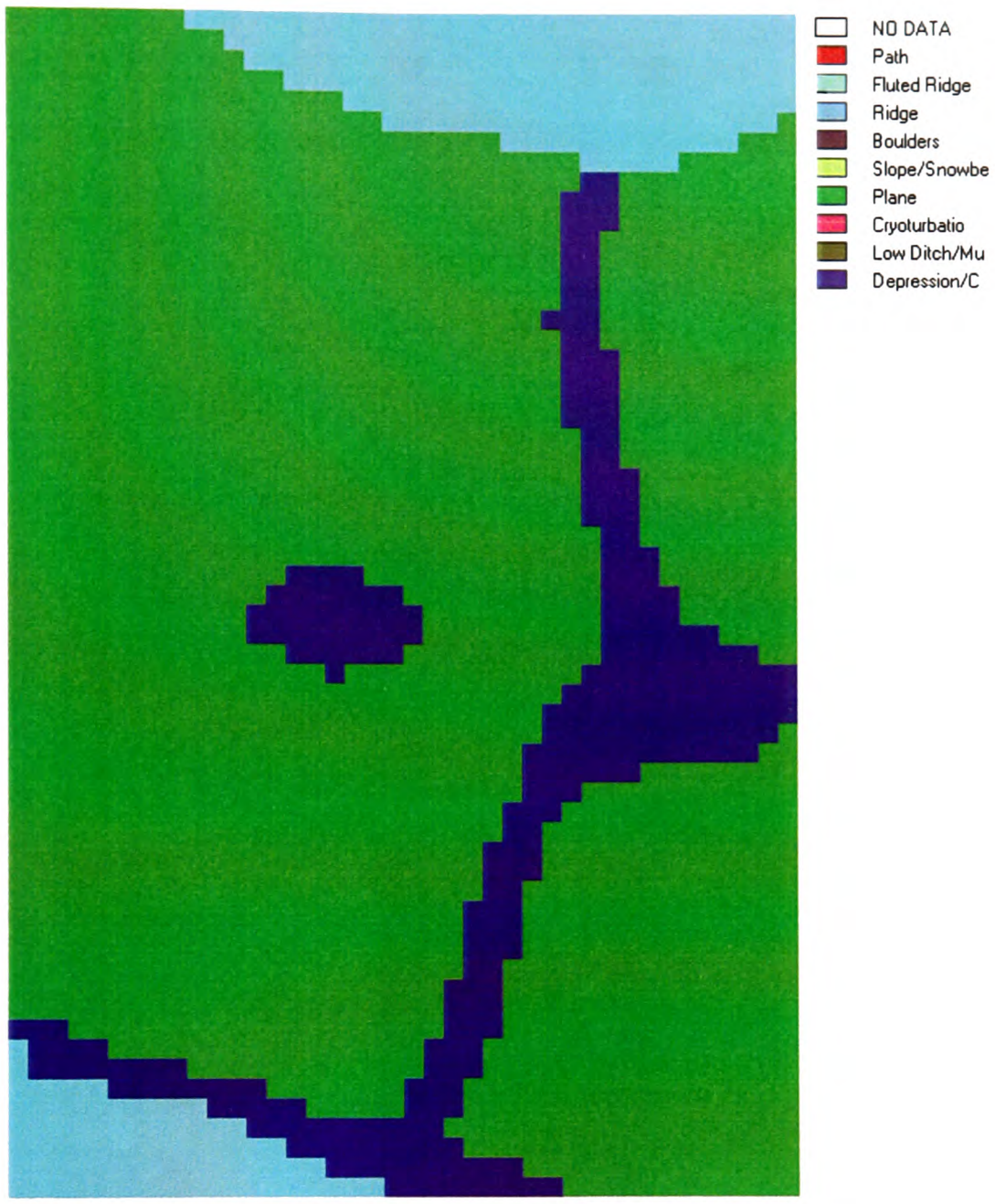


Salix herbacea

salher135

Høgvaglbreen foreland block II (Hog2)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



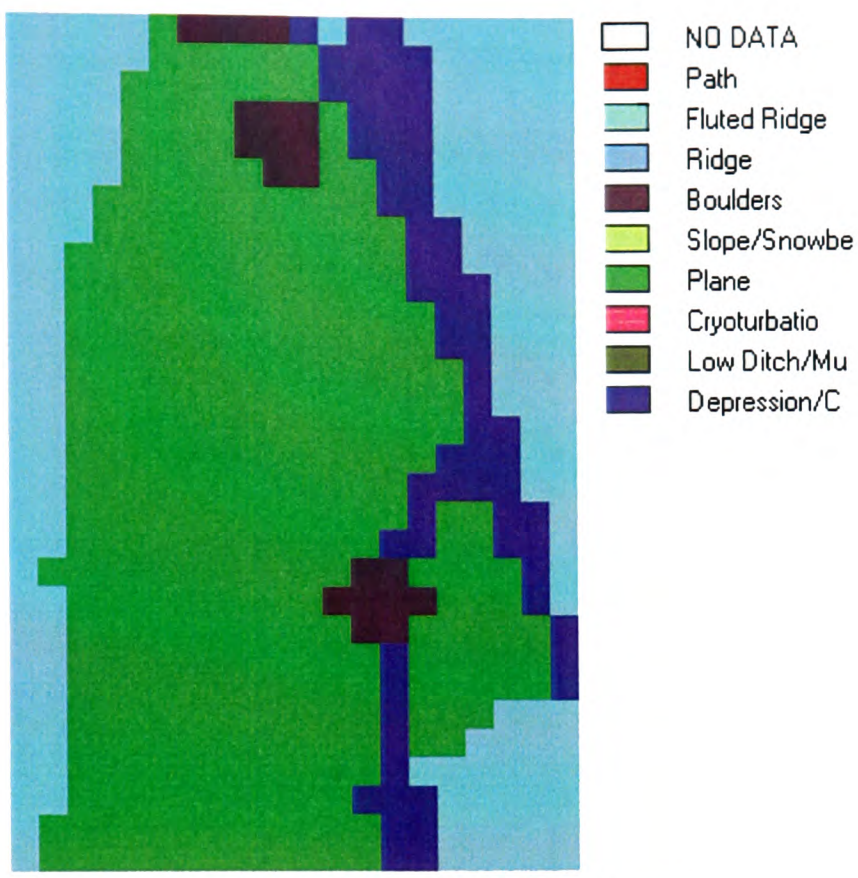
Environmental sketch-map

Salix herbacea

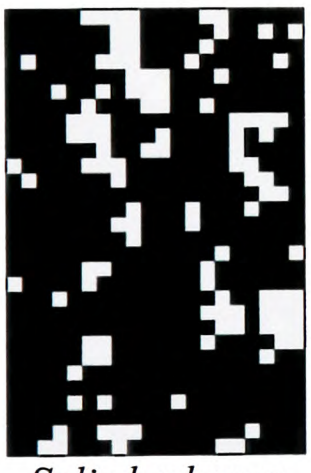
salher132

Høgvaglbreen foreland block III (Hog3)

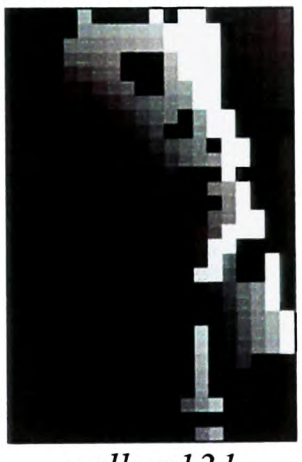
Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 15m.



Environmental sketch-map



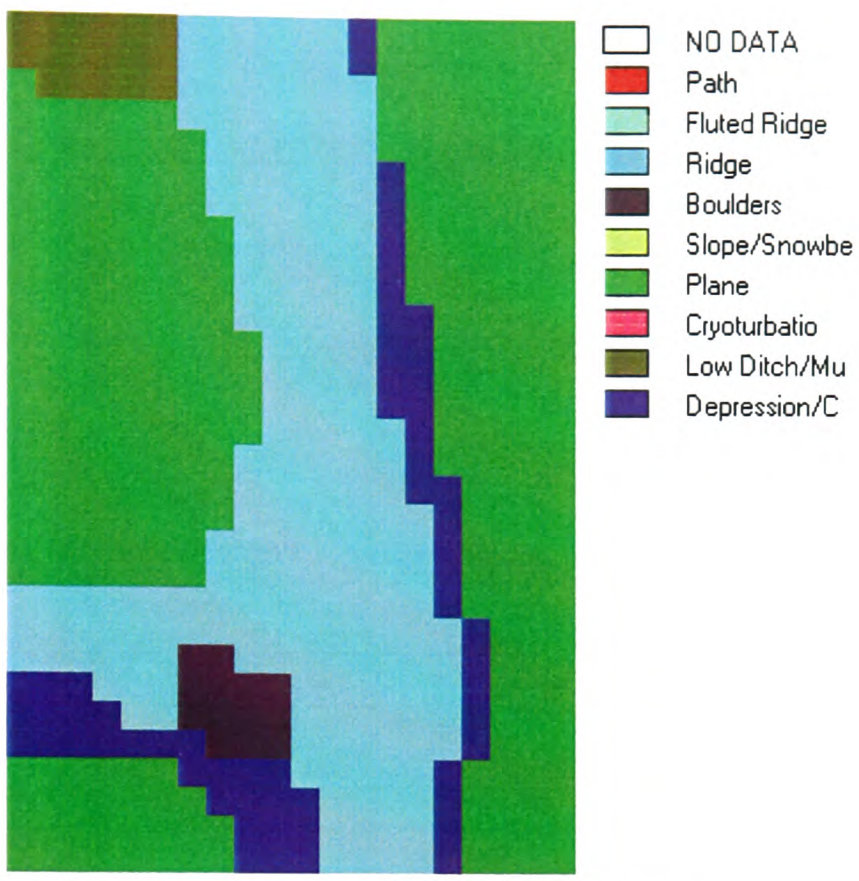
Salix herbacea



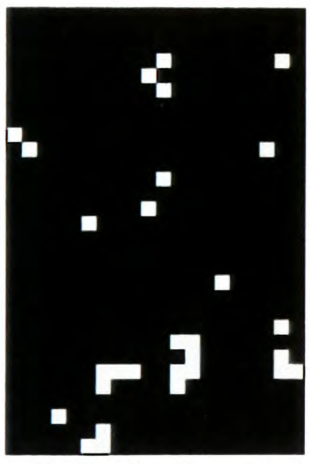
salher131

Høgvaglbreen foreland block IV (Hog4)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 15m.



Environmental sketch-map

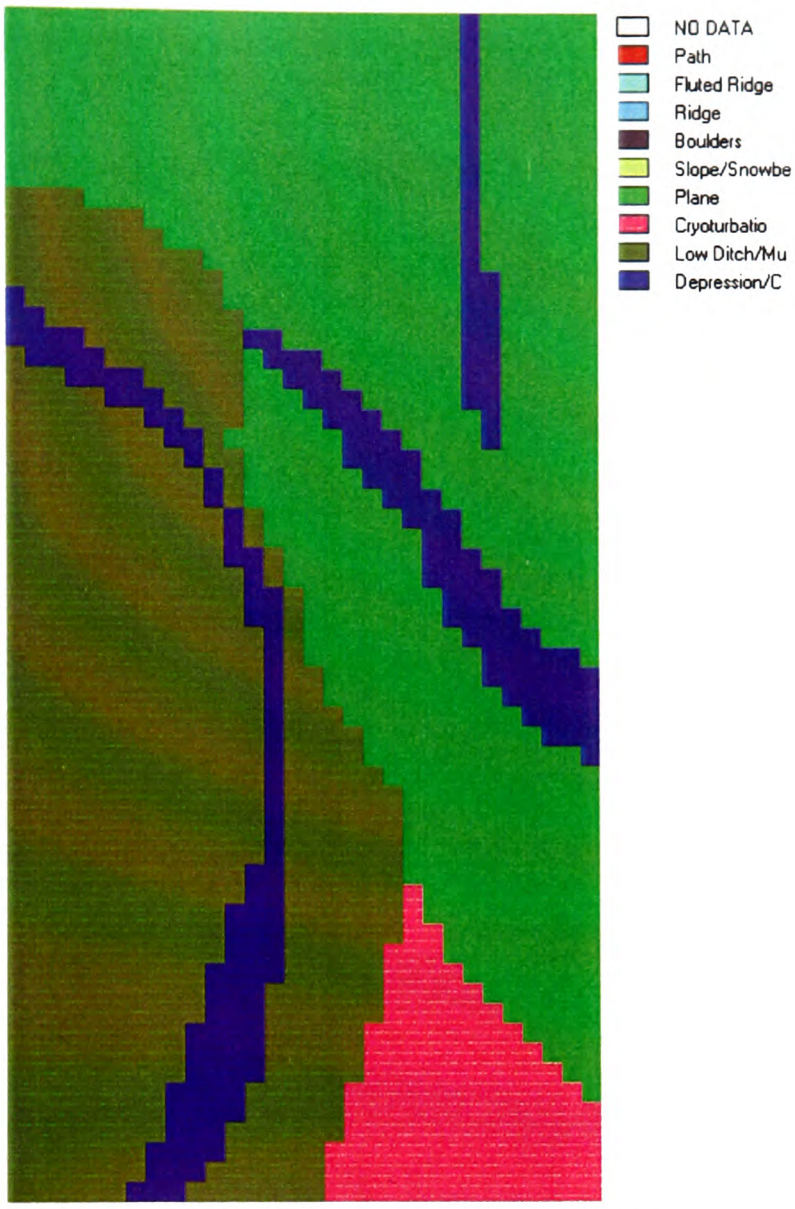


Salix herbacea

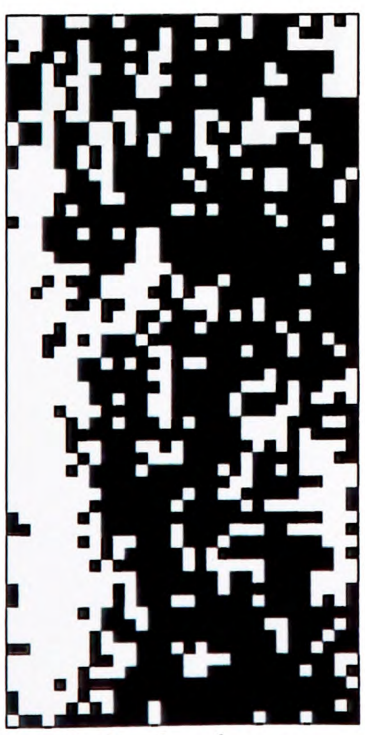
salher135

Høgvaglbreen foreland block V (Hog5)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 15 x 30m.



Environmental sketch-map

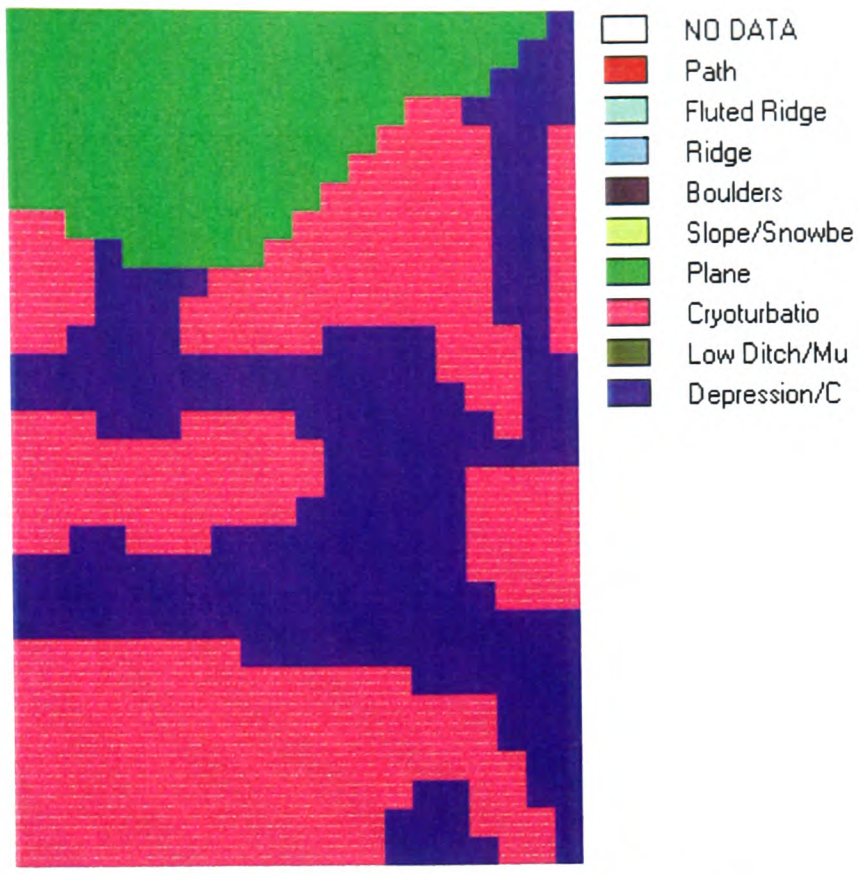


Salix herbacea

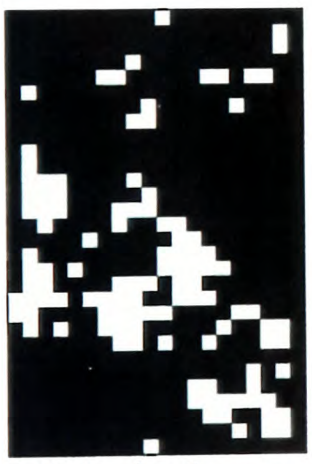
salher145

Høgvaglbreen foreland block VI (Hog6)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 15m.



Environmental sketch-map

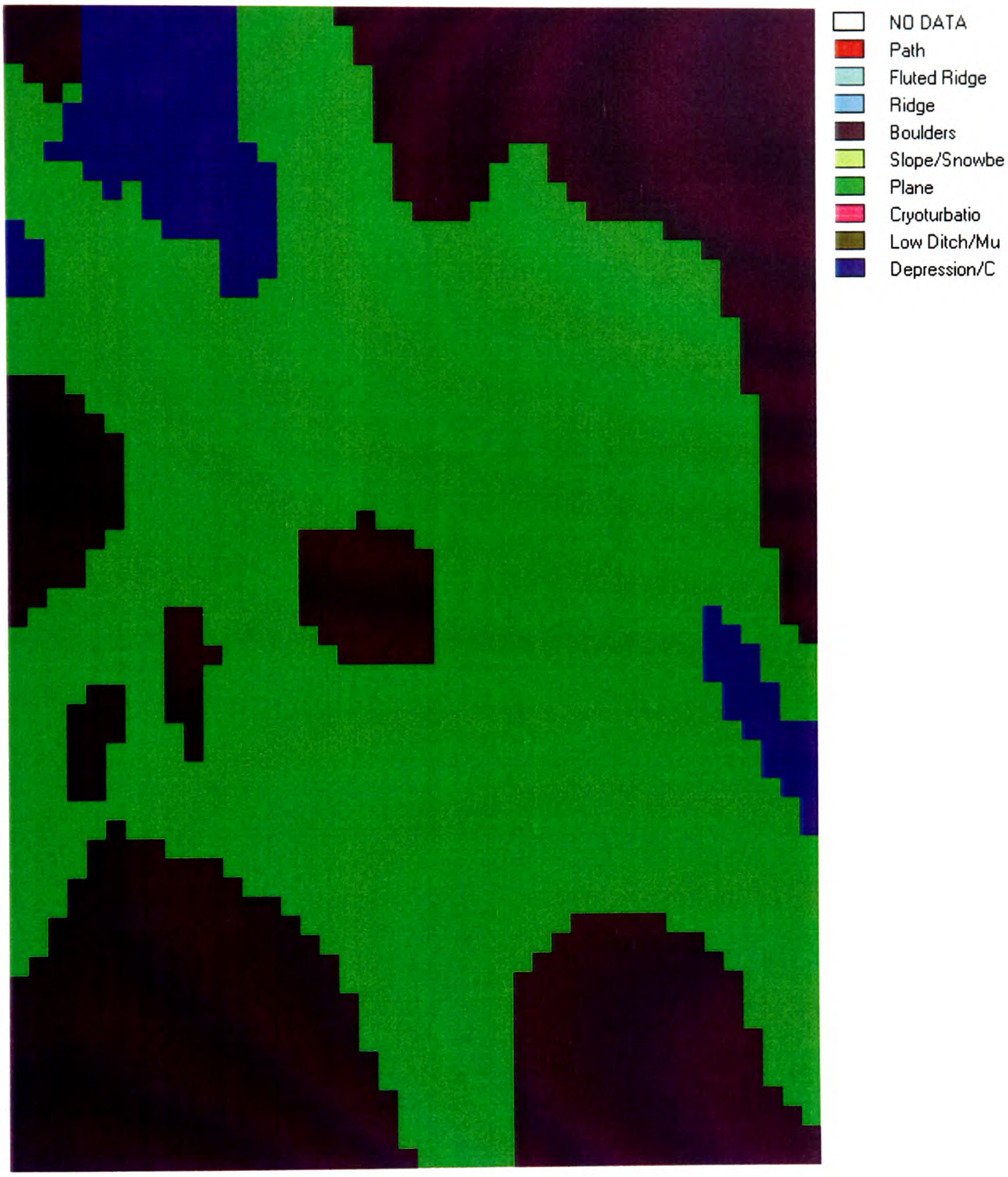


Salix herbacea

salher132

Nigardsbreen foreland block I (Nig1)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 21 x 30m.

