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THE UNIVERSITY OF ALBERTA

A STUDY OF SPATIAL PATTERN AND ITS DETERMINANTS AMONGST THE SPECIES OF A SAXICOLOUS LICHEN COMMUNITY AT JONAS ROCKSLIDE, JASPER NATIONAL PARK, ALBERTA.

BY

ELIZABETH ANNE JOHN

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
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Mark R.T. Dale

Mark R. T. Dale

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Date: 6 December 1988

Philosophy, like lichens,

takes centuries to grow

and is always ignored in the Book of Instructions.

Elizabeth Smart.

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate studies and Research for acceptance, a thesis entitled A STUDY OF SPATIAL PATTERN AND ITS DETERMINANTS AMONGST THE SPECIES OF A SAXICOLOUS LICHEN COMMUNITY AT JONAS ROCKSLIDE, JASPER NATIONAL PARK, ALBERTA submited by Elizabeth Anne John in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

(supervisor)

Dale H. Vitt

Walter Moser

Date: September 29 1988

ABSTRACT

The spatial patterning of saxicolous lichens is studied at Jonas Rockslide in the Rocky Mountains at Jasper National Park, Alberta, Canada. The rockslide is composed of quartzite sandstone blocks, ranges in altitude from 1500m to 22[illegible]m and is 3km in length and 1km wide. The sizes of the largest Rhizocarpon (sub-genus Rhizocarpon) thalli lead to the hypothesis that it is over 500 years old. Single rockfaces are sampled on altitudinal transects. Each rockface is sampled with a grid of points, retaining positional information, and the species of lichen present at each point is recorded. Environmental information such as aspect, altitude and slope of the rockface is also recorded at each rockface.

One hundred and six species of saxicolous lichens are recorded at this site, of which 21 have a cover value greater than 1%. An analysis using the within rockface positional information shows that a number of species are not randomly distributed over the rock surface. Some species are more often found on the upper and outer parts of the rockface, whereas others are more often on the lower and inner portions. These non-random distributions are hypothesised to reflect microenvironmental differences across a rockface and this is supported by the available microclimatic evidence.

A canonical correpondence analysis, CANOCO, is used to investigate the correlation of environmental factors such as slope of the rockface and altitude of the rockface with lichen distributions over whole rockfaces divided into sections. The variables slope, altitude and insolation received are important correlates of lichen distributions overall, however, the lichens cannot be readily delimited into discrete groups.

Biotic interactions are investigated in a series of association analyses and thallus size data is used to investigate dynamic processes amongst the species present. The large number of small thalli indicates that this is a dynamic community with recruitment occurring into lichen populations. Associations between species reflect shared microhabitat requirements.

The genus Rhizocarpon is represented by twelve species at this site and raises the question of how so many apparently similar species can co-exist. Each Rhizocarpon species is found to occupy a different position in the complex of environmental gradients and thus competition between the members of this genus is likely to be small.

The study reveals a complex and dynamic community of saxicolous lichens.

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I. INTRODUCTION

Pattern and Process in Plant Communities

The study of the ecology of plant communities has been dominated by the search for pattern in the spatial and temporal arrangement of the individual organisms comprising a community. A knowledge of pattern is the first step towards an understanding of the organising processes in a community, the elucidation of which is the ultimate goal of most community ecologists. Pattern arises as a result of processes occurring in the community and thus contains clues as to what those processes might be. However the detection of pattern is not always easy and ecologists have devoted much effort to finding statistically sound methods of determining whether species are randomly distributed, and if not, the form of their non-random distribution and whether it can be related to any underlying environmental gradients.

Once an understanding of pattern is gained, the ecologist has next to consider what processes may have led to that pattern. There are numerous plausible hypotheses to explain the existence of a particular pattern, and choice between them requires manipulative experimentation enabling falsification of incorrect hypotheses (see Bender *et*. *al*. 1984). This is perhaps the most difficult step in community ecology because of the difficulty of designing replicable experiments that have relevance to the situation in an undisturbed community. Occasionally 'natural experiments' occur, but these have inherent problems due to their lack of replicability and uncontrolled conditions.