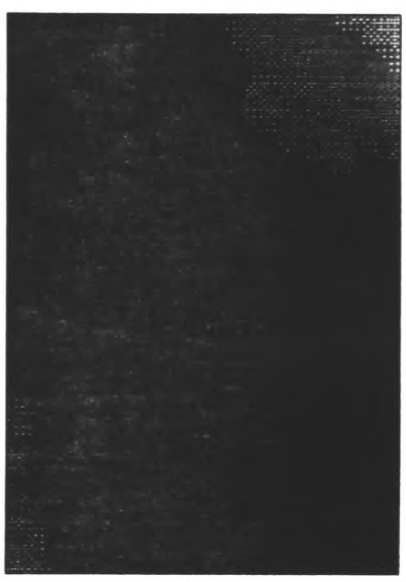


Environmental sketch-map

Calluna vulgaris

Empetrum hermaphroditum

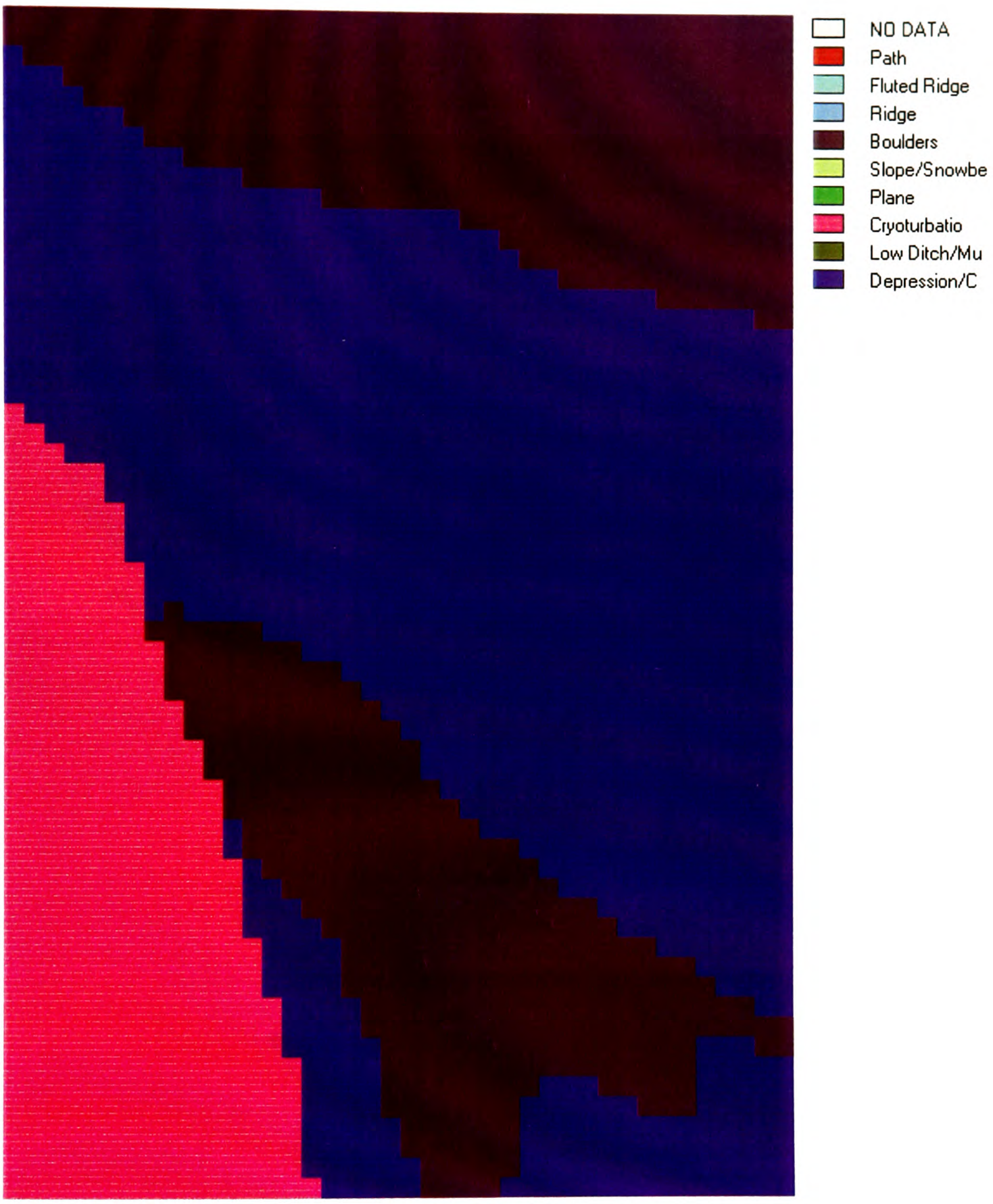
calvul155



empher355

Nigardsbreen foreland block II (Nig2)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



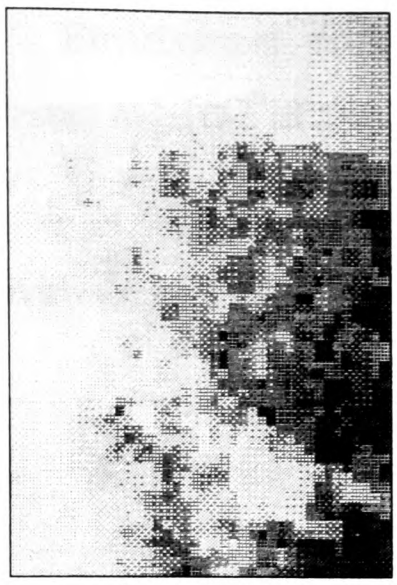
Environmental sketch-map

Betula pubescens

Calluna vulgaris

Empetrum hermaphroditum

Vaccinium vitis-idaea



betpub131

calvul235

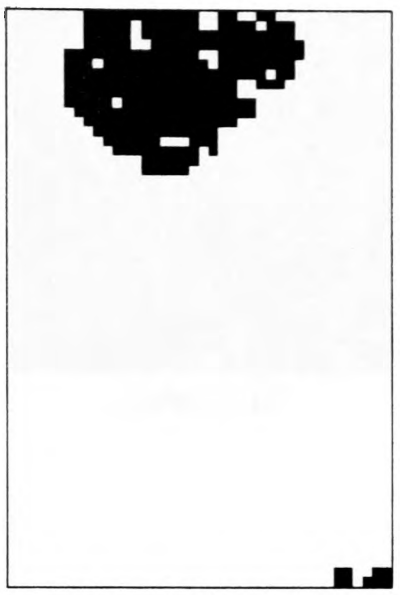
empher135

vacvit152

Nigardsbreen foreland block III (Nig3)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

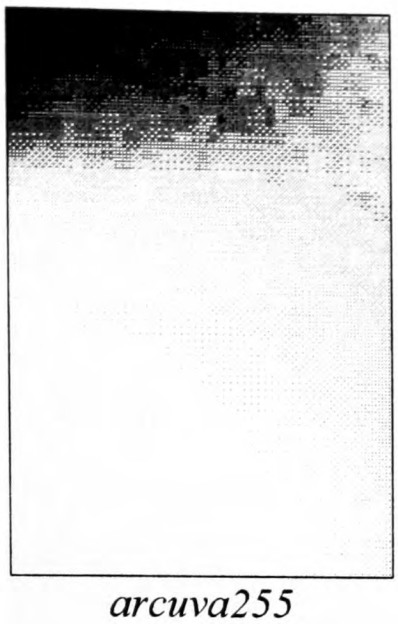
No Environmental sketch-map available



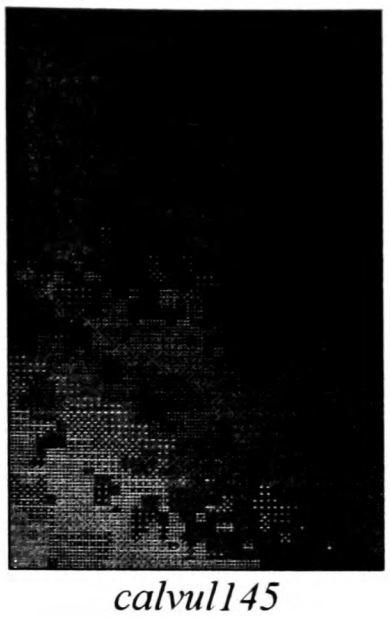
Arctostaphylos uva-ursi

Calluna vulgaris

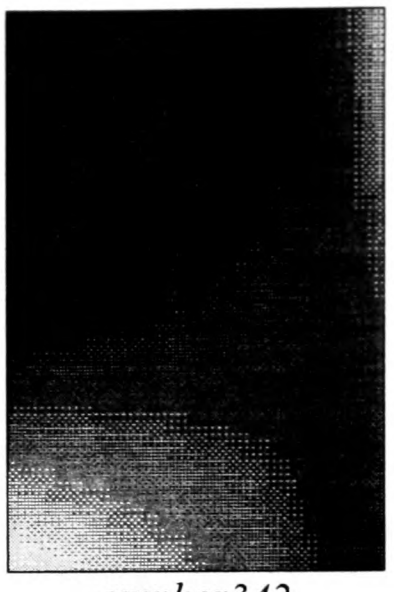
Empetrum hermaphroditum



arcuva255



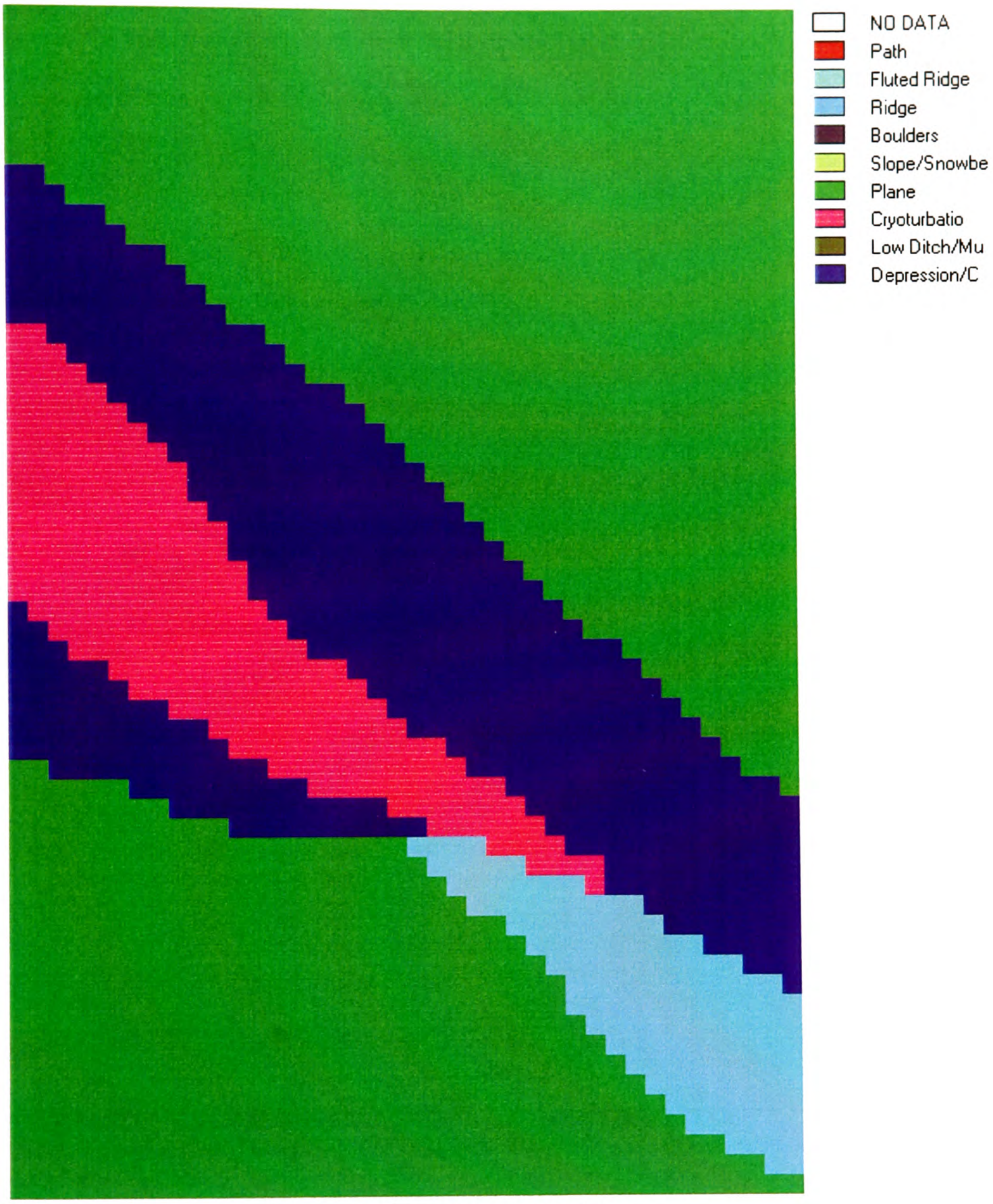
calvul145



empher342

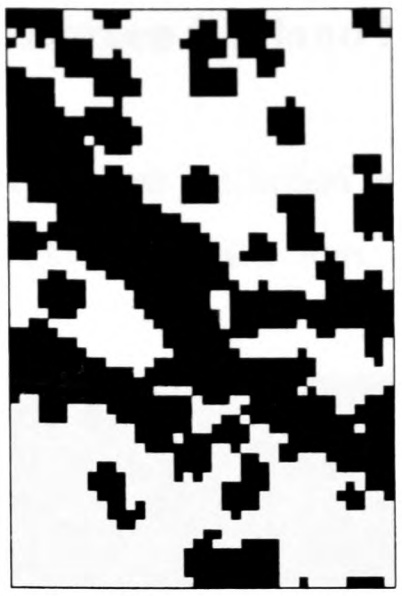
Nigardsbreen foreland block IV (Nig4)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



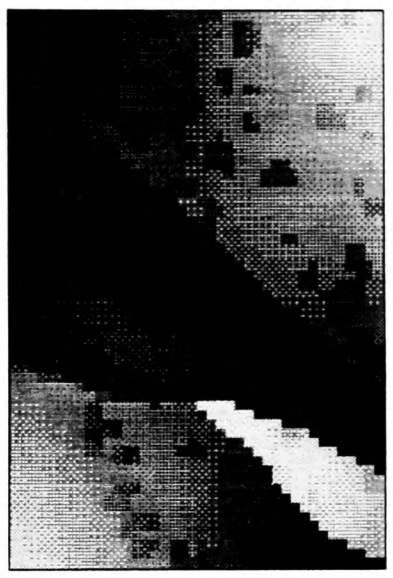
Environmental sketch-map

Calluna vulgaris



Empetrum hermaphroditum

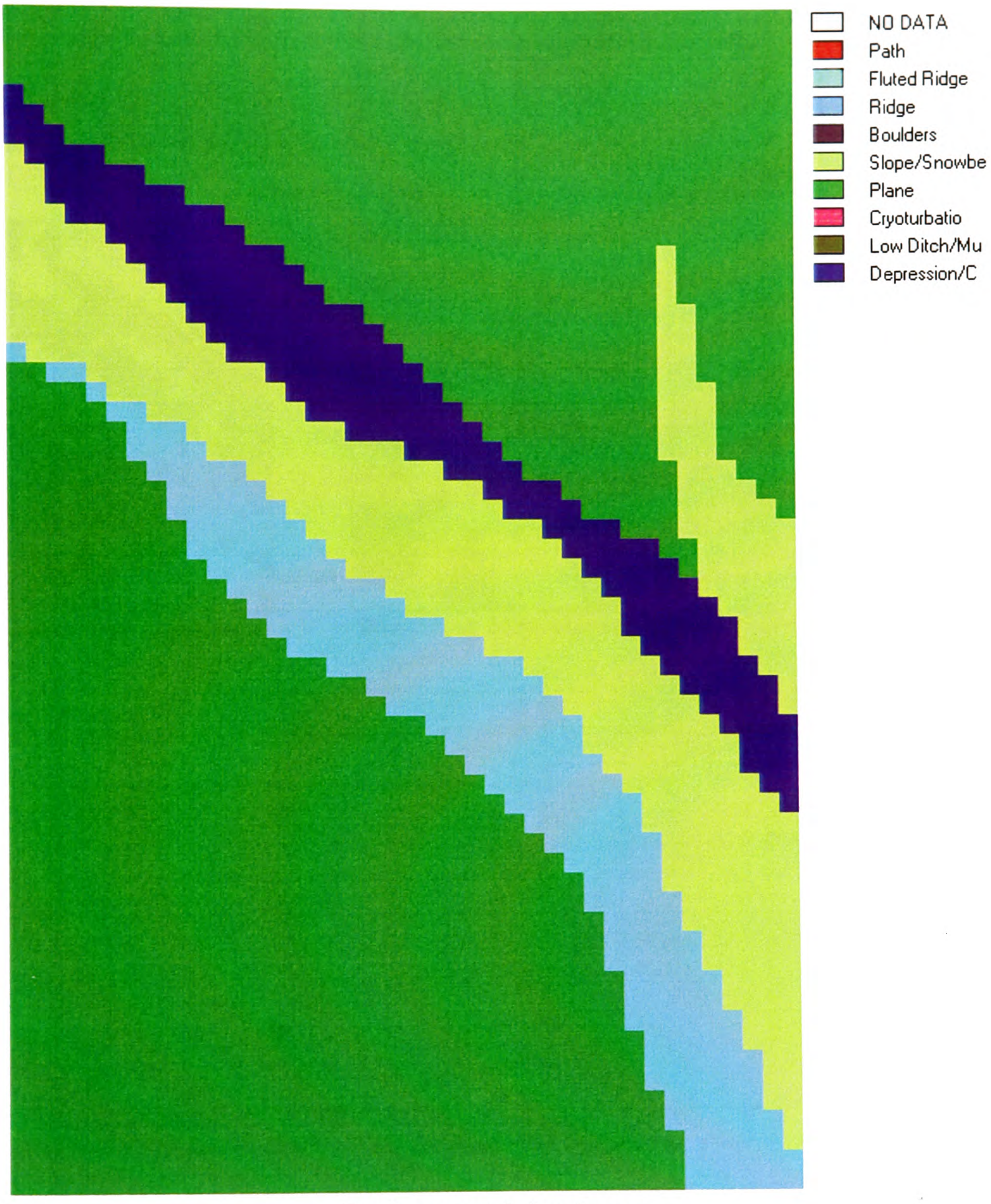
calvul135



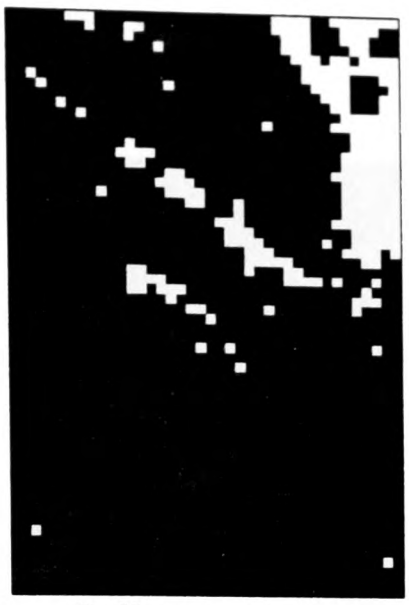
empher245

Nigardsbreen foreland block V (Nig5)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



Environmental sketch-map



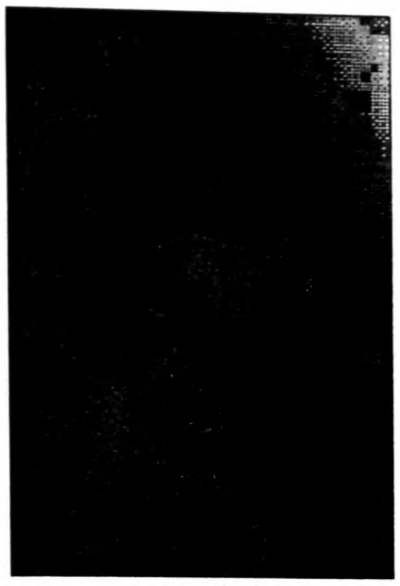
Calluna vulgaris

Empetrum hermaphroditum

Vaccinium myrtillus

Vaccinium uliginosum

Vaccinium vitis-idaea



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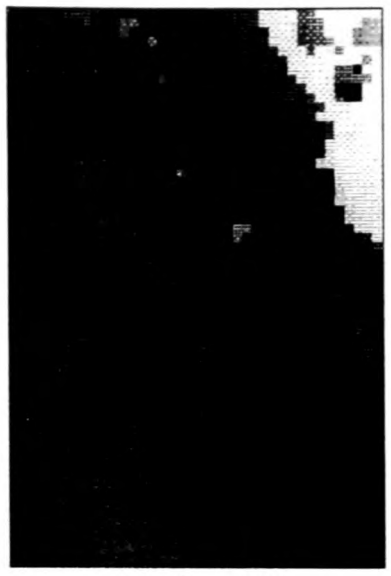

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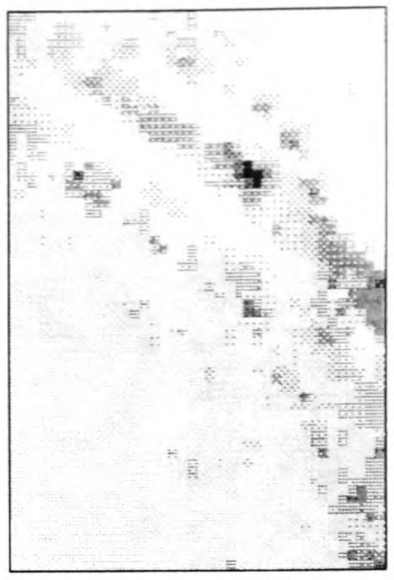
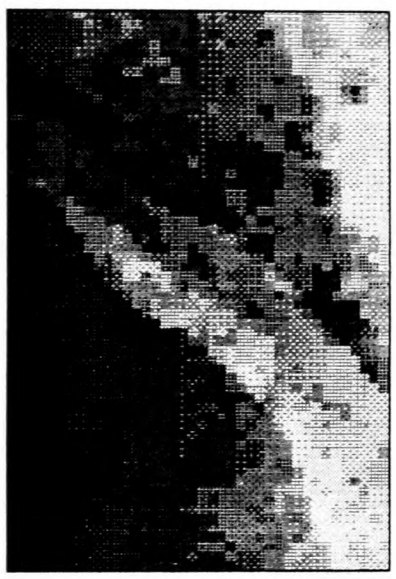
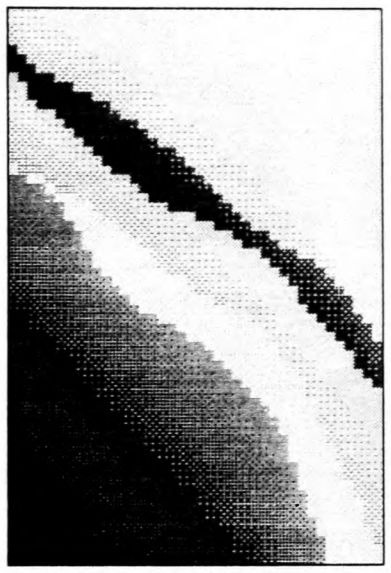


vacmyr135



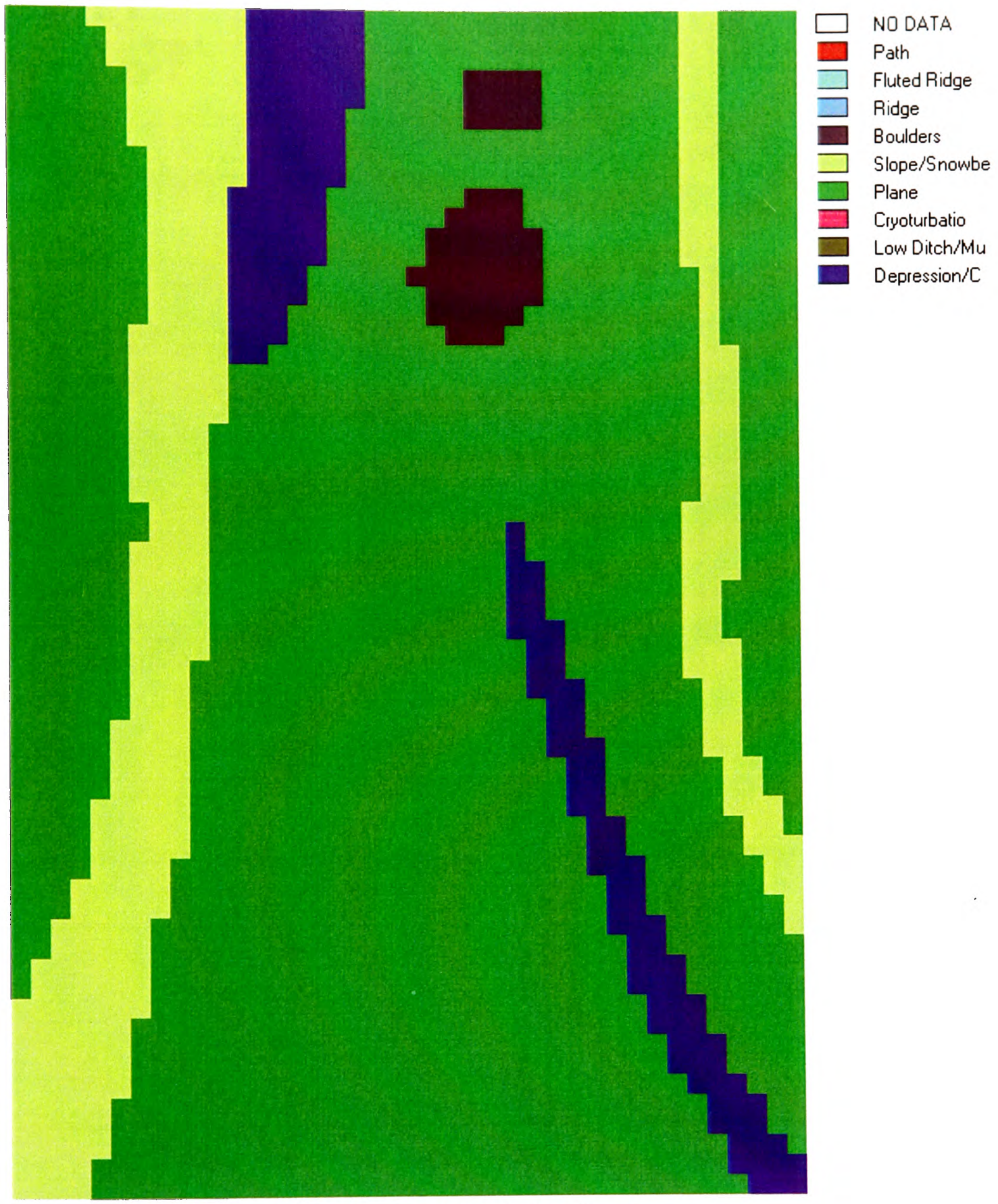
vaculi155



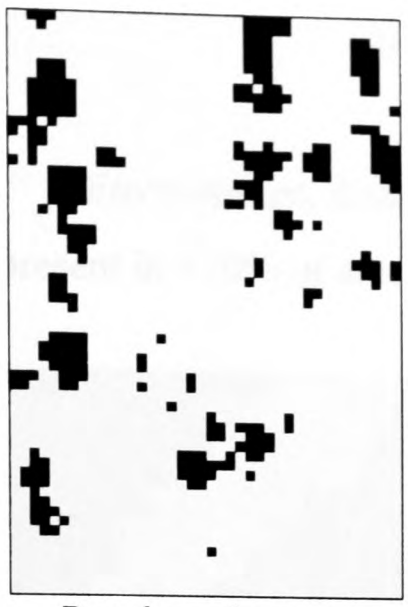
vacvit135

Nigardsbreen foreland block VI (Nig6)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



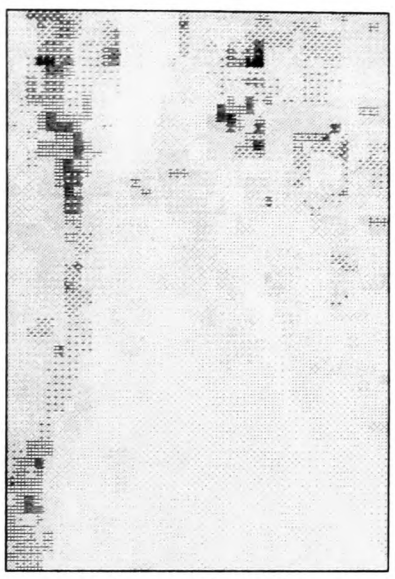
Environmental sketch-map



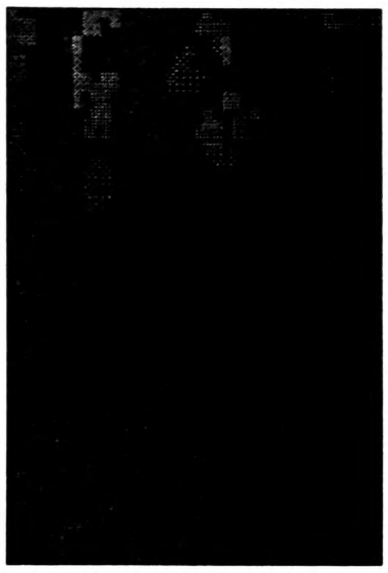
Betula pubescens

Calluna vulgaris

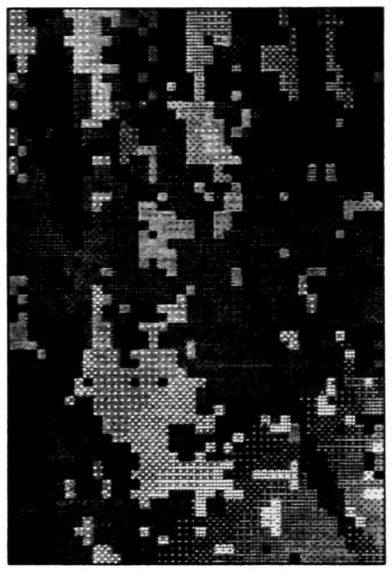
Empetrum hermaphroditum



betpub255



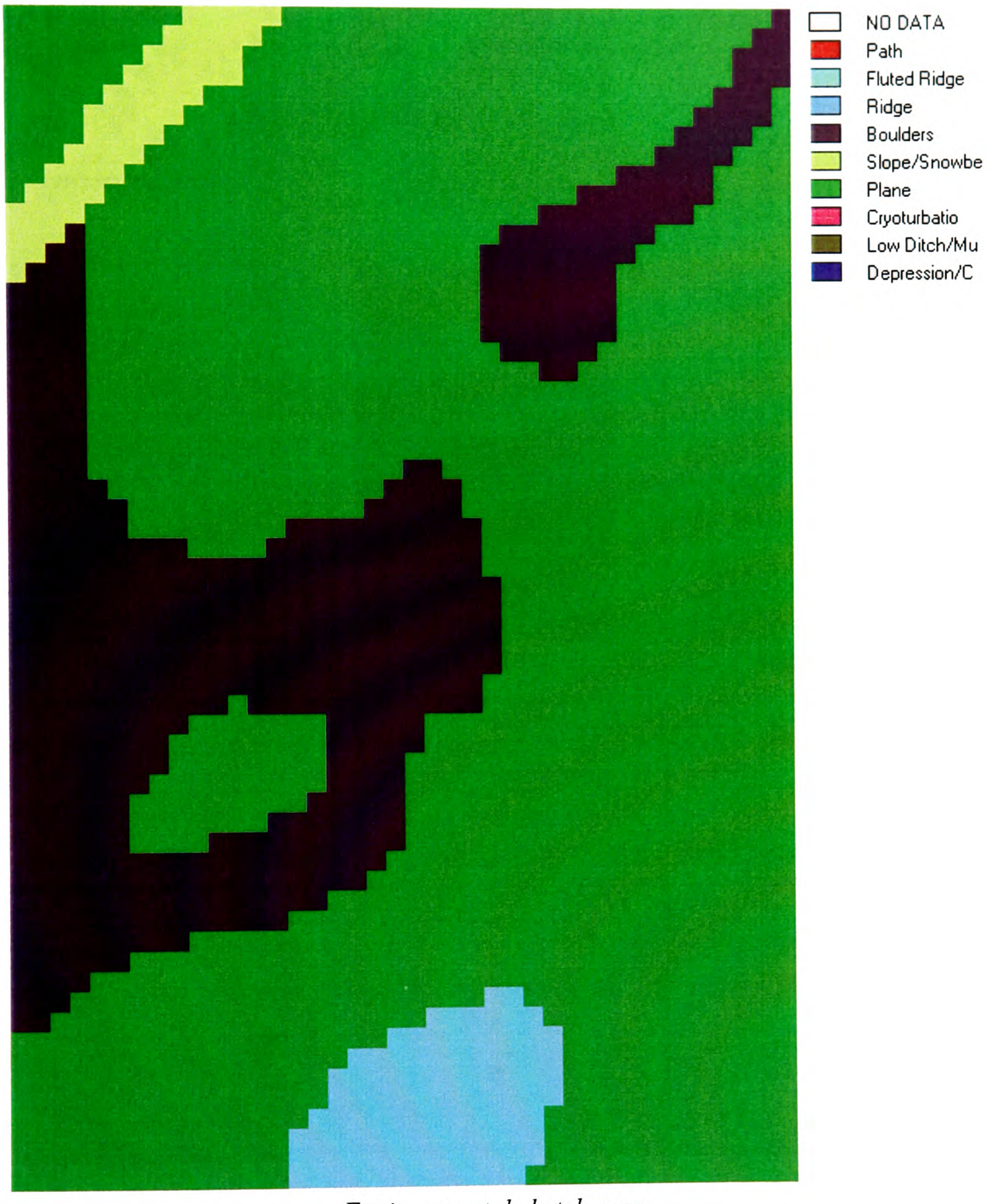
calvul155



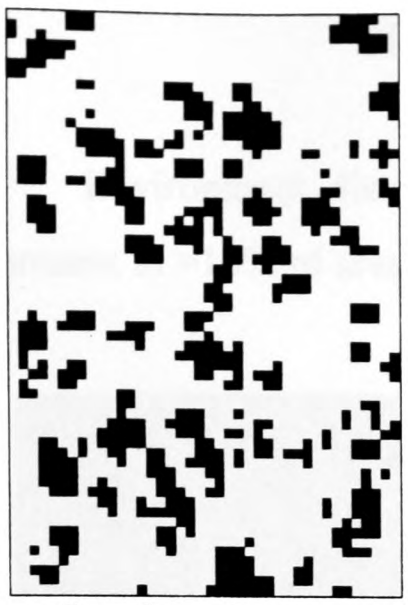
empher155

Nigardsbreen foreland block VII (Nig7)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

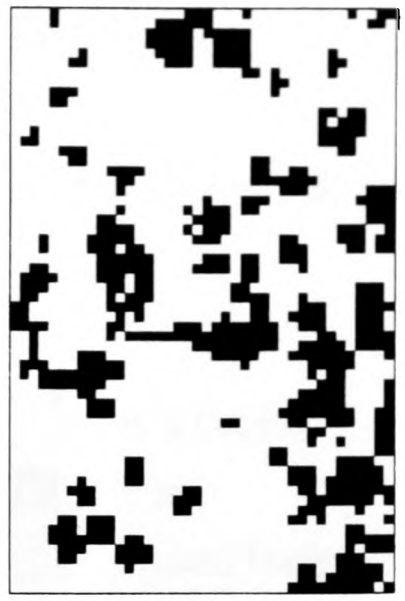


Environmental sketch-map

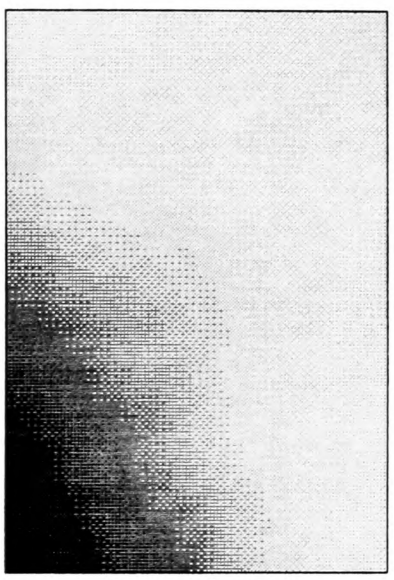


Betula pubescens

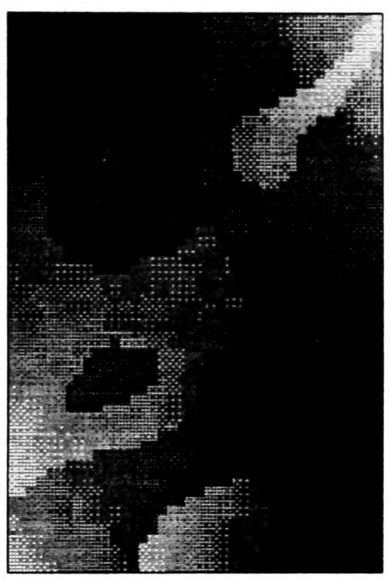
Calluna vulgaris



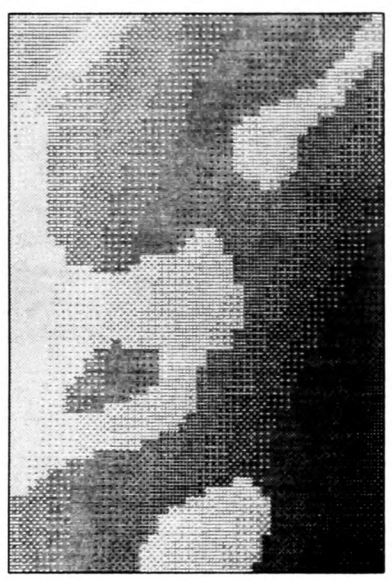
Empetrum hermaphroditum



betpub351



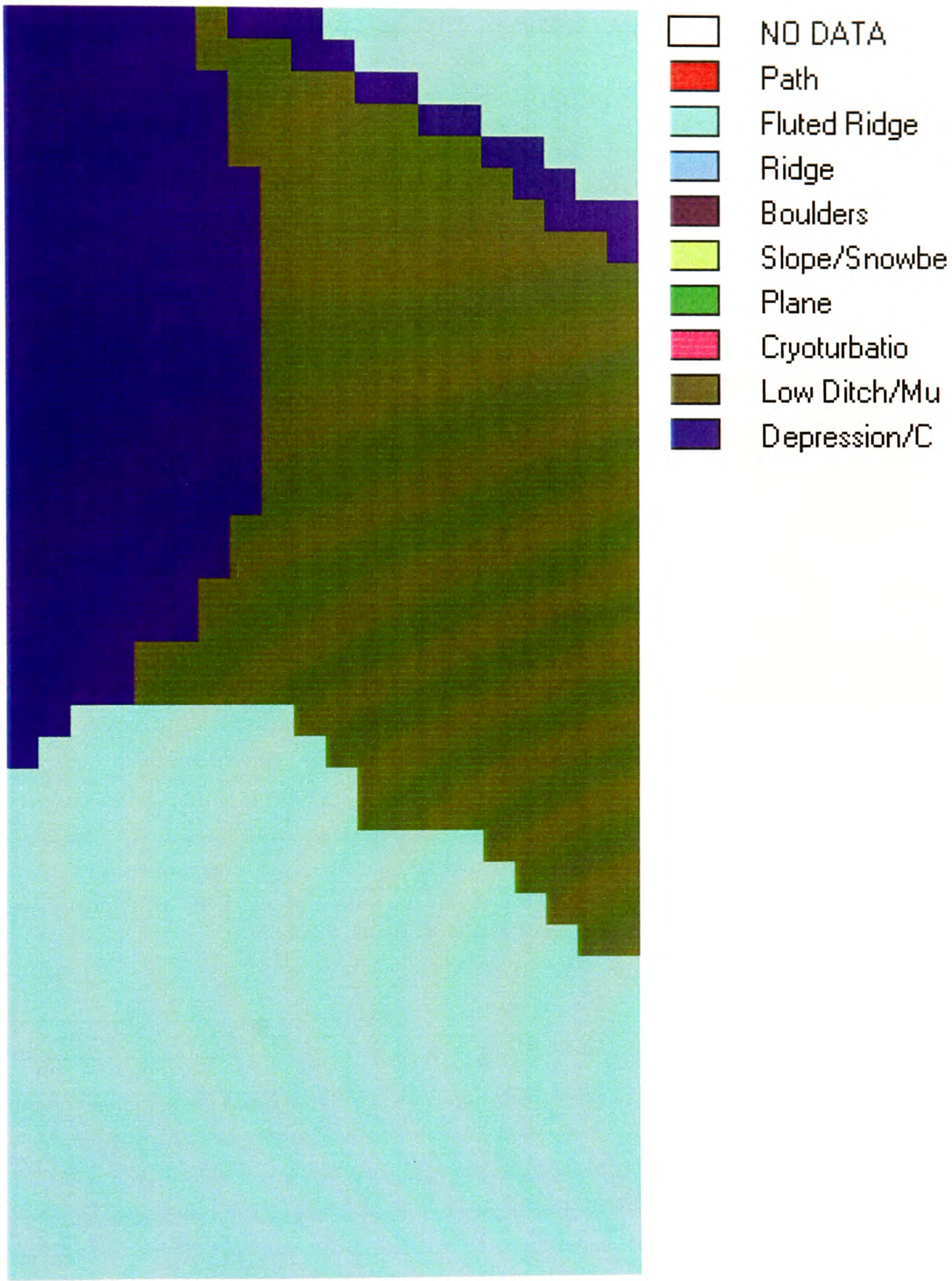
calvul242



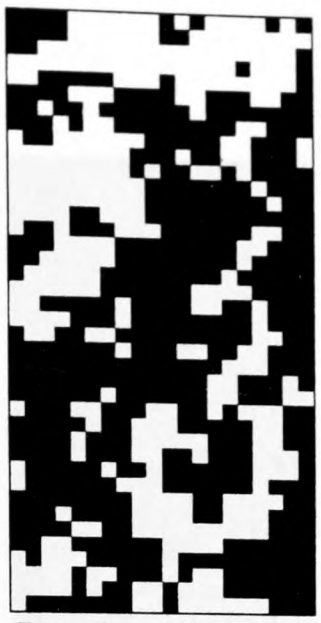
empher135

Nigardsbreen foreland block VIII (Nig8)

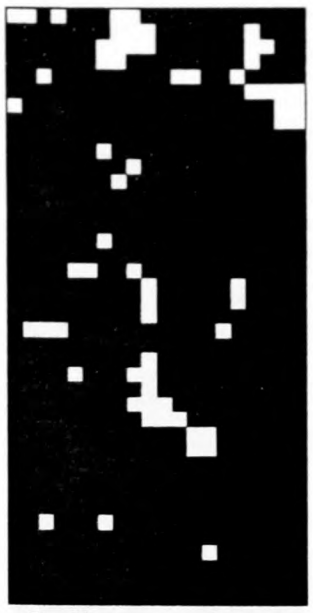
Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 20m.