In addition, in communities of long-lived organisms, there is an historical problem in understanding observed pattern, in that pattern is a result of past processes. The processes producing a currently observed pattern may no longer be acting (Bender *et*. *al*. 1984).

As a community is composed of individual organisms, any organising process affecting the distributions of species within the community must act at the level of the individual organism. Although this seems intuitive, it is only in the last three decades that this idea has been reflected in the sampling techniques and experiments of many plant community ecologists. Much ecological work has relied on the quadrat as the sampling unit, and assumed that all species occurring together in the same quadrat share the same 'position' in the community. However, plant distributions may be correlated with minutely separated microhabitats, many of which may occur in one quadrat, so that although a number of species may share a quadrat, they may all be there for different reasons. The extent of this problem will obviously depend on the scale of the quadrat: point sampling can be regarded as the ultimate in quadrat reduction, such that only one plant can be sampled. Some recent work has used $2cm^2$ quadrats to overcome some of the difficulties inherent in larger quadrats (Mahdi & Law 1987).

Quadrat sampling may be particularly misleading when considering associations between species as evidence of biological interactions. As sessile organisms, plants only encounter their immediate neighbours, and interactions between individuals are restricted to those cases where they are close enough to touch or overtop one another (or possibly for chemical diffusion in cases where allelopathy occurs). Thus two species may always occur together in the same quadrat, yet never interact. Alternatives to quadrat sampling include point sampling, nearest neighbour and plant centered sampling techniques, which allow the assessment of the position of individual organisms within the community, and an assessment of 'neighbours' with which an individual may be interacting (Turkington & Harper 1979, Turkington _et_. _al_ 1977, Mahdi & Law 1987, Yarranton 1966).

Two species may tend to occur together significantly often because they share microhabitat requirements, or because one species provides a resource neccessary for the other (_e_._g_. fixed nitrogen), or because they have evolved the ability to coexist without detrimental competitive interactions (competitive combining ability (Aarssen 1983)). Two species may 'avoid' one another because they have different microhabitat requirements or because they are unable to coexist because of competitive interactions. Associations between species may be due to 'influence' of one species on another or due to 'ecological coincidence' because microhabitats are shared.

Processes are the ultimate factors controlling species distributions, and therefore organising a community. When considering details, there are probably as many processes by which a plant community could be organised as there are species in the community, however, it is worth briefly discussing some of the major kinds of processes that could dominate in a community as a whole. The triangular model of Grime (1979), although originally conceived for discussion of individual species strategies, can usefully be applied to community processes. The model proposes a three-way spectrum of plant strategies, with competitors, stress-tolerators and ruderals as the three extremes.

Much discussion has centered around the importance of competition as an organising force in plant communities (e.g. Watson 1980, Wilson & Keddy 1986, Fowler & Antonovics 1981, Werner 1979), and it is likely that in some communities it is of great importance, with many species restricted in their distributions due to their varying abilities to compete along an environmental gradient. This would be the case in situations where abiotic conditions were suitable for the rapid growth of a number of species. Observed (realised) niches of most species are probably small in comparison to fundamental niches and some species may be eliminated from the community. In such communities biotic interactions are important organising factors. Assessment of the role of competition in a community involves removal of species, and observation of the effects of removal on the niche space occupied by neighbouring species. This has been done in a number of communities, (e.g. Wilson & Keddy 1986, Bertness & Ellison 1987, Fowler 1981) and competition shown to be a determinate of species distributions to varying degrees.

In some environments the effects of the abiotic environment may be more important than biotic interactions. This would occur in situations where the environment is unsuitable for rapid growth of any species, and abiotic stresses are more important than competition induced stresses in ranking species along environmental gradients. There is probably little interaction between the species of the community. Observed niches are likely to be close to potential niches in that community. Alpert (1985) studied a community of saxicolous mosses believed to be of this nature. In such a community removal of species would have little effect on the niche space occupied by other species.