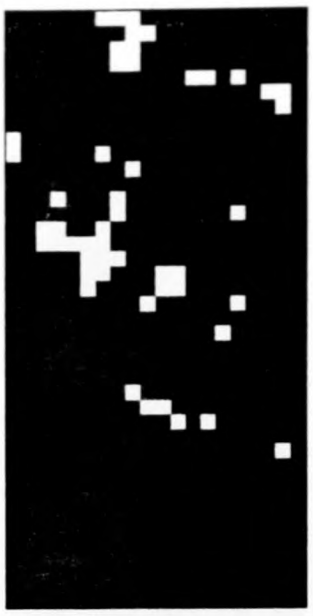
Environmental sketch-map



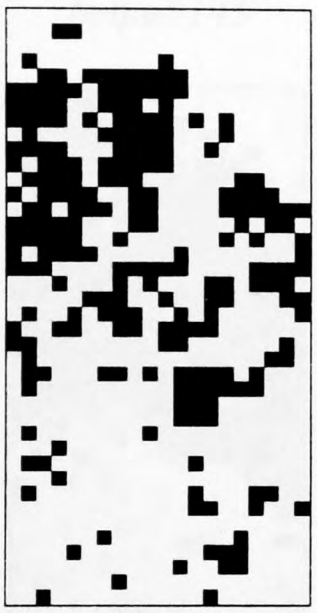
Betula pubescens



Calluna vulgaris



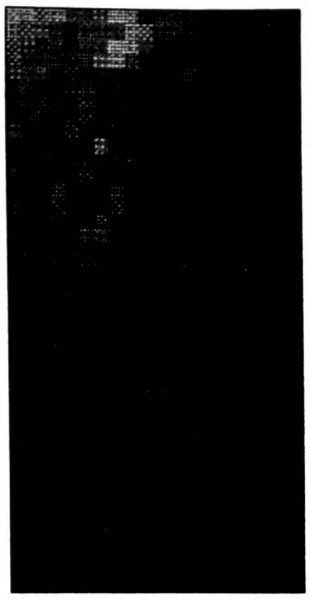
Empetrum hermaphroditum



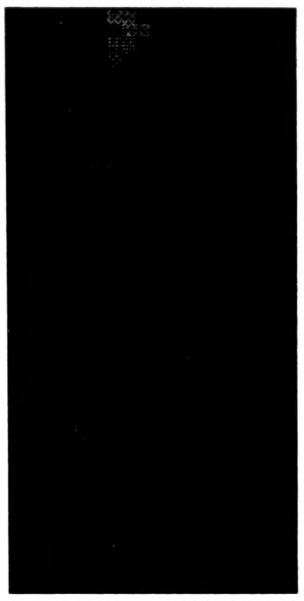
Phyllodoce caerulea

Vaccinium uliginosum

Vaccinium vitis-idaea

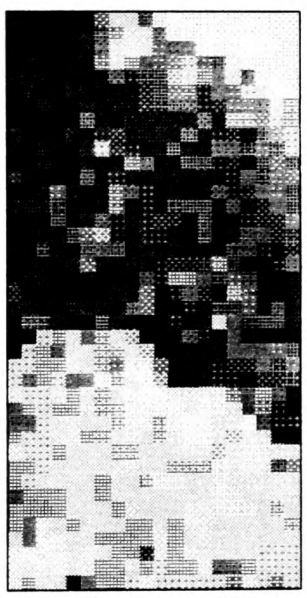


betpub145

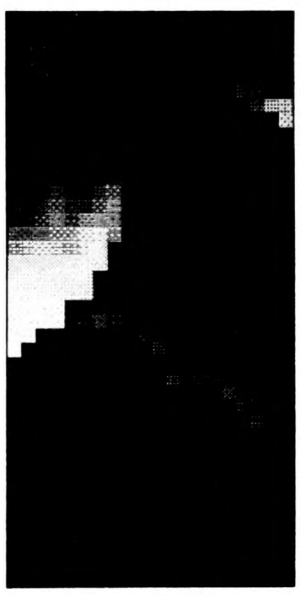


calvul135

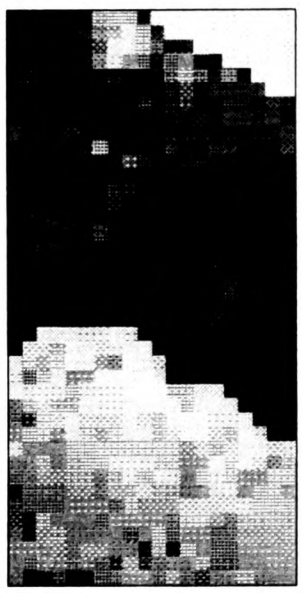
empher135



phycae235



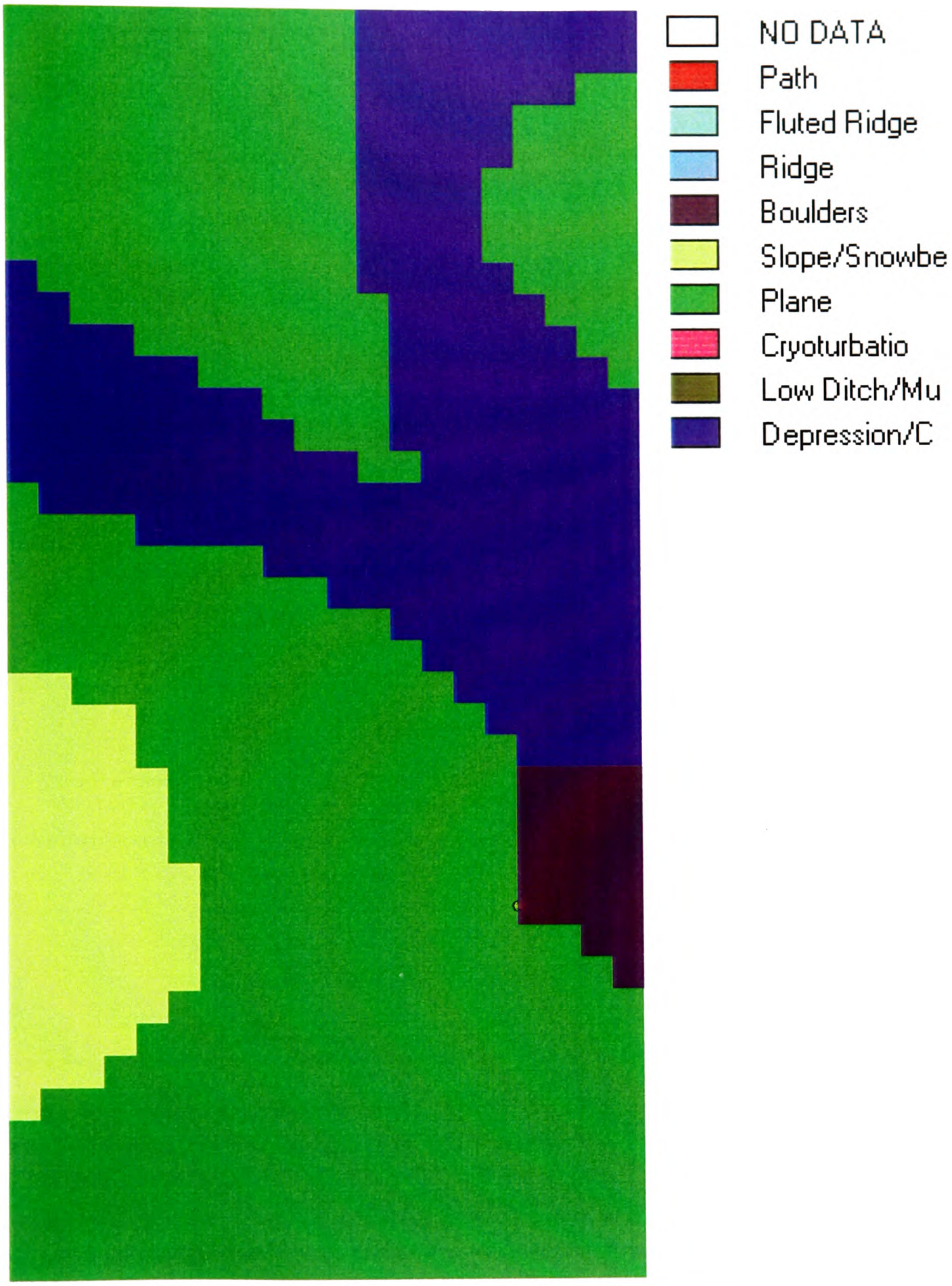
vaculi131



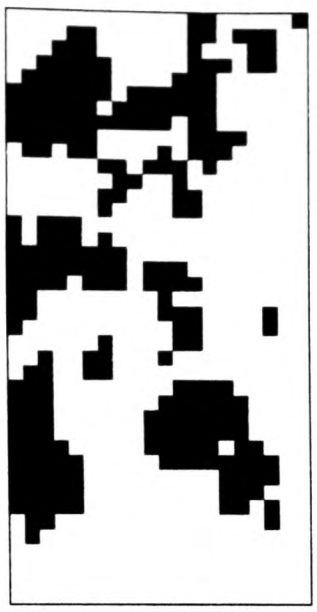
vacvit135

Nigardsbreen foreland block IX (Nig9)

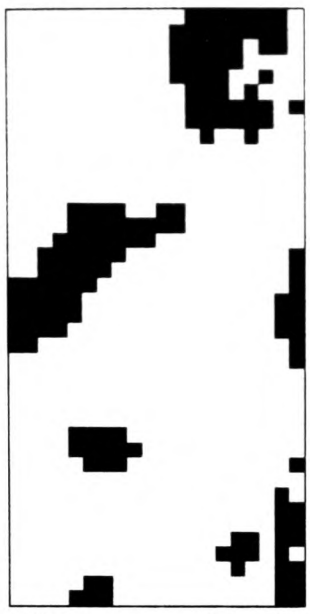
Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 20m.



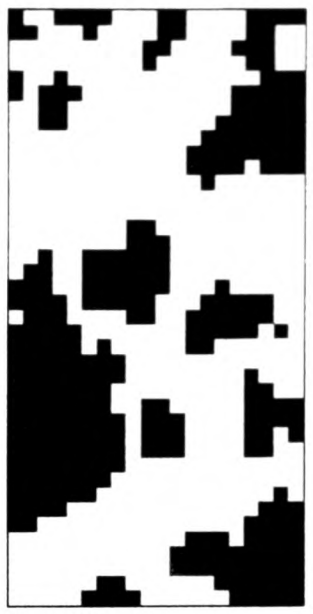
Environmental sketch-map



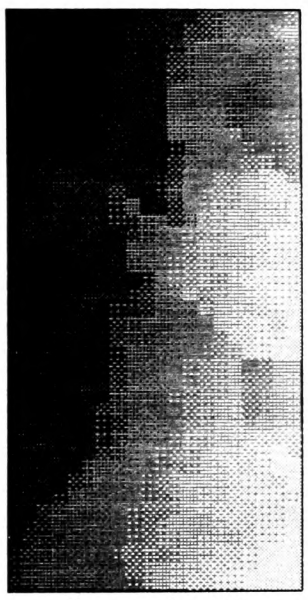
Betula pubescens



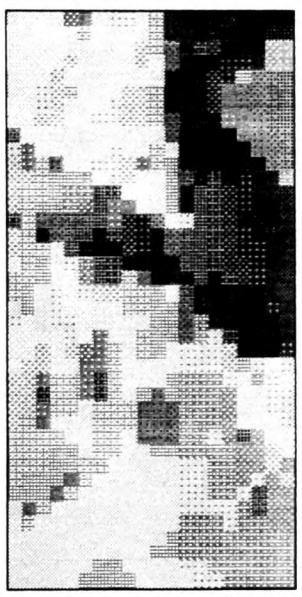
Calluna vulgaris



Empetrum hermaphroditum



betpub135

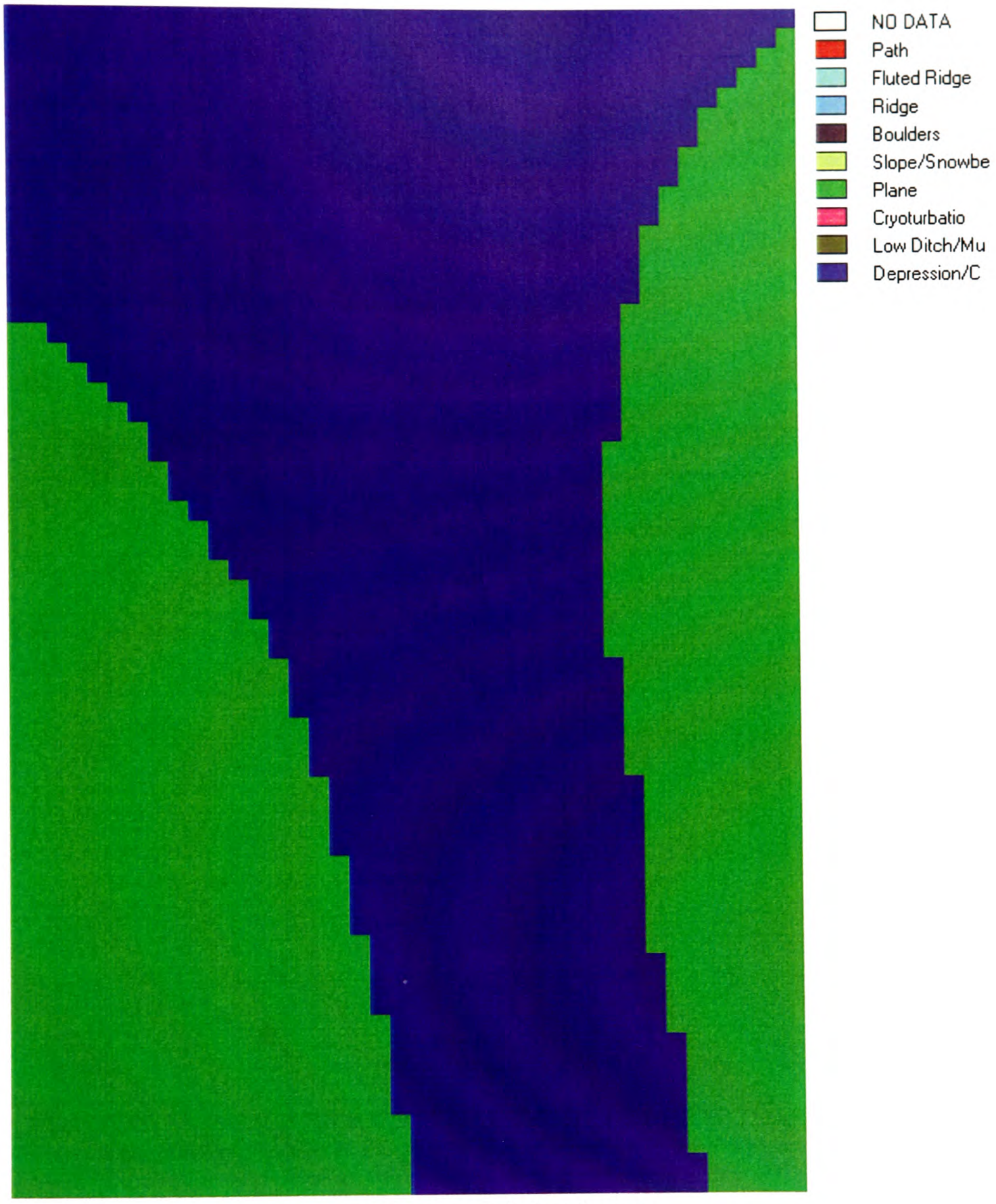


calvul155

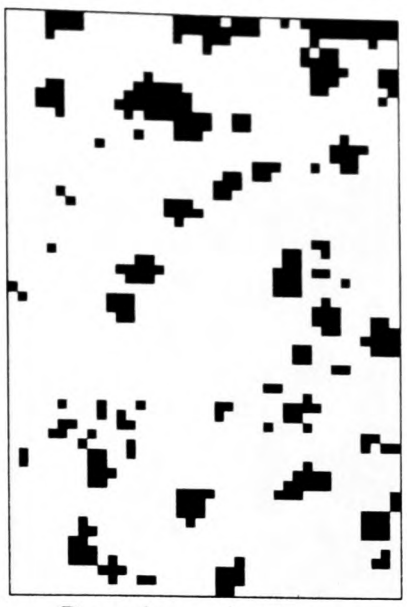
empher135

Nigardsbreen foreland block X (Nig10)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



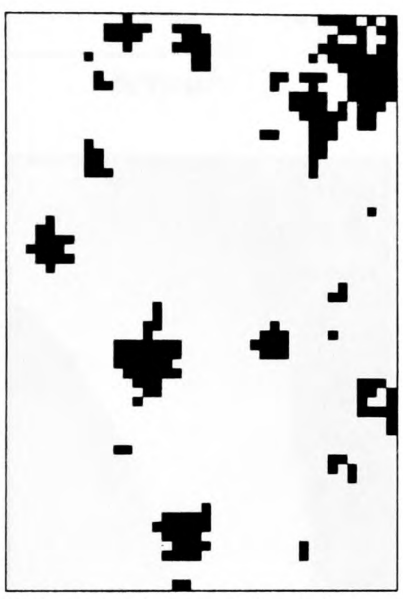
Environmental sketch-map



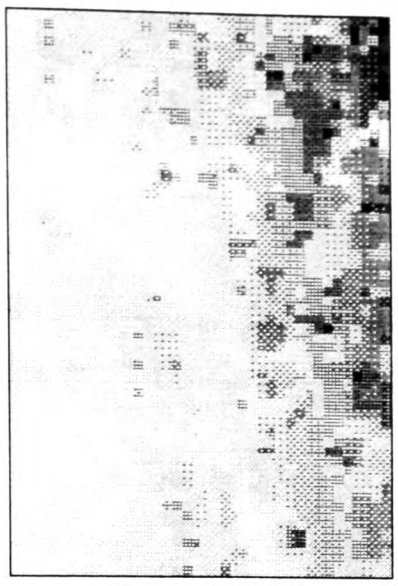
Betula pubescens

Calluna vulgaris

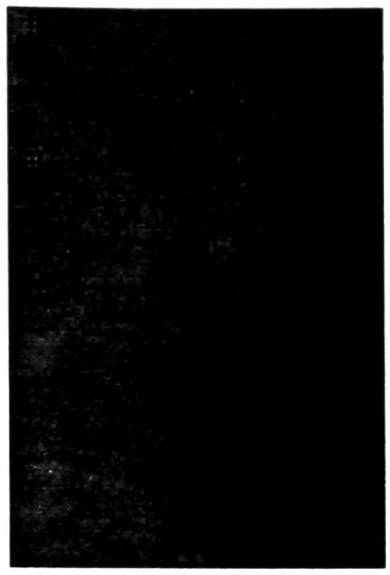
Empetrum hermaphroditum



Vaccinium vitis-idaea

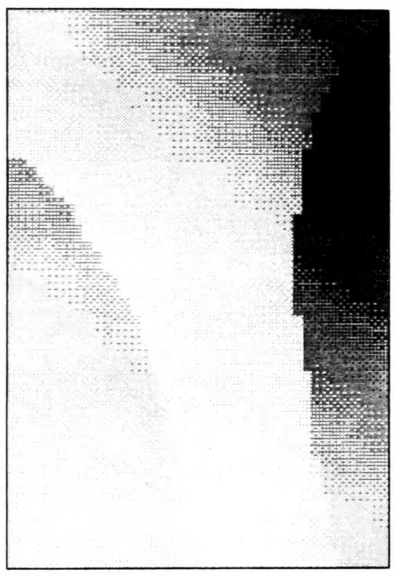


betpub252



calvul135

empher155

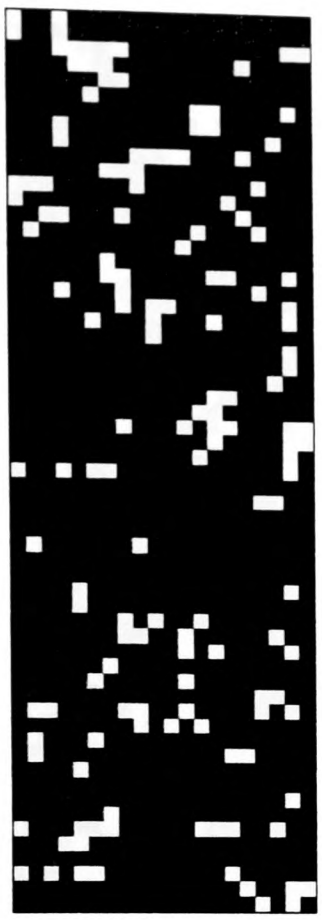


vacvit141

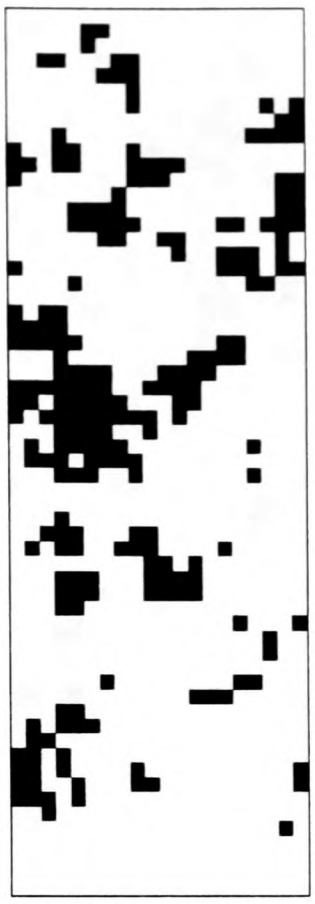
Storbreen foreland block I (Sto1)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 10 x 30m.

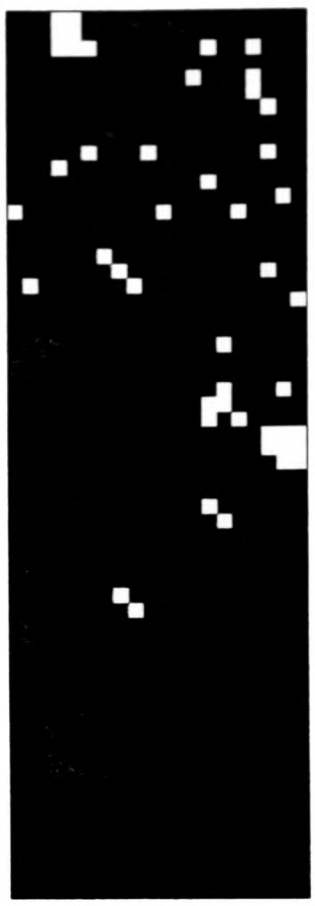
Environmental sketch-map



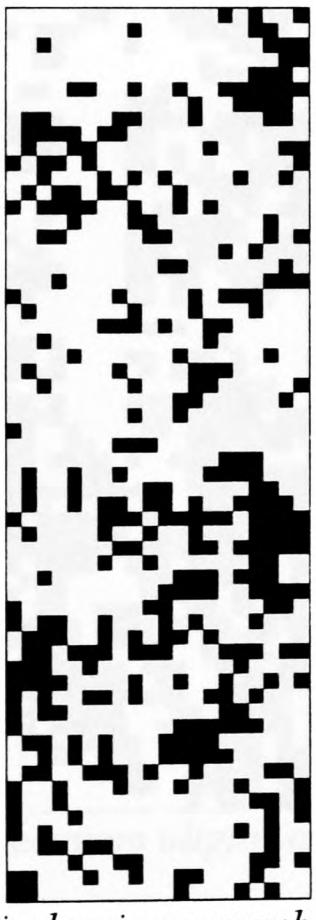
Betula nana



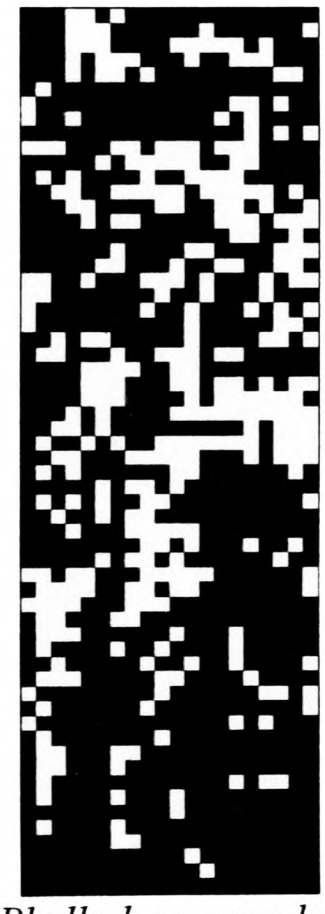
Calluna vulgaris



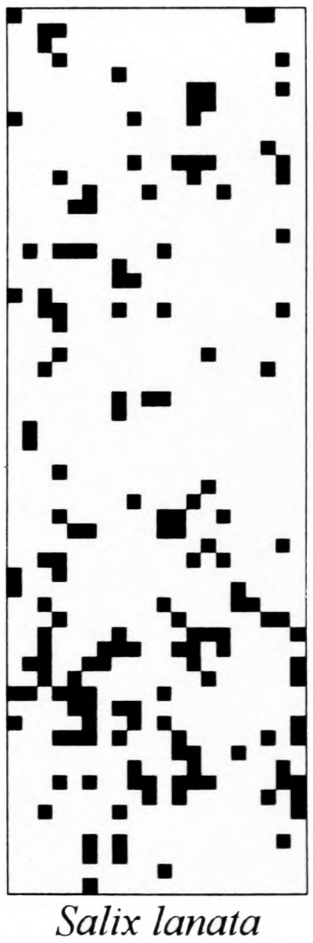
Empetrum hermaphroditum



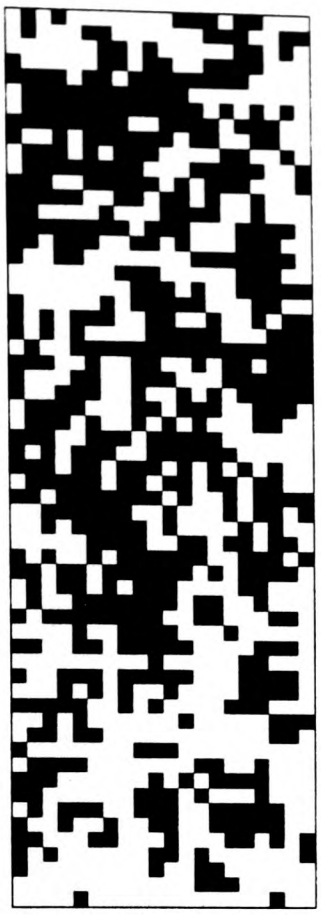
Loiseleuria procumbens



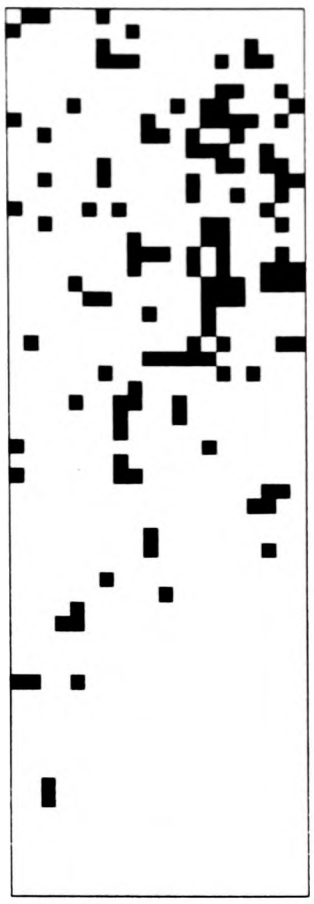
Phyllodoce caerulea



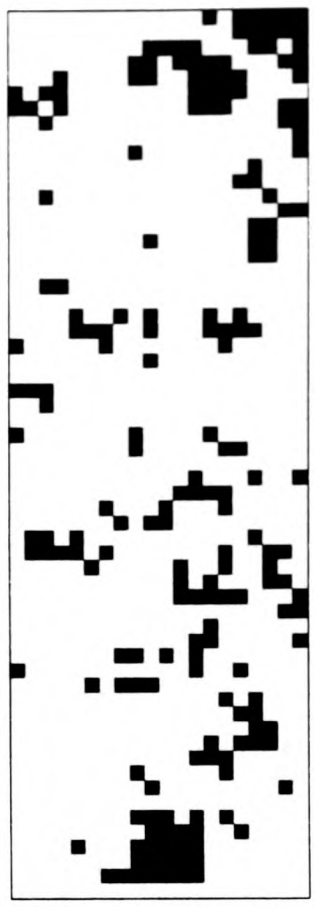
Salix lanata



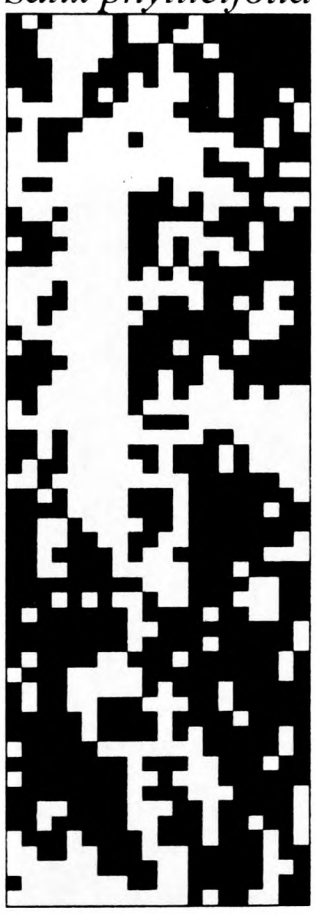
Salix phyllicifolia



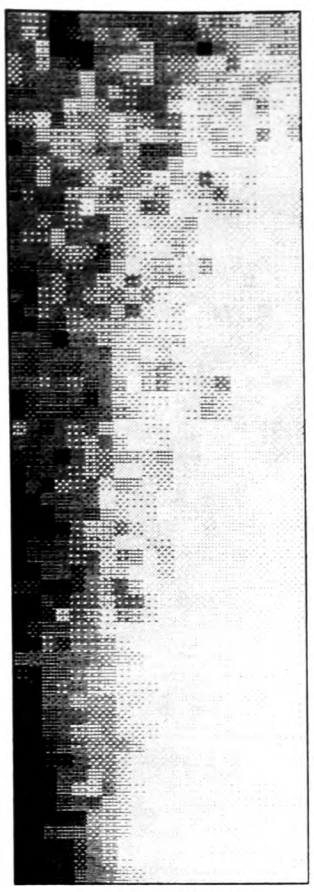
Salix reticulata



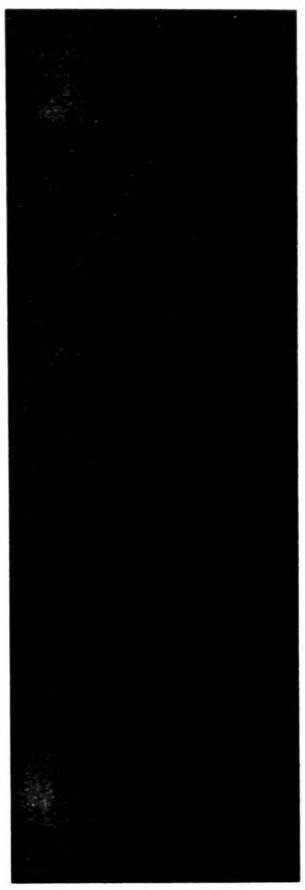
Vaccinium myrtillus



Vaccinium uliginosum

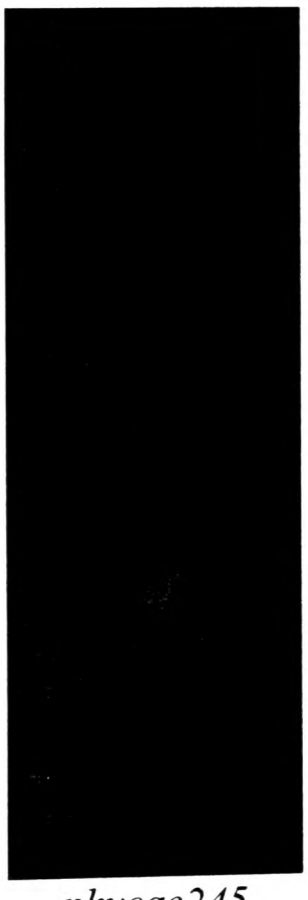


calvul132

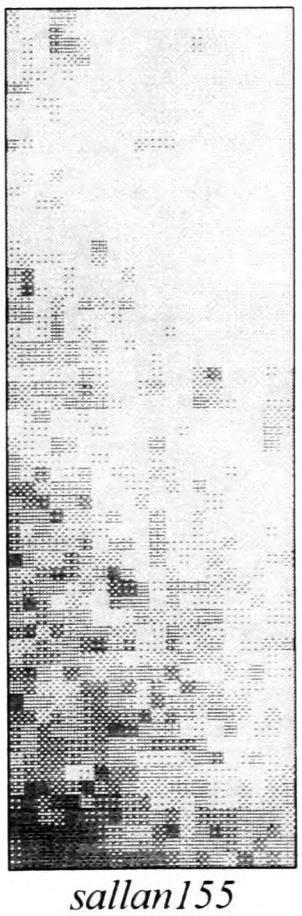


empher145

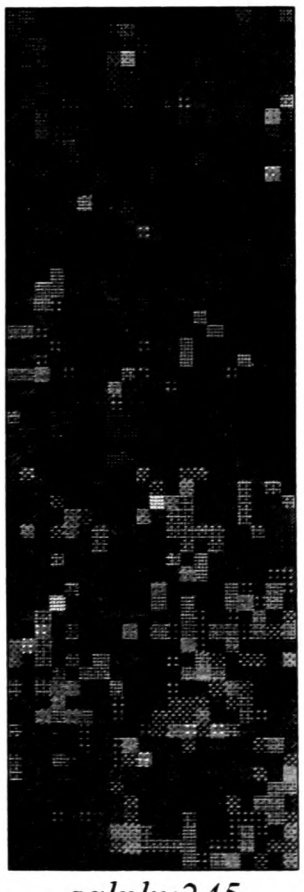
loipro155



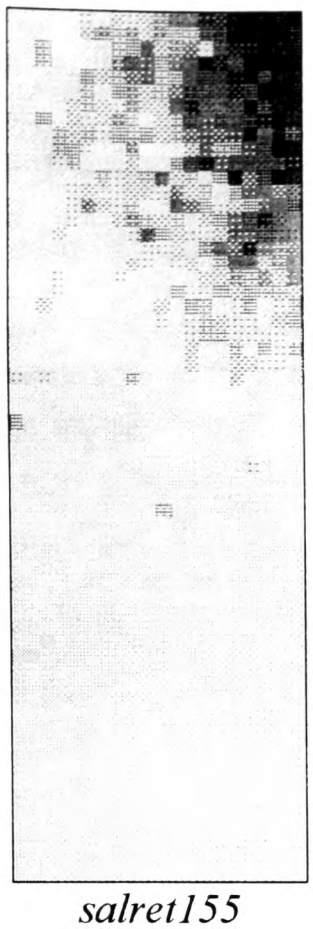
phycae245



sallan155



salphy245



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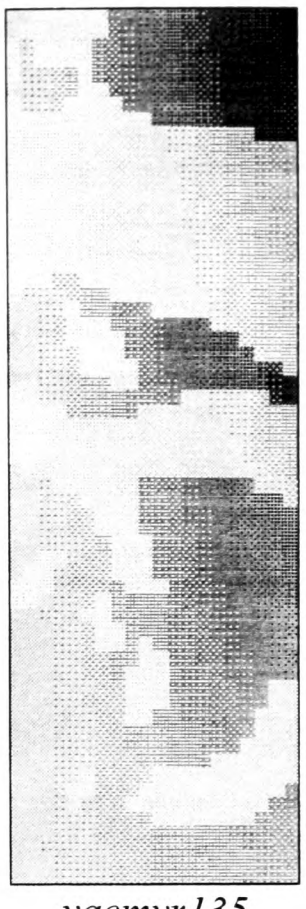
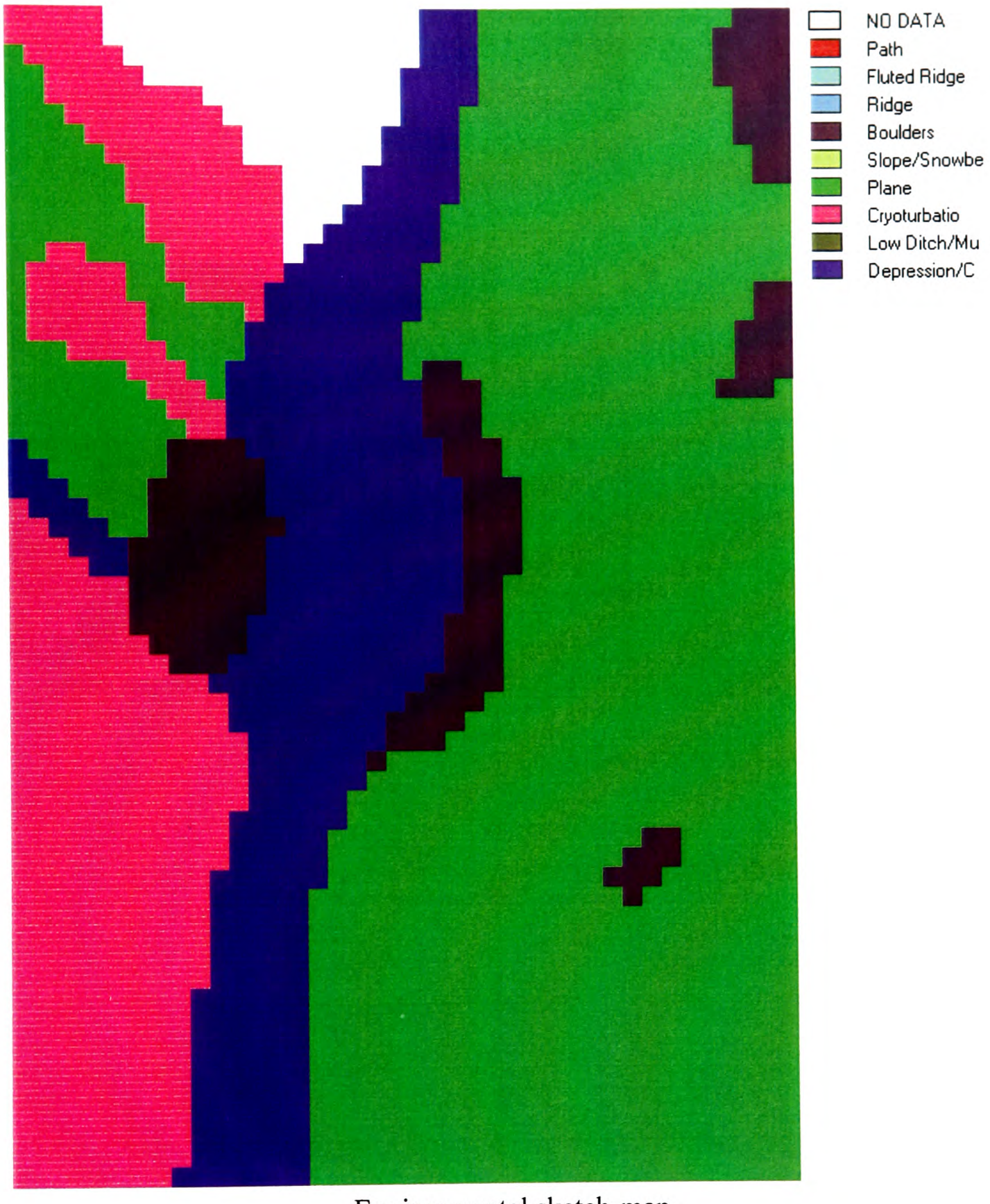


vacmyr135

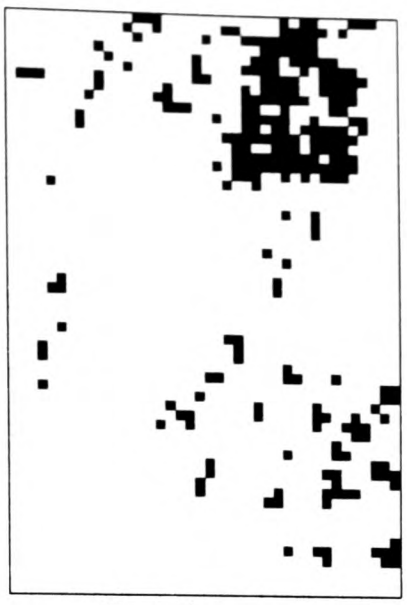
vaculi335

Storbreen foreland block II (Sto2)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



Environmental sketch-map

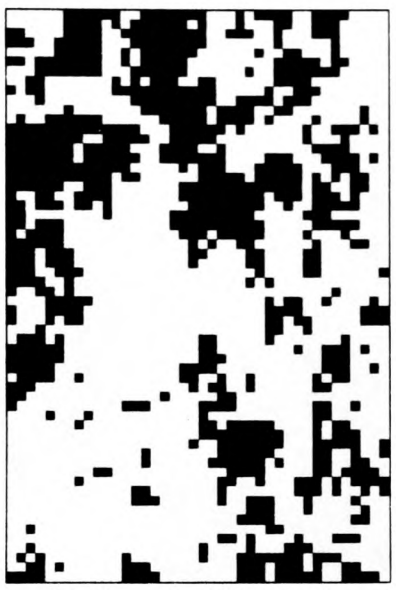


Betula nana

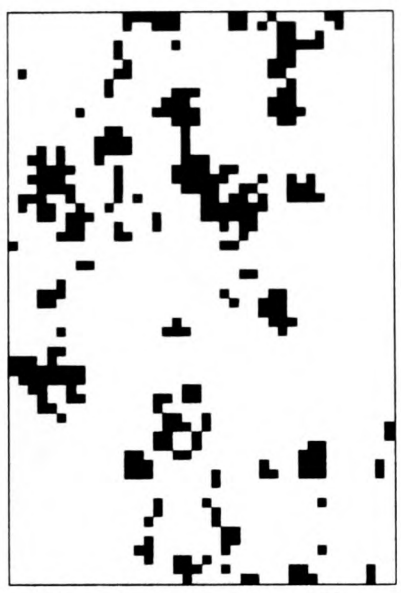
Empetrum hermaphroditum

Phyllodoce caerulea

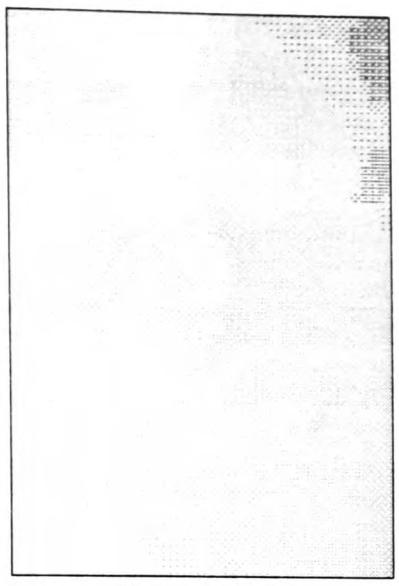
Salix herbacea



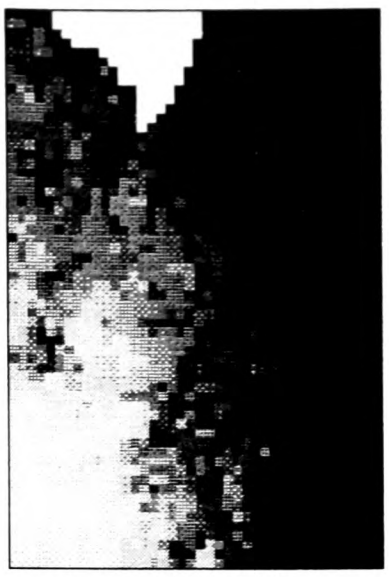
Salix phyllicifolia



Vaccinium myrtillus

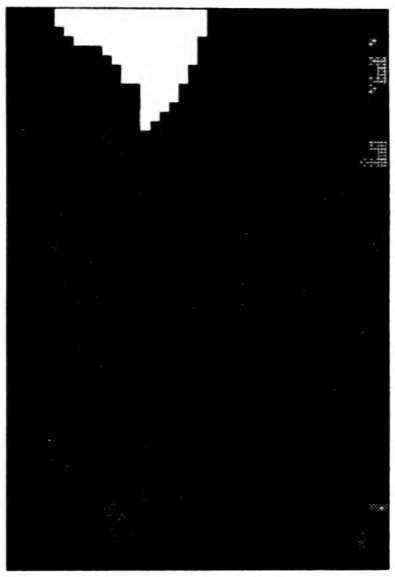


betnan345



empher152

phycae145



salher145

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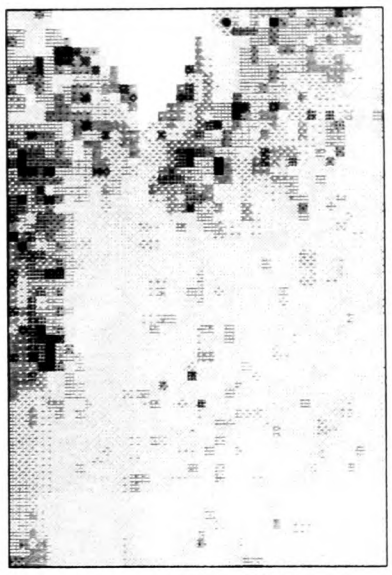
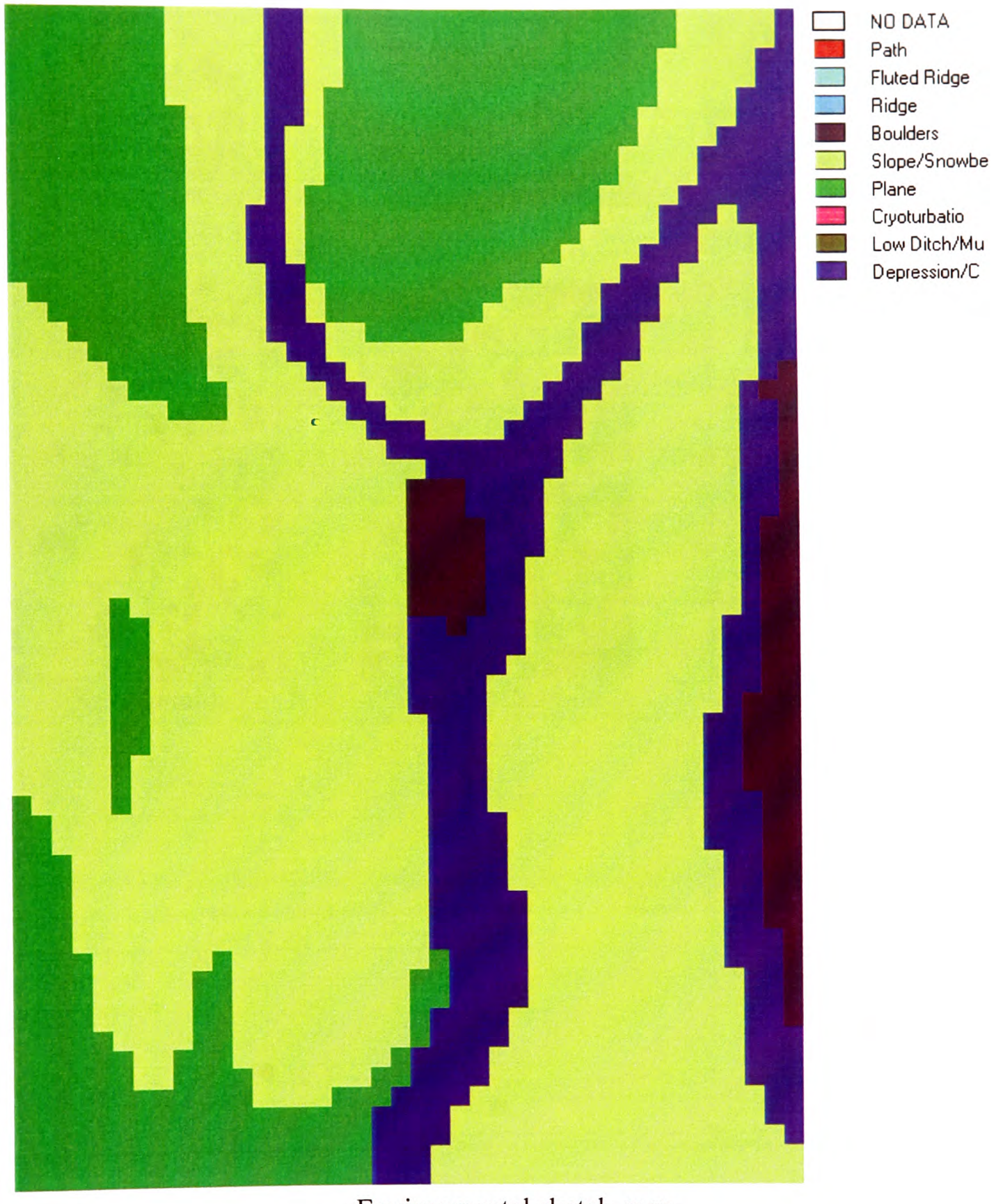