Finally, disturbance may occur frequently and unpredictably such that equilibrium in the community is never reached and a community dominated by ruderals will persist. The community is 'organised' by stochastic processes.

A Suitable Community for the Study of Pattern

One problem with the detection of pattern, let alone the understanding of processes, is the complexity of temporal and spatial arrangements of most communities. Species may interact at a range of vertical levels, from root to shoot, and may have different phenological patterns, making the assessment of interactons complex, and neccessitating a study in many dimensions! Thus, it is not surprising that some of the most detailed studies of pattern and interactions in communities have been done on structurally relatively simple communities, such as short grass meadows (Turkington & Harper 1979, Turkington et. al. 1977), and other grasslands (Mahdi & Law 1987, Fowler & Antonovics 1981), marine intertidal communities of sessile organisms (Sebens 1986)and lichen and bryophyte communities (Oksanen 1984, Yarranton 1966, Alpert 1985).

The community studied here is composed of saxicolous plants, mostly lichens. Forty-five per cent of the rock is colonised by crustose lichens, which have simple, essentially two-dimensional thalli, inseparable from the substrate. Contacts between crustose lichens are easily visible at the rock surface. A few of the crustose lichens are endolithic; their hyphae and algae live within the rock, but are restricted to within a few millimetres of the rock surface. Approximately 25% of the rock surface is covered by foliose lichens which have a lower cortex and are able to grow over other lichens. However, all the forms present at this exposed site are highly adpressed and rarely project more than a few millimetres above the rock surface. The community is essentially two-dimensional and can be easily sampled. The nature and number of plant-plant contacts can be readily assessed, and the community is suitable for using a grid sampling system.

However there are a number of drawbacks to the study of pattern amongst saxicolous lichens. Among crustose lichens the variation in form is slight, and many species are very difficult to tell apart without first dissecting apothecia or applying chemicals to the thallus. In a less detailed study the collection of voucher specime s may overcome this difficulty but when it is necessary to identify every sampled thallus, special techniques must be adopted. A related difficulty is the complexity of lichen taxonomy, and a lack of clarity as to the delimitation of species and genera, although recent advances in lichen taxonomy are rapidly improving this situation (Egan 1987). It is of great importance to the ecologist to be able to distinguish species from ecotypes, but this distinction has often been blurred by taxonomists working on herbarium material (Weber 1966). Lichens are difficult to cultivate, and this adds to the difficulties of delimiting species.

A recent study has suggested another complicating factor in the study of lichens at an individual level. Larson and Carey (1987) have found evidence indicating that an individual lichen may consist of a number of genotypes. This is probably due to the complexities of fungal genetics and possibly the lichen growth form which may allow a single thallus to be composed of more than one individual.

Another problem in the use of saxicolous lichens for ecological studies, especially in a relatively harsh subalpine environment, is their extremely slow growth rates. This makes them relatively unsuitable for manipulative studies, within the community, and restricts the study to one of pattern, in which only hypotheses can be formed about organising processes, at least in the short term.

A conceptual difficulty in dealing with a slow growing plant community is that of the time scale. The slow growth rate and small size of saxicolous lichens lead one to think of them as 'stress tolerators' in the terminology of Grime (1979), that is, slow growing, non-competitive species. In fact Grime uses lichens as an example of a stress tolerating group. However within any lichen community there is almost certainly a range of strategies, with the initial colonisers behaving like ruderals, and more competitive species supplanting them as a dense mosaic of lichens builds up. The success of a species as a competitor depends largely on the plants with which it is competing.

Previous Studies on Saxicolous Lichen Communities

Most work on saxicolous lichens has dealt with descriptive aspects of their ecology, both qualitatively (Creveld 1981) and quantitatively (e.g. Armstrong 1974, Pentecost 1979, Larson 1980, Yarranton & Green 1966). Lichen distributions have been correlated with variables of the rock surfaces on which they are growing such as slope, aspect, depth of snow cover, altitude, substrate type, microtopography and age of surface. The correlations have been thought to be due to the effects of these variables in determining the microenvironment at the rock surface, particularly with respect to substrate chemistry, water availability and temperature, and the importance of these variables in lichen ecophysiology. Occasionally competition between lichens has been cited as a factor affecting lichen distributions (Lawrey 1981, Yarranton & Green 1966). While some workers have commented on the apparent broadness of lichen distributions with respect to microenvironmental variables (Armstrong 1974, Pentecost 1979), others have observed distinct microhabitat specificity (Creveld 1981). Most studies have used quadrats to sample these communities, point sampling has occassionally been used (Yarranton 1966).

The Saxicolous Environment

The saxicolous environment is dominated by boundary layer conditions (Kershaw 1983) and this is particularly true in an exposed environment. Temperatures can fluctuate greatly as rocks absorb and re-radiate heat sometimes leading to dramatic & rapid freeze-thaw cycles in certain conditions (McKay & Friedman 1985). The temperature gradient above a rockface can be very steep, with surface temperatures differing dramatically from air temperatures, and even a distance of a few millimetres making a large difference (see, for instance, Coxson & Kershaw 1983a). Unless the rock has water holding capacities, drying will occur very rapidly after precipitation in sunny conditions, leading to large fluctuations in water availability at the rock surface. In winter, radiation may penetrate snow, warming the rock beneath and creating melt pockets (Larson & Kershaw 1974).

The rate of reception and retention of precipitation, whether snow or rain, and the amount of radiation received by a rockface will depend on the slope and aspect of the rocksurface, and so could vary greatly at one site. A single rock surface is not a uniform environment, and as shown by the work of Coxson & Kershaw (1983a), it is quite possible that lichens on sheltered parts of a rockface may have surface temperatures 13°C above those cooled by a light breeze.

Lichen Ecophysiology

Due to their small size, intimate substrate contact in boundary layer conditions, and lack of active regulatory mechanisms for the control of temperature or water, it might be expected that lichens would show extreme microhabitat specificity. Some of the earliest work dealing with lichen ecophysiology lead to the conclusion that lichens have broad ecological tolerances, especially with respect to temperature. Using respiratory rates as an indicator it was shown that lichens could be subject to severe stresses of temperatures as high as 100°C yet not appear to be damaged (Kappen 1973). However, more recent work using photosynthetic rates has not supported these findings (McFarlane & Kershaw 1984). The difference is thought to be due to the differences between the fungal and algal partners involved in the lichen symbiosis; the fungus is responsible for most of the respiration and is less sensitive to heat stress than the alga.

There is now a growing body of evidence indicating that lichens are highly adapted to specific environments (Kershaw 1985). Some lichens are damaged at temperatures as low as 25°C while others show little stress at temperatures of 45°C. Differences can usually be correlated with the normal microenvironment of the lichen in question. Two saxicolous examples are Rhizocarpon superficiale which lives on the edges of rockfaces unlikely to reach high temperatures and is intolerant of temperatures of 45°C (Coxson & Kershaw 1983b) and Melanelia granulosa (studied under the name Parmelia disjuncta) which grows on parts of rockfaces that are likely to reach higher temperatures and is not damaged at this temperature (Kershaw & Watson 1983). Both these species are present at Jonas Rockslide.

Some lichens have been found to show seasonal adaptations to their light and temperature regimes (Kershaw 1985), indicating that for these species phenotypic flexibility is very important in their ecological adaptation.

It is likely that early and late winter conditions will be important in saxicolous lichen ecology. The combination of sunshine and snow melt provide conditions for photosynthesis that may not be available at other times of the year when rocks dry out rapidly after rain. Many lichen species are able to photosynthesize at appropriate temperatures for this to be the case (0°C to 10°C).