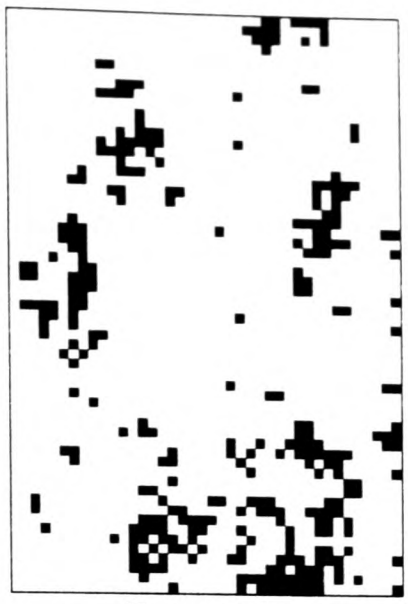
vacmyr135

Storbreen foreland block III (Sto3)

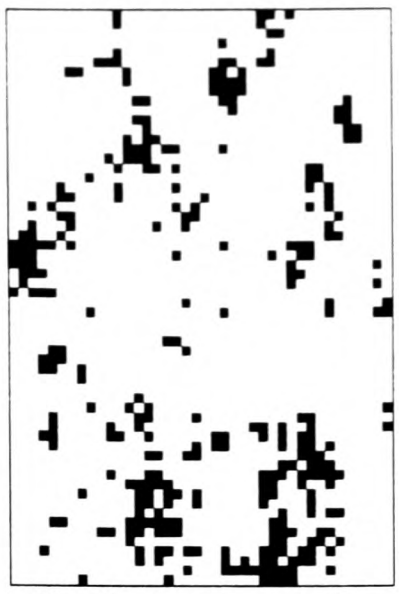
Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



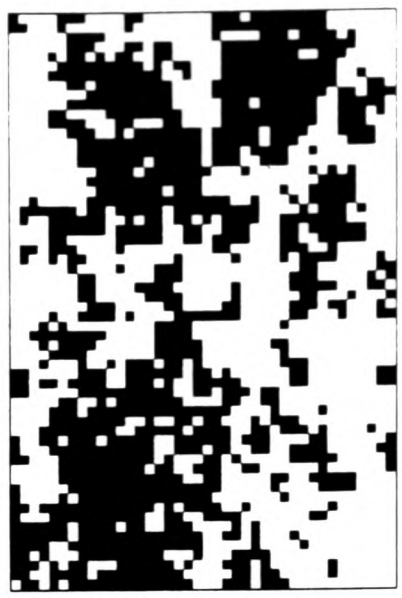
Environmental sketch-map



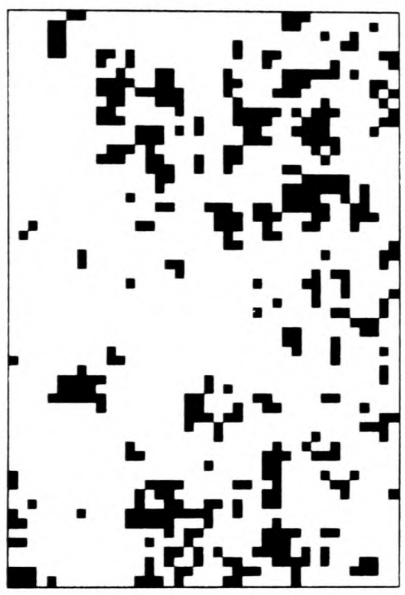
Empetrum hermaphroditum



Phyllodoce caerulea

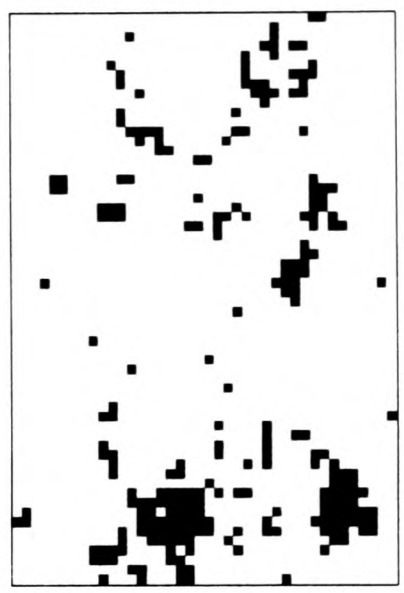


Salix herbacea

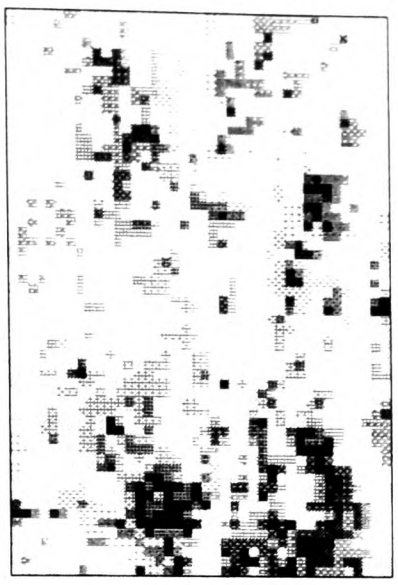


Salix lanata

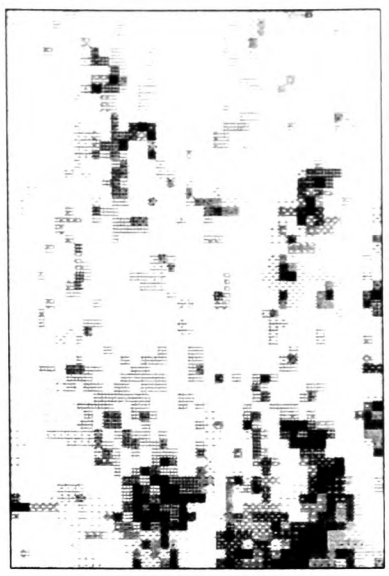
Salix phyllicifolia



Vaccinium myrtillus



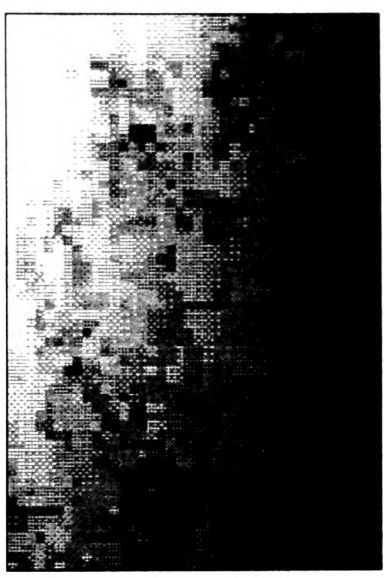
empher145



phycae135

salher235

sallan155

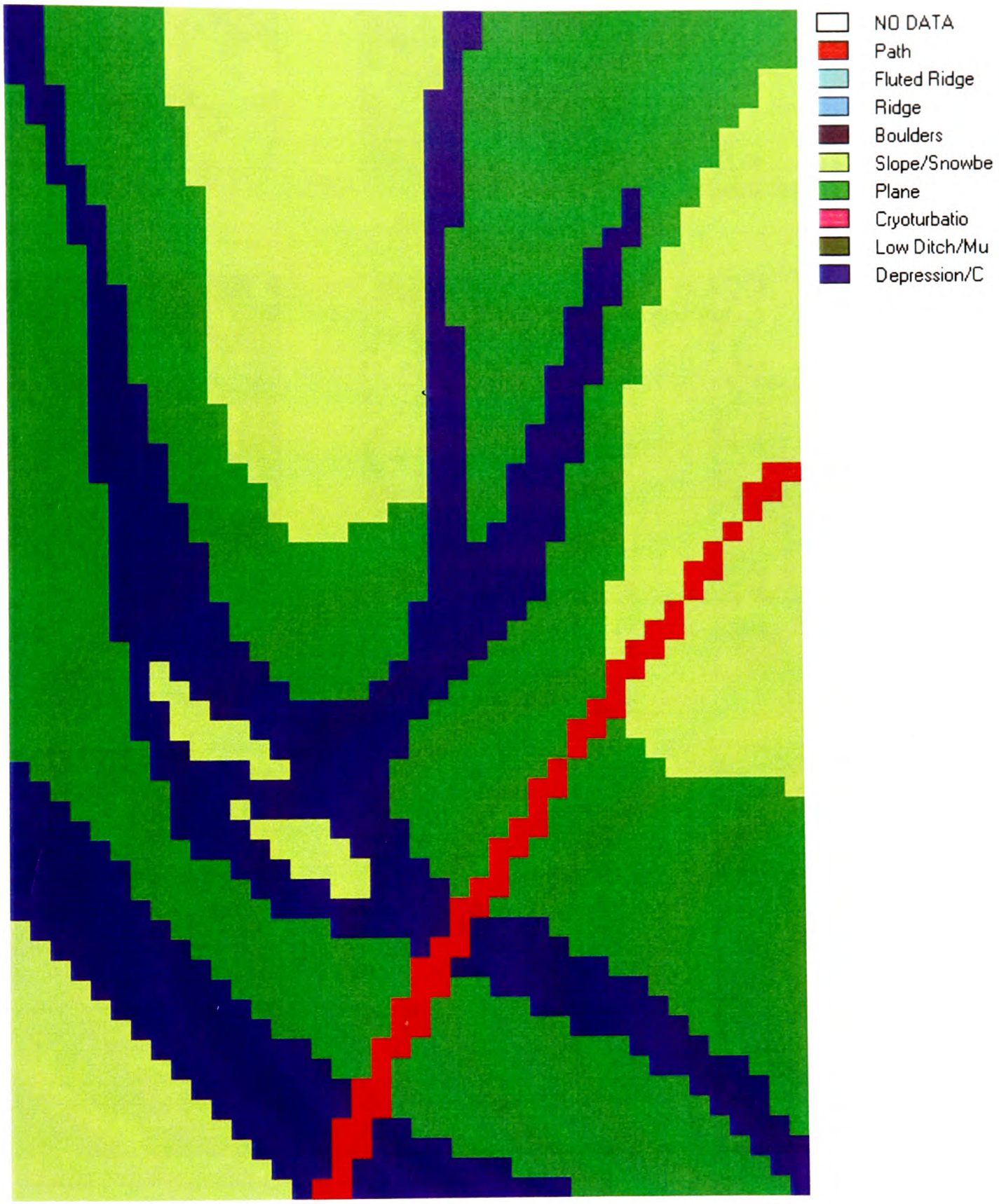


salphy135

vacmyr135

Storbreen foreland block IV (Sto4)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



Environmental sketch-map

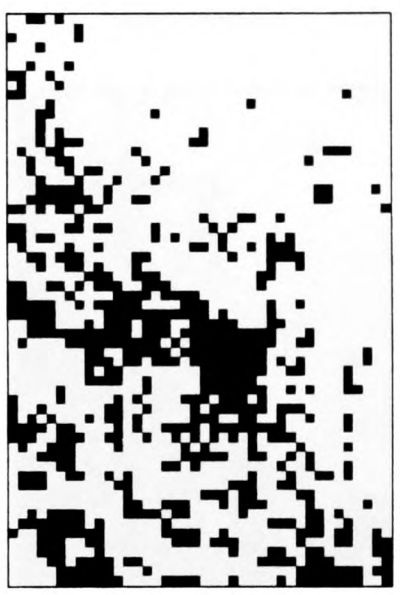
Betula nana

Empetrum hermaphroditum

Loiseleuria procumbens

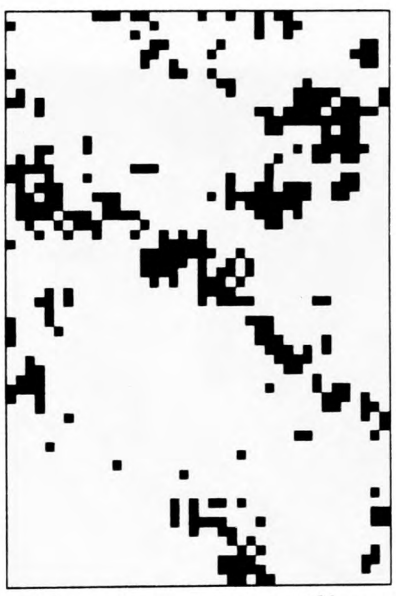
Phyllodoce caerulea

Salix herbacea



Salix lanata

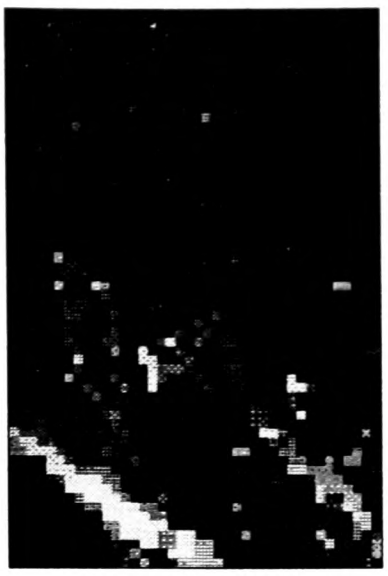
Salix phyllicifolia



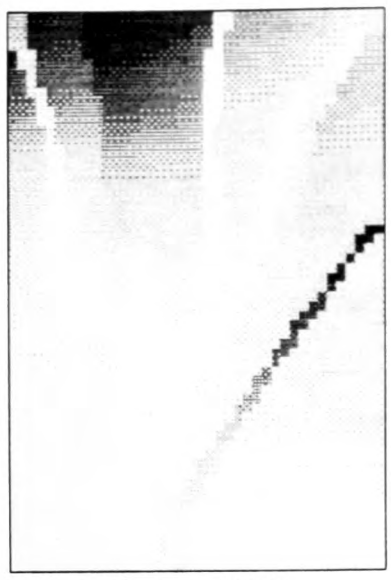
Vaccinium myrtillus

Vaccinium uliginosum

betnan155

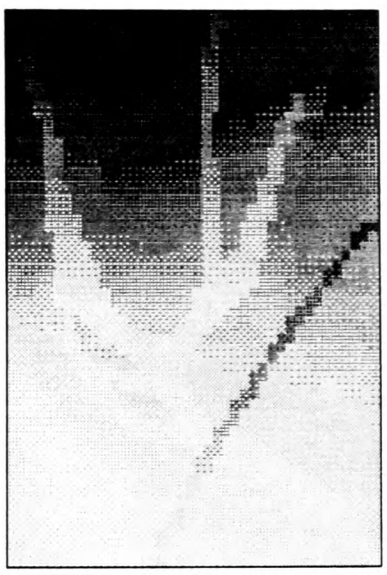


empher135

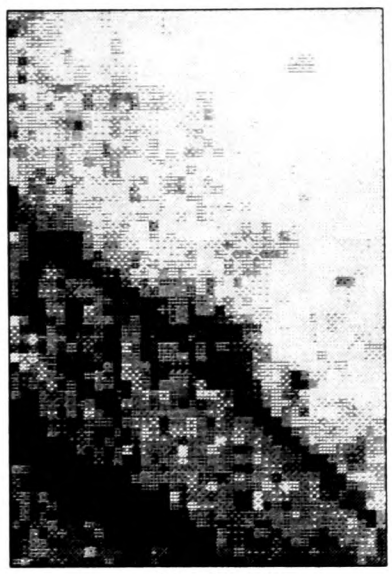


loipro332

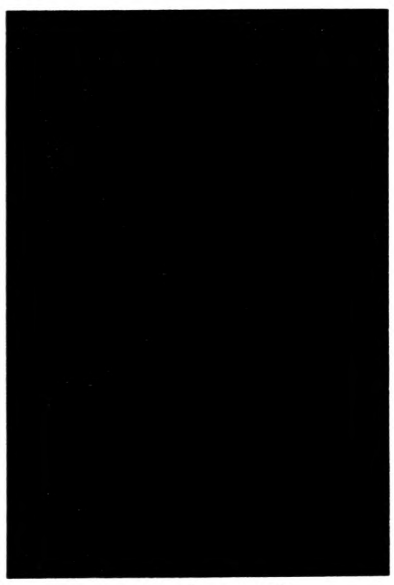
phycae145



salher141



sallan255



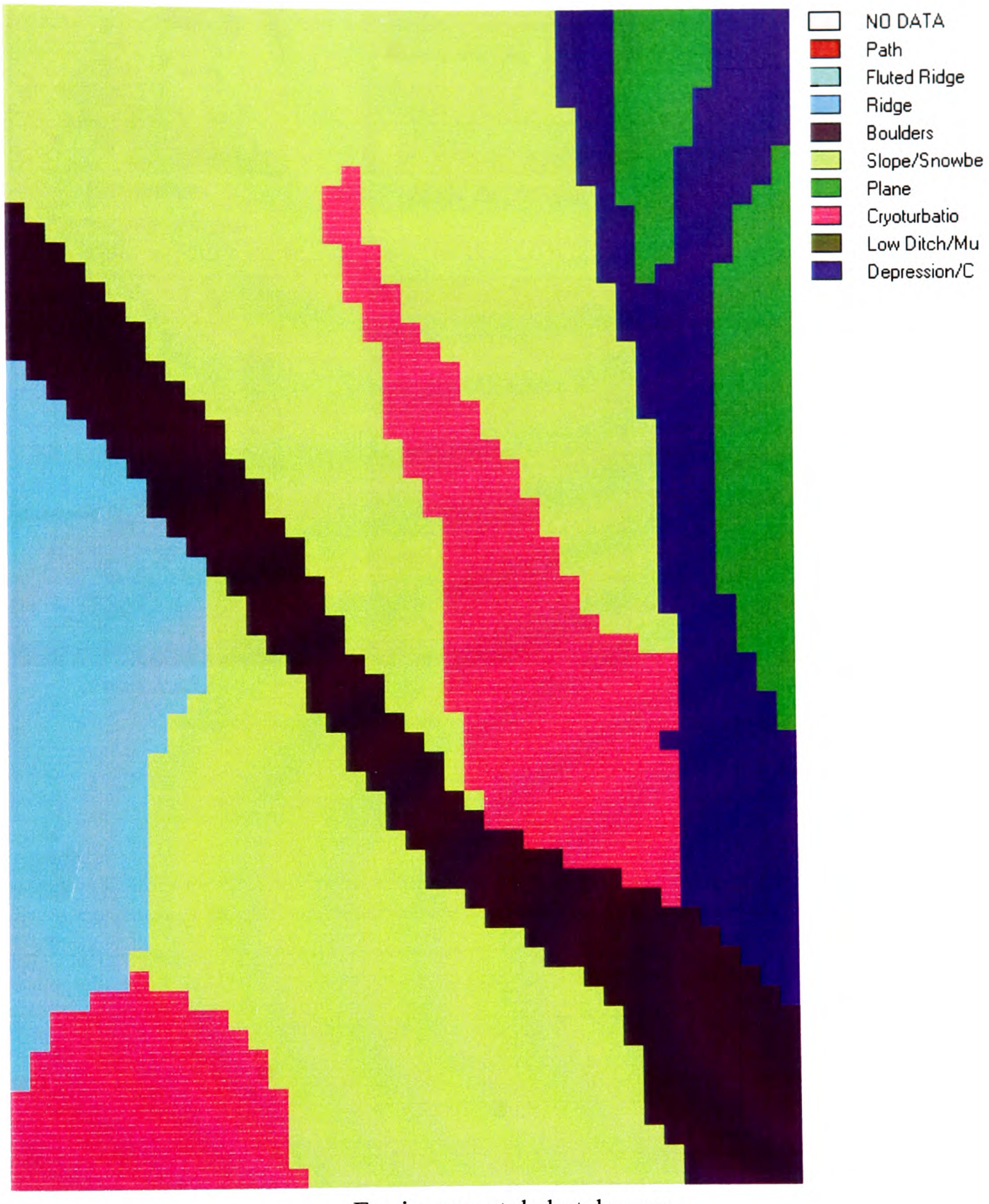
salphy145

vacmyr135

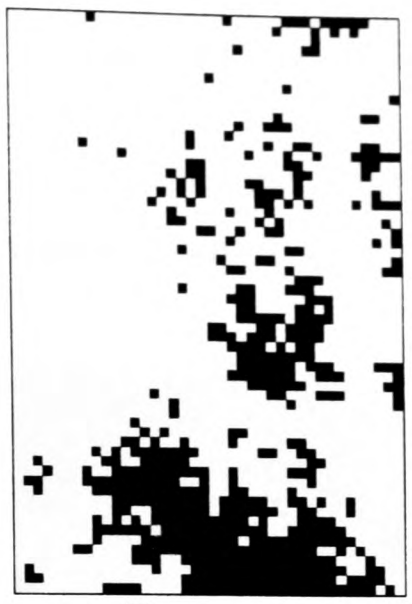
vaculi135

Storbreen foreland block V (Sto5)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.

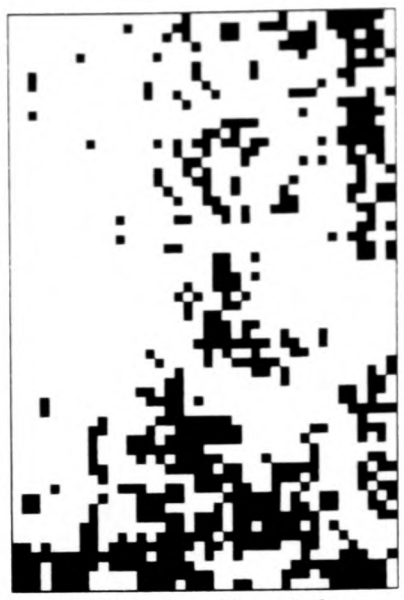


Environmental sketch-map

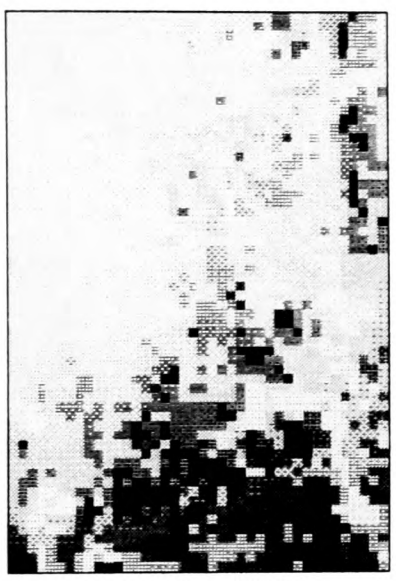


Empetrum hermaphroditum

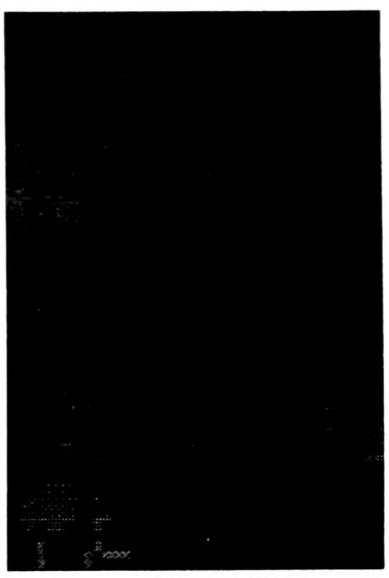
Salix herbacea



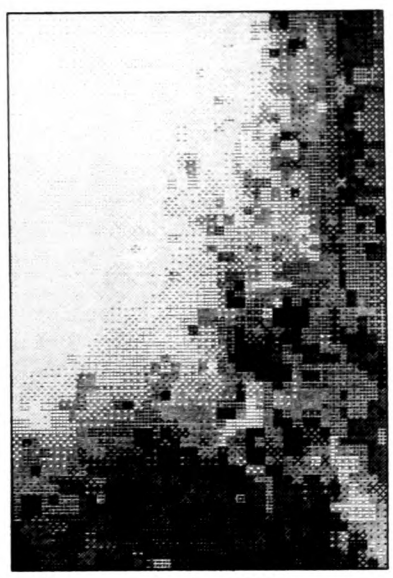
Salix phyllicifolia



empher252



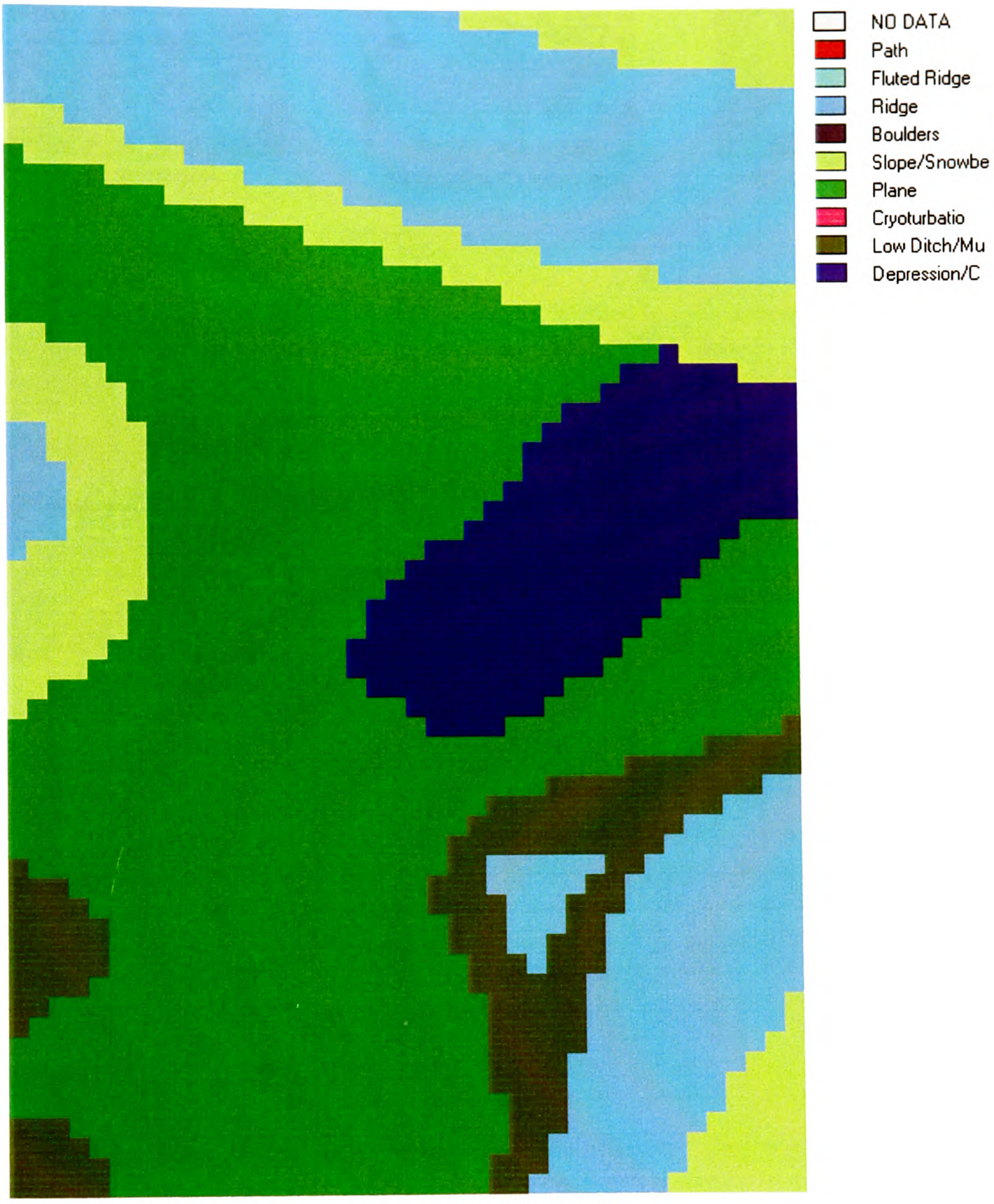
salher155



salphy132

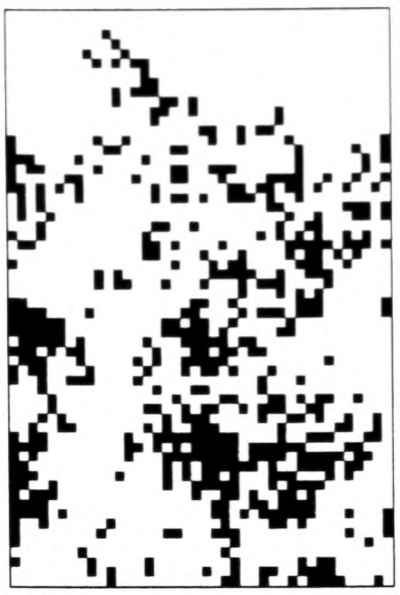
Storbreen foreland block VI (Sto6)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 20 x 30m.



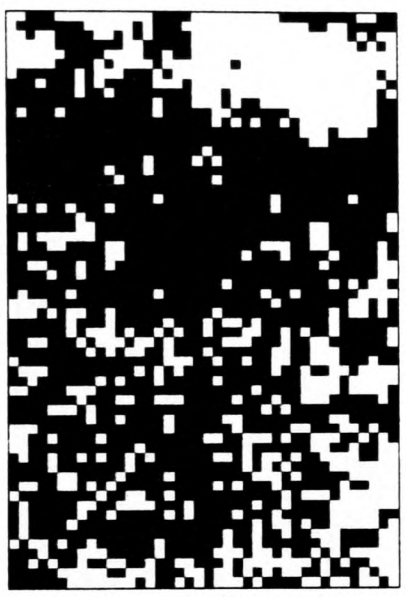
Environmental sketch-map

Empetrum hermaphroditum

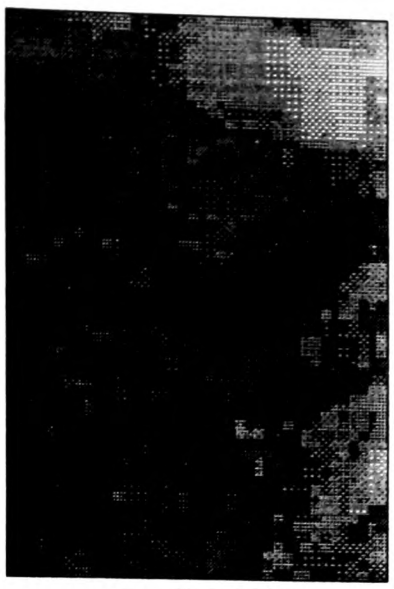


Phyllodoce caerulea

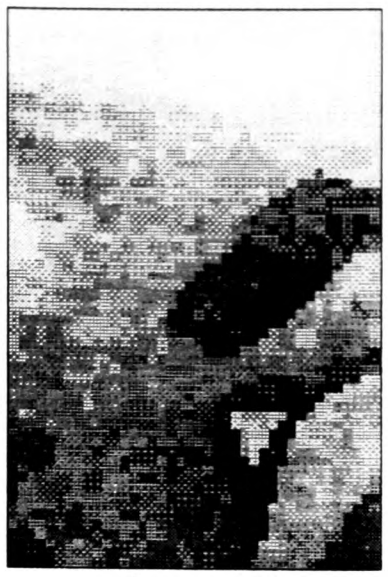
Salix herbacea



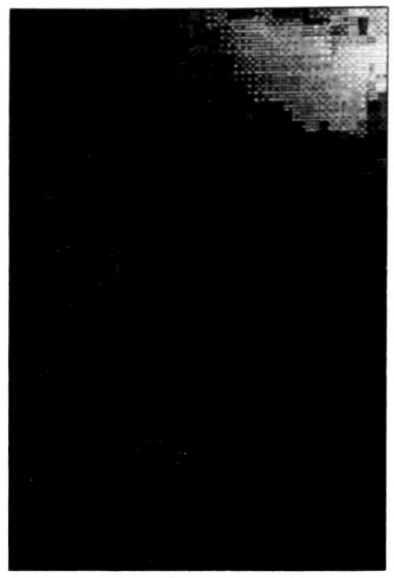
Salix phyllicifolia



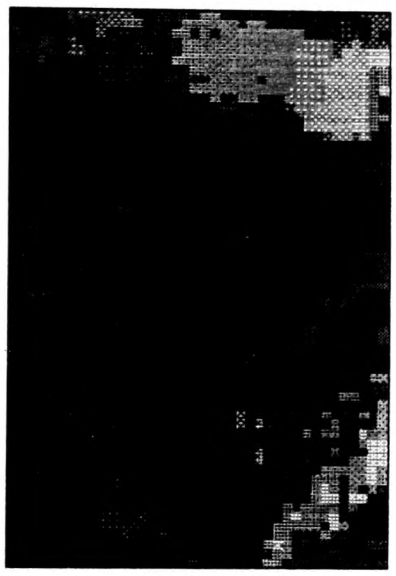
empher145



phycae152



salher135



salphy155

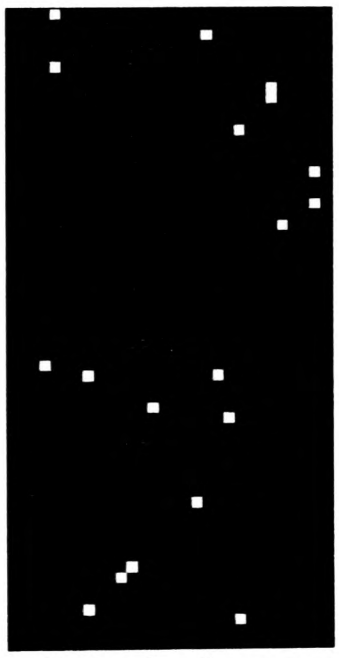
Storbreen foreland block VII (Sto7)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 15 x 30m.

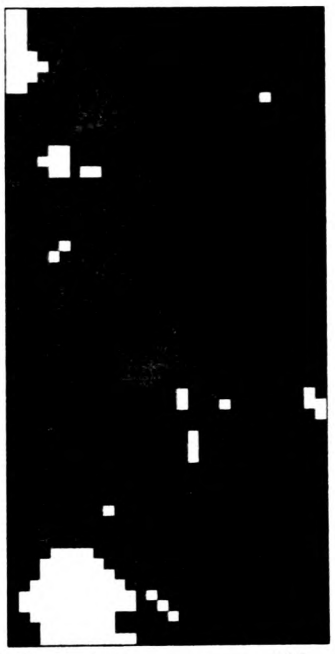
No Environmental sketch-map available

Empetrum hermaphroditum

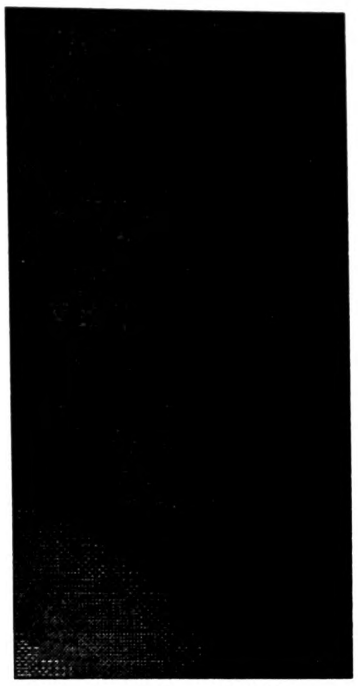
Phyllodoce caerulea



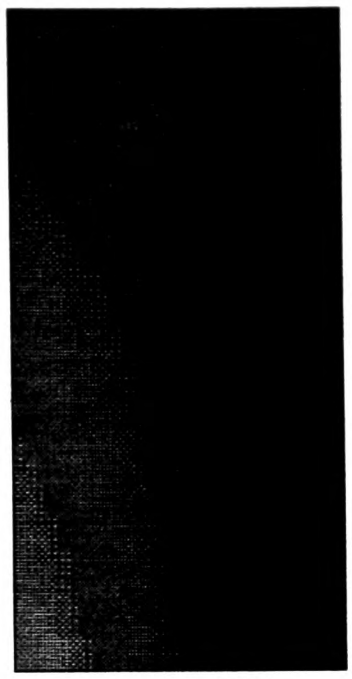
Salix herbacea



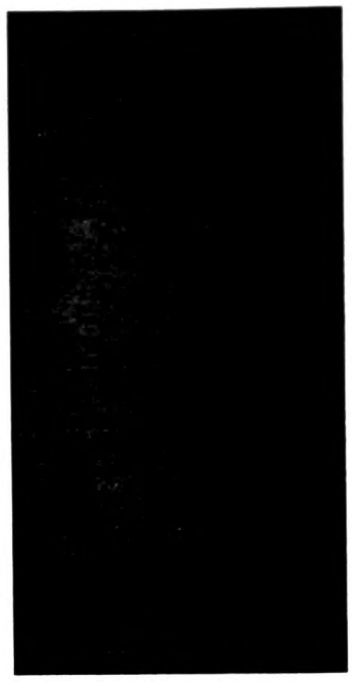
Vaccinium myrtillus



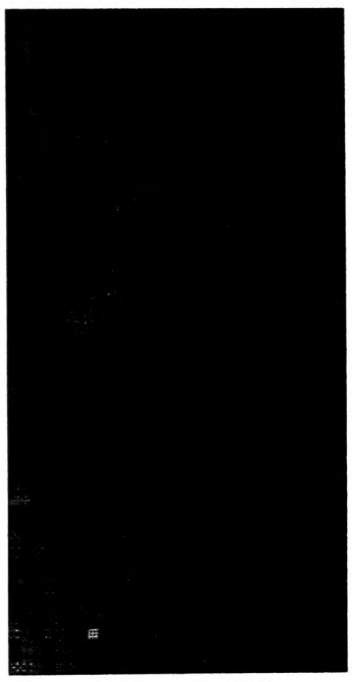
empher345



phycae355



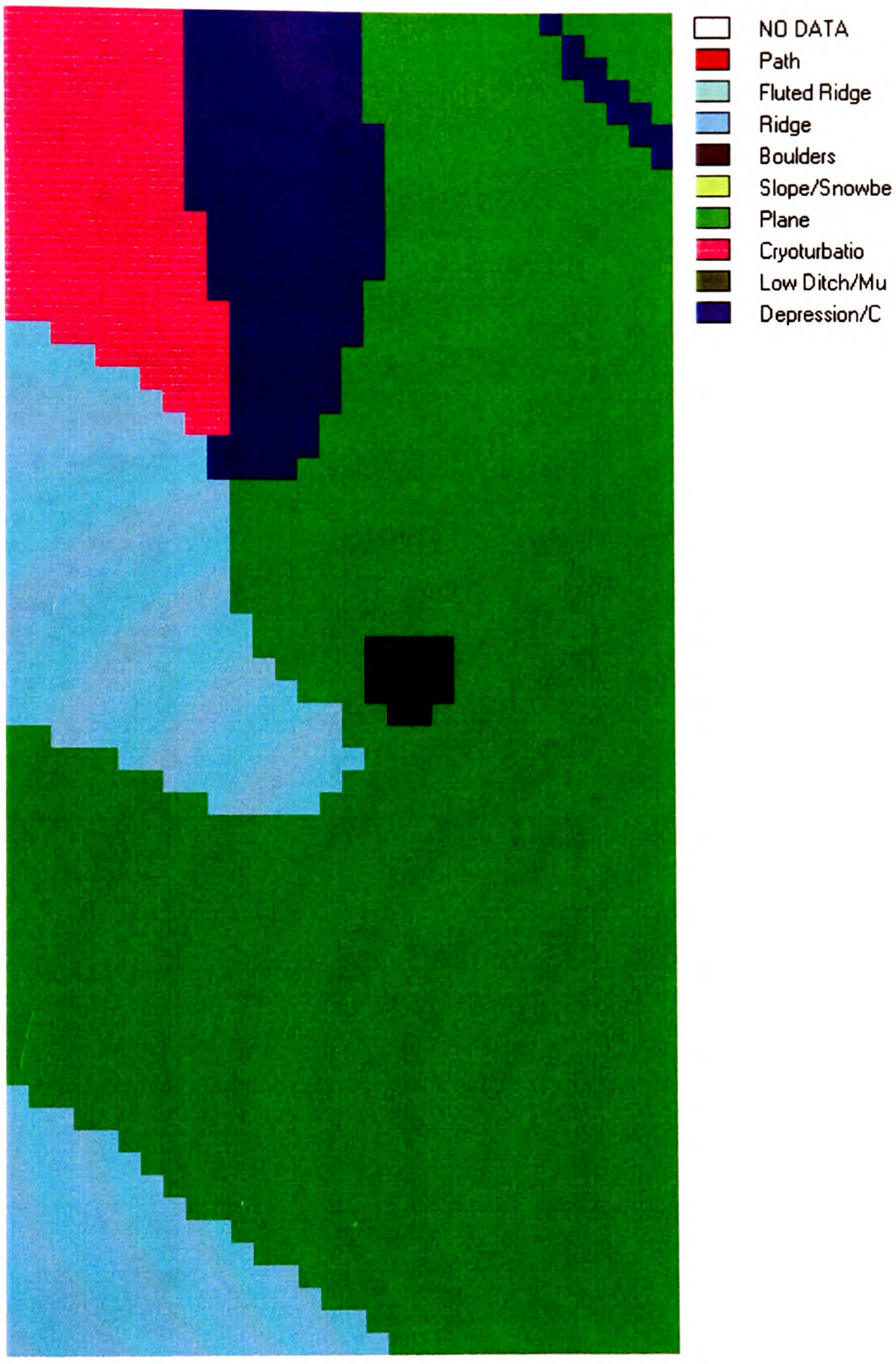
salher135



vacmyr135

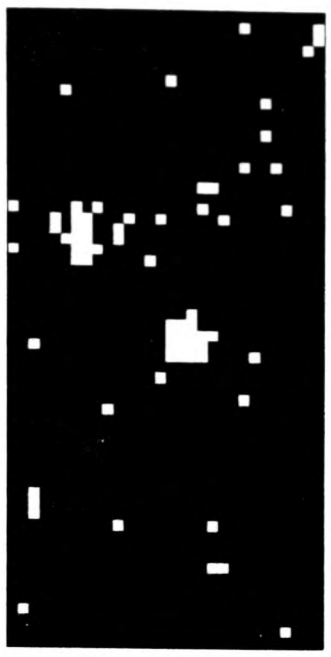
Storbreen foreland block VIII (Sto8)

Environment, distribution and best prediction maps of all dominant woody species (present in >10% of area). Size of block = 15 x 30m.



Environmental sketch-map

Betula nana

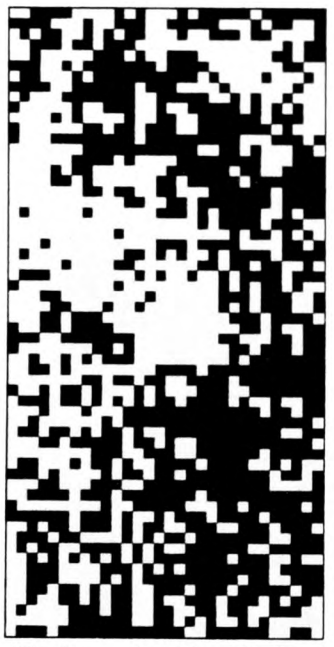


Empetrum hermaphroditum

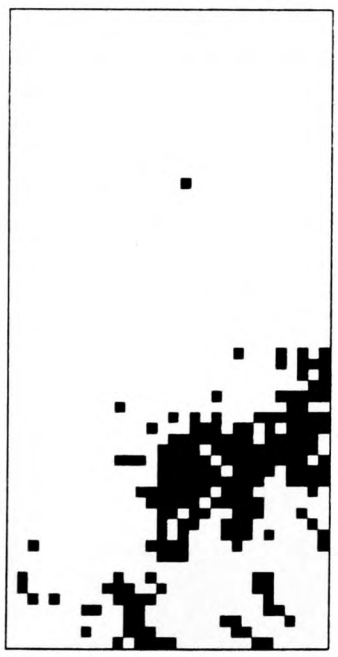
Phyllodoce caerulea

Salix herbacea

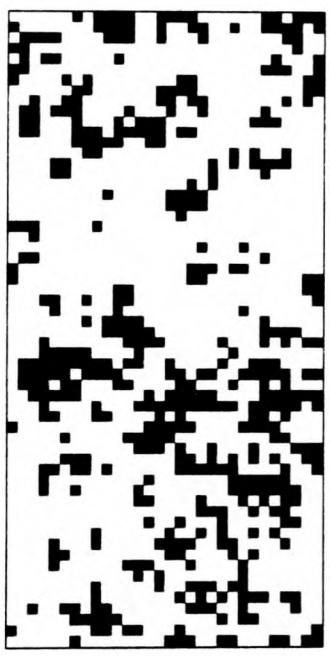
Salix lanata



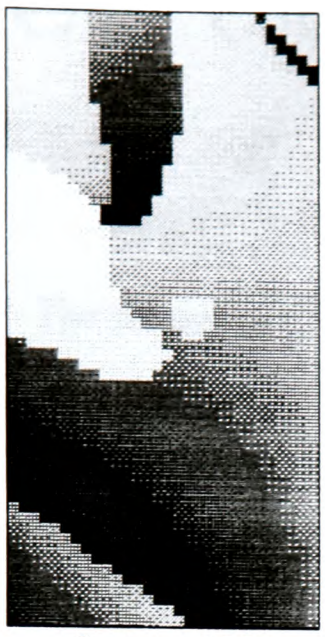
Salix phyllicifolia



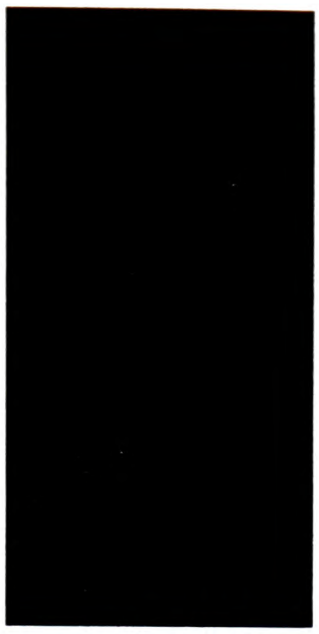
Vaccinium myrtillus



Vaccinium uliginosum

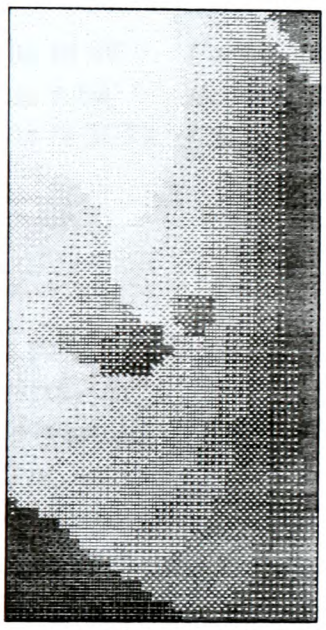


betnan155

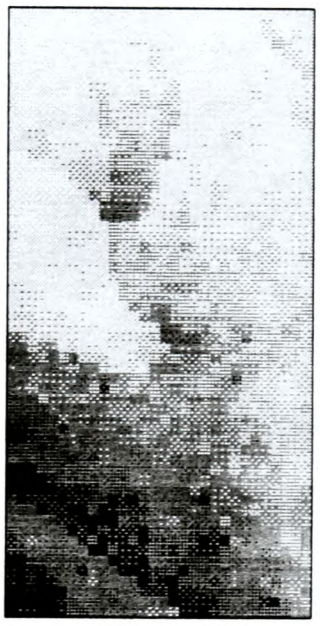


empher145

phycae145

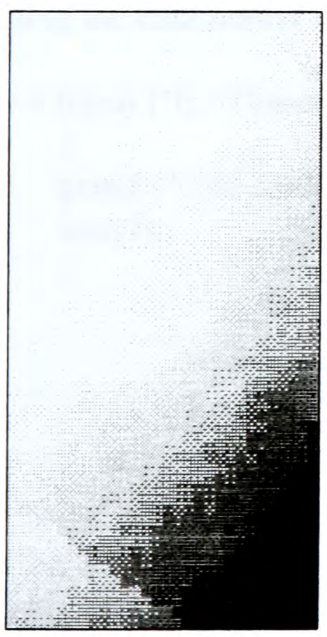


salher345

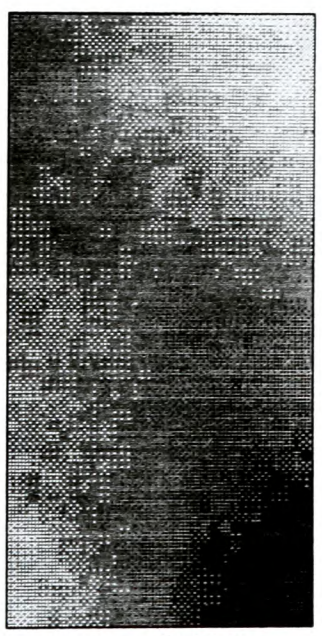


sallan155

salphy145



vacmyr145



vaculi135

2. C/C++ Code

TTLQV program

The following C/C++ code was used for the calculation of the TTLQV values.

```
/*
 * ttlqvasc.C
 * Program reads ascii matrix files and performs
 * 2 dimensional pattern analysis (Dale, 1990) with vl, vr, v2, vx and vy
*/

#include <stdio.h>
#include <stdlib.h>

#define m 48      //rows
#define n 64      //cols
#define N 3072    //blocksize

void main ()
{

int  i,j,row,col,c,b,d,p,q,count;
int xyarray[m][n], xarray[N];
double  varleft, varileft,vleft, varianceleft,valueleft1, valueleft2, valueleft3, valueleft4, vright, varright,
variright, varianceright, vall;
double  var,v,vtemp, variance, mvariance[48][64],auxvariance, meanvariance[70];
const ncol=64,mrow=48;

FILE *fp,*outp;

// reading the data matrix into 2 dimensional array

if ((fp = fopen ("E:\\Thesis\\difcheck.txt", "r")) == NULL)
        {
        printf (" File could not be opened! \n\n");
        exit(1);
        }
j=0;
                while (!feof(fp))
                {
                        fscanf(fp,"%d",&d);
                        xarray[j]=(int)d;
                        j++;
                }
fclose(fp);
j=0;
                for (row=0 ; row<mrow ; row++)
                {
                        for (col=0 ; col<ncol ; col++)
                {
                        xyarray[row][col] = (int)xarray[j];
                        j++;
```

```
                    }
                    }
// end reading the data matrix

if ((outp = fopen ("E:\\Thesis\\difcheck.out", "a+")) == NULL)
        {
                printf (" File could not be opened! \n\n");
                exit(1);
        }
j=0;
varleft = 0.0;
varianceleft = 0.0;
varright = 0.0;
varileft =0.0;
varirright = 0.0;
varianceright = 0.0;
vleft = 0.0;
vright = 0.0;
valueleft1 = 0.0;
valueleft2 = 0.0;
valueleft3 = 0.0;
valueleft4 = 0.0;

for (b=1; b <= (ncol/2); b++)                   // set maximal sample block size
{
        for (i=1; i<=(ncol+1-2*b); i++)         //first summation for Vl
        {
                for (j=1; j<=(mrow+1-2*b); j++)   //second summation for Vl
                {
                                                                        // This is the
tricky bit
                        for (p=i-1; p<=i+b-2; p++)          //first summation for topleft
                        {
                                for (q=j-1; q<=j+b-2; q++)// second summation for topleft
                                {
                                        valueleft1 = valueleft1 + (float)xyarray[q][p];
                                }                                       // end second
summation for topleft
                        }                                               // end first
summation for topleft

                        for (p=i-1+b; p<=i+2*b-2; p++) // first summation for topright
                        {
                                for (q=j-1; q<=j+b-2; q++)// second summation for topright
                                {
                                        valueleft2 = valueleft2 + (float)xyarray[q][p];
                                }                                       // end second
summation for topright
                        }                                               // end first
summation for topright

                        for (p=i-1; p<=i+b-2; p++)          //first summation for lowleft
                        {
                                for (q=j-1+b; q<=j+2*b-2; q++)// second summation for lowleft
                                {
                                        valueleft3 = valueleft3 + (float)xyarray[q][p];
                                }                                       // end second
summation for lowleft
```

```
                    }                                                    // end first
summation for lowleft

                    for (p=i-1+b; p<=i+2*b-2; p++) // first summation for lowright
                    {
                            for (q=j-1+b; q<=j+2*b-2; q++)// second summation for lowright
                            {
                                    valueleft4 = valueleft4 + (float)xyarray[q][p];
                            }                                            // end second
summation for lowright
                    }                                                    // end first
summation for lowright

                    vleft=(3*valueleft1- valueleft2-valueleft3-valueleft4);
                    varleft=(vleft*vleft)/(18*((float)ncol+1-(2*(float)b))*((float)mrow+1-
(2*(float)b))*((float)b*(float)b));
                    varileft = varileft + varleft;
                    //varianceleft = varianceleft + varleft;
                    vright=(3*valueleft2-valueleft1-valueleft3-valueleft4);
                    varright=(vright*vright)/(18*((float)ncol+1-(2*(float)b))*((float)mrow+1-
(2*(float)b))*((float)b*(float)b));
                    variright = variright + varright;
                    //varianceright = varianceright + varright;
                    valueleft1 = 0.0;
                    valueleft2 = 0.0;
                    valueleft3 = 0.0;
                    valueleft4 = 0.0;
                }                                                        // end second
summation for Vl
                            varianceleft = varianceleft + varileft;
                            varianceright = varianceright + variright;
                            varileft = 0.0;
                            variright = 0.0;
            }                                                            // end first
summation for Vl
            vall =(varianceleft + varianceright)/2;
            fprintf(outp, "%d%6.3f    %6.3f    %6.3f\n",b,varianceleft,varianceright, vall);
            varianceleft = 0.0;
            varleft = 0.0;
            varileft=0.0;
            vleft = 0.0;
            varianceright = 0.0;
            varright = 0.0;
            variright=0.0;
            vright = 0.0;
            vall = 0.0;
                                                                         // end block for
}
scales

v=0.0;
variance=0.0;
//this starts the column variance
for (c=0; c <= ncol-1; c++)
                                                    // loops the column transects
{
            for (b=1; b <= (mrow/2); b++)
                                                                         //loops the scales
            {
                    for (i=0; i<=mrow-2*b; i++)
```

```
                {                                                                   //first sum

                        for (j=i; j<=(i+b-1); j++)
                        {                                                           //second sum
                                vtemp = (float)xyarray[j][c] - (float)xyarray[j+b][c];
                                v = v + vtemp;
                        }                                                           //end second sum
                        var = (v * v)/(2*(float)b*((float)mrow+1-2*(float)b));
                        variance = variance + var ;
                        v=0;
                }                                                                   //end first sum
                mvariance[b-1][c] = variance;
                variance = 0.0;
                vtemp = 0.0;
                var = 0.0;
                v = 0.0;
        }                                                                           //end loop scales
}                                                                                   // ends the loop for the 40
transects
for (b=0; b <= (mrow/2)-1; b++)
{                                                                   // loops the 30 scales
        for (c=0; c <= ncol-1; c++)
        {                                                           // loops the 40 transects
//              fprintf(outp,"scale %d, column %d, variance %6.3f\n",b+1,c,mvariance[b][c]);
                auxvariance = auxvariance + mvariance[b][c];        // add up the variances across all
transcects in each scale
        }
        meanvariance[b]= auxvariance/ncol;
        auxvariance = 0.0;
}
fprintf(outp,"\n\nThis is the mean of the column variance\n\n");
for (count=0; count<=(mrow/2)-1; count++)
{
fprintf(outp, "%d%6.3f\n",count+1,meanvariance[count]);
}
//
//this starts the row variance
//
variance = 0.0;
v=0.0;

for (c=0; c <= mrow-1; c++)
{                                                                   // loops the 60 transects
        for (b=1; b <= (ncol/2); b++)
        {                                                                           //loops the scales
                for (i=0; i<=ncol-2*b; i++)
                {                                                                   //first sum

                        for (j=i; j<=(i+b-1); j++)  //second sum
                        {
                                vtemp = (float)xyarray[c][j] - (float)xyarray[c][j+b];
                                v = v + vtemp;
                        }                                                           //end second sum
                        var = (v * v)/(2*(float)b*((float)ncol+1-2*(float)b));
                        variance = variance + var ;
                        v=0;
                }                                                                   //end first sum
                mvariance[c][b-1] = variance;
```

```
                variance = 0.0;
                vtemp = 0.0;
                var = 0.0;
                v = 0.0;
        }                                                       //end loop scales
}                                                               // ends the loop for the 60
transects

for (b=0; b <= (ncol/2)-1; b++)
{                                                               // loops the 20 scales
        for (c=0; c <= mrow-1; c++)
        {                                                       // loops the 60 transects
//                      fprintf(outp,"scale %d, row %d, variance %6.3f\n",b+1,c,mvariance[c][b]);
                auxvariance = auxvariance + mvariance[c][b];        // add up the variances of the
transects for each scale
        }
        meanvariance[b]= auxvariance/mrow;
        auxvariance = 0.0;
}
fprintf(outp,"\n\nThis is the mean of the row variance\n\n");
for (count=0; count<=(ncol/2)-1; count++)
{
fprintf(outp, "%d %6.3f\n",count+1,meanvariance[count]);
}
fclose(outp);
}
```

Model error and AUC program

The following is the C/C^{++} code used for the calculation of error measures for the model performance. It produces two output files, which contain the error measures and the AUC-values.

```
/*
 * crosstab.C
 * Program reads two asci files from sas2 output procedure and produces
 * a confusion matrix for 1000 different cutlevels and the error measures
 * prevalence,sensitivity, specificity, FP, FN, misclassification rate, correct classification rate
 * Odds Ratio, Kappa and NMI for each of the cutlevels. Output can be used for ROC-plots.
 * AUC is also calculated as an approximation
 * The names of the forelands are in foreland.txt and the name of the species in forelandcodelis.txt
 *
*/

#include <stdio.h>
#include <stdlib.h>
#include <math.h>
#include <string.h>

#define N 2600  //maximal number of cells in the datablock caters for(42*60)

struct errors                   //this structure will contain sensitivity and 1-specificity values for auc
{
        double sensity;
        double invspec;
};
struct species                  //this structure will contain the speciesnames (up to 20 characters per name)
{
        char str[20];
};
struct forcode                  //this structure will contain the foreland codes (up to 20 characters per name)
{
        char str[20];
};


void main ()
{

int  i,j,s,t,u,k,l,m,n;
int model[27] =
{131,132,135,141,142,145,151,152,155,231,232,235,241,242,245,251,252,255,331,332,335,341,342,34
5,351,352,355};
double  x1array[N],x2array[N],x3array[N];
double prev,sens,spec,fpos,fneg,miscl,corcl,oddr,kappa,nmi,ad,bd,cd,dd,nd,cut,auctemp,auc,x;
float var1;
char path1[100] = """E:\\thesis\\sas2\\""";
char path2[10];
char path3[5]= ".txt";
char path4[5]= ".out";
```

```
char pathall1[150];
char pathall2[150];
char pathlist1[100] = """E:\\thesis\\sas2\\code\\""";
char pathlist2[10] = """lis.txt""";
char pathlist3[110];
char pathout1[100] = """E:\\thesis\\sas2\\""";
char pathout2[100] = "auc2.out";   // contains the area under the curve values
char pathout3[100] = "modcros2.out";        // contains the error estimations
char pathoutall1[150];
char pathoutall2[150];
struct errors trigon[1000];          // max 100 members of the structure contain trigonometric values
struct species specname[12];                 // max 12 species at the moment
struct forcode forelands[30];                // max 30 forelands at the moment
char buffer[20];                             // for conversion of the int model value


FILE *fp1,*fp2,*outp,*outp2,*speclist, *forlist;



//filling the structure with the foreland codes !! use forland.txt for selective processing of forelands
//and forelandall.txt to process all forelands.


if ((forlist = fopen ("""E:\\thesis\\sas2\\code\\foreland.txt""", "r")) == NULL)
        {
        printf (" File could not be opened! \n\n");
        exit(1);
        }
j=0;

        while (!feof(forlist))
                {
                        fscanf(forlist,"%s",forelands[j].str);
                         j++;
                }
n= j-1;  // number of forelands to be processed
// end reading the foreland list



        for (m= 0; m < n ; m++)  // start of the loop over forelands
{


                strcpy(path2,forelands[m].str);      // put the foreland code into path2

                printf("\n Working on foreland %s!\n" ,path2);


                //filling the structure with the speciesnames

                strcpy(pathlist3,pathlist1);
                strcat(pathlist3,path2);
                strcat(pathlist3,pathlist2);


                if ((speclist = fopen (pathlist3, "r")) == NULL)
```

```
                {
                printf (" File could not be opened! \n\n");
                exit(1);
                }
j=0;

                while (!feof(speclist))
                {
                        fscanf(speclist,"%s",specname[j].str);
                         j++;
                }
l= j-1;   // number of species in the species list
// end reading the specieslist



        strcpy(pathoutall1,pathout1);
        strcpy(pathoutall2,pathoutall1);
        strcat(pathoutall1,path2);
        strcat(pathoutall1,"\\");
        strcat(pathoutall1,pathout2);
        strcat(pathoutall2,path2);
        strcat(pathoutall2,"\\");
        strcat(pathoutall2,pathout3);

//opening the AUC file to contain all the AUC values and writing column headers

        if ((outp2 = fopen (pathoutall1, "a+")) == NULL)
                {
                        printf (" File could not be opened! \n\n");
                        exit(1);
                }
                fprintf(outp2, "Model      AUC\n");

// end opening the AUC file

// opening the cutlevel file for all error measures

        if ((outp = fopen (pathoutall2,  "a+")) == NULL)
                {
                        printf (" File could not be opened! \n\n");
                        exit(1);
                }
                fprintf(outp, "Cutlevel    Prev     Sens     Spec     1-Spec  FP       FN       Miscl
        Corcl    Oddr     Kappa   NMI\n");

// end opening the cutlevel file

auctemp=0;
auc=0;

for (t=0; t<l;t++)
{                       //start of the loop over the j species (from counter j reading speclist)
                printf("\n Species %s!" ,specname[t].str);
        for (u=0; u<27;u++)
        {               //start the loop over the 27 models
```

```
                fprintf(outp, "Model %s%d
                                \n",specname[t].str.model[u]);

// concatenating the path information

        _itoa( model[u], buffer, 10 );

        strcpy(pathall1,path1);
        strcat(pathall1,path2);
        strcat(pathall1,"\\");
        strcpy(pathall2,pathall1);
        strncat(pathall1 +18, specname[t].str, 1);
        strncat(pathall1 +19, specname[t].str + 3,1);
        strcat(pathall1, "mod");
        strcat(pathall1, buffer);
        strcat(pathall1, path3);
        strcat(pathall2, specname[t].str);
        strcat(pathall2, path3);


 // reading the probability data into 1 dimensional array

 if ((fp1 = fopen ( pathall1 , "r")) == NULL)
        {
        printf (" File could not be opened! \n\n");
        exit(1);
        }
j=0;

                while (!feof(fp1))
                {
                        fscanf(fp1,"%f",&var1);
                        x1array[j]=(double)var1;
                        j++;
                }

fclose(fp1);
j=0;

// reading the presence/absence data into 1 dimensional array

if ((fp2 = fopen ( pathall2 , "r")) == NULL)
        {
        printf (" File could not be opened! \n\n");
        exit(1);
        }
j=0;
s=-1;

                while (!feof(fp2))
                {
                        fscanf(fp2,"%f",&var1);
                        x2array[j]=(double)var1;
                        j++;
                        s++;
                }
```

```
fclose(fp2);
j=0;
x=0.0;
k=0;

for (cut=0.001; cut<1; cut=cut+0.001)          //running through the cutlevels and computing
{                                                                                    //the stats for all
cutlevels

        ad =bd =cd =dd = 0.0;

        for (i=0; i<s;i++)
        {
                if (x1array[i]<= cut)
                        x3array[i]=0.0;
                else
                        x3array[i]=1.0;

                if (x2array[i] == 0.0 && x3array[i] == 0.0)
                        dd=dd+1.0;
                if (x2array[i] == 0.0 && x3array[i] == 1.0)
                        bd=bd+1.0;
                if (x2array[i] == 1.0 && x3array[i] == 0.0)
                        cd=cd+1.0;
                if (x2array[i] == 1.0 && x3array[i] == 1.0)
                        ad=ad+1.0;
        }

        nd = ad+bd+cd+dd;

        j=0;
        i=0;


                        if ((nd) !=0.0)
                                prev = (ad+cd)/nd;
                        else
                                prev = 999.0;
                        if ((ad+cd) !=0.0)
                                sens = ad/(ad+cd);
                        else
                                sens = 999.0;
                        if ((bd + dd) != 0.0)
                                spec = dd/(bd+dd);
                        else
                                spec = 999.0;
                        if ((bd+ad) !=0.0)
                                fpos = bd/(bd+ad);
                        else
                                fpos = 999.0;
                        if ((cd+dd) !=0.0)
                                fneg = cd/(cd+dd);
                        else
                                fneg = 999.0;
                        if (nd !=0.0)
```

```
                        {
                                miscl = (bd+cd)/(nd);
                                corcl = (ad+dd)/(nd);
                        }
                        else
                        {
                                miscl = 999.0;
                                corcl = 999.0;
                        }
                        if (cd != 0.0 && bd != 0.0)
                                oddr = (ad*dd)/(cd*bd);
                        else
                                oddr = 999.0;
                        if ((nd-(((ad+cd)*(ad+bd)+(bd+dd)*(cd+dd))/nd)) != 0.0)
                                kappa = ((ad+dd)-(((ad+cd)*(ad+bd)+(bd+dd)*(cd+dd))/nd))/(nd-
(((ad+cd)*(ad+bd)+(bd+dd)*(cd+dd))/nd));
                        else
                                kappa = 999.0;
                        if (ad !=0.0 && bd !=0.0 && cd !=0.0 && dd!=0.0 && (nd*log(nd)-
((ad+cd)*log(ad+cd)+(bd+dd)*log(bd+dd))) !=0.0)
                                nmi = (-ad*log(ad)-bd*log(bd)-cd*log(cd)-
dd*log(dd)+(ad+bd)*log(ad+bd)+(cd+dd)*log(cd+dd))/(nd*log(nd)-
((ad+cd)*log(ad+cd)+(bd+dd)*log(bd+dd)));
                        else
                                nmi = 999.0;
// store 1-specificity and sensitivity values in structure

                                (trigon[k].invspec) = (1.0-spec);
                                (trigon[k].sensity) = sens;
                                k++;


        if (x == 9.0)       //writing every 10th cutlevel into outputfile
        {
//                      printf("\n cut == x is %d",(cut==x));
                        fprintf(outp, "%8.4f       %8.5f   %8.5f   %8.5f   %8.5f   %8.5f   %8.5f   %8.5f
        %8.5f   %8.5f   %8.5f   %8.5f\n",cut,prev,sens,spec,1-
spec,fpos,fneg,miscl,corcl,oddr,kappa,nmi);
                        x=-1.0;
        }
        x=x++;
//      printf("\n cut == x is %d",(cut==x));
}

for (k=998; k>= 0; k--)     //calculate the AUC
{
        if (k==998)
        {
                auctemp = (trigon[k].invspec*trigon[k].sensity)/2;
                auc = auc + auctemp;
        }
        else
        {
                auctemp = (((trigon[k].invspec)-
(trigon[k+1].invspec))*(trigon[k+1].sensity))+(((trigon[k].invspec)-
(trigon[k+1].invspec))*((trigon[k].sensity)-(trigon[k+1].sensity))/2);
```

```
                auc = auc + auctemp;
        }
}
        k=-1;
        auctemp = ((1-(trigon[k+1].invspec))*(trigon[k+1].sensity))+((1-(trigon[k+1].invspec))*(1-
(trigon[k+1].sensity))/2);
        auc = auc + auctemp;

        fprintf(outp2, "%s%d      %8.5f\n",specname[t].str,model[u],auc);

        // printf("\n The area under curve for %s%d is %8.5f !\n\n", specname[t].str,model[u],auc);
        auc=0;
}               // end of the for loop over the 27 models
}               // end of the for loop over the j species
fclose(outp);
fclose(outp2);
}               // end of loop over the n forelands
}
```