Lichen colour has been widely discussed as a means of ecological adaptation (Gaussla 1986, Kershaw 1974, Thomson 1982). Saxicolous lichens can differ widely in colour and there is no doubt that this in itself is a factor altering microclimatic conditions. There is an inexact correlation between a lichens colour and its reflectivity (Gaussla 1986). Darker lichens are likely to absorb more radiation and have higher thallus temperatures in a high radiation environment and in some circumstances this may allow them to photosynthesize at substrate temperatures that are otherwise too cold. On the other hand, paler, more reflective thalli, are less likely to suffer summer heat stress. It has also been suggested that pale thalli, by reflecting radiation, remain cooler than their substrate, and enhance their water balance by acting as a substrate for condensation (Gaussla 1986).

Community Diversity

A perennial problem addressed by plant community ecologists is how to explain the persistent diversity of species in many plant communities (*e.g.* Grubb 1977, Werner 1979, Watson 1983). In theory, competition should eliminate species whose niches are not sufficiently different. This problem can be applied to the situation at Jonas Rockslide where over one hundred saxicolous lichen species coexist, in an environment that provides very little structural diversity (consisting mostly of planar surfaces), and in a community where the plants themselves provide little in the way of structural or phenological diversity. There are a number of hypotheses that could account for the lack of competitive exclusion at this site:

1. The microenvironment is highly diverse and each species has a sufficiently distinct ecological niche during its adult phase that they are not in direct competition.

2. Although niches of established thalli may overlap considerably, there is sufficient differentiation during the establishment phase of the lichen life cycle for competitive exclusion to be avoided.

3. Continuous cyclic successional processes, due, at least in part, to senescence patterns, maintain species diversity at the site (Watt 1947).

4. Interspecific competition is not important because:

   a) the environment is too stressful

   b) equilibrium has not yet been reached in this community because of the slow growth rates of the species involved, and in the future competitive exclusion may occur if the site remains undisturbed.

Given the microhabitat specificity of lichens discussed above, and the extreme environment of the rockslide, one might expect a good deal of niche separation among species at this site. Very little is known of the importance of the regeneration stage in lichen ecology, indeed, even the mechanisms of regeneration are only just being understood. This is especially true for those species that reproduce via ascospores, entailing the necessity of recombining with an alga (Ott 1987). Many saxicolous species apparently reproduce only by ascospores. Very little work has been done on the colonisation of rock surfaces, however Armstrong (1981, 1978) studied the colonisation of a slate surface, and found that there were many propagules present in water run-off from lichen colonised surfaces, but that regeneration seemed highly dependent on minor details of surface topography, and that there seemed to be a shortage of suitable attachment sites for propagules. Some species were able to colonise more readily than others. This study implies a potentially important role of regeneration in saxicolous lichen ecology.

The process of colonisation has been studied indirectly by investigating whole populations of thalli and using thallus size as a measure of age. (That there is a direct correlation between thallus size and age is a somewhat questionable assumption, see Chapter 6). These studies indicate that recruitment into lichen populations occurs at varying rates and may depend on the successional stage of the community.

Competition does undoubtedly occur amongst saxicolous lichens in some situations. It has been demonstrated experimentally among some foliose species (Armstrong 1986, 1982). These experiments indicated that competition could be a mechanism for change in the species composition of a community, but also showed that the outcome of competition among species growing in a mixture cannot be easily predicted as a strong competitor in a two species mixture was weaker in a three species mixture.

It is easy to imagine competition between foliose lichens or between foliose and crustose lichens, as foliose lichens are able to grow over the thallus of the other lichens. Competition has also been observed between crustose lichens, by both direct methods such as time-lapse photography (Hale 1956, Hawksworth & Chater 1982) and indirect methods such as observations at one point in time (Pentecost 1980). Competition between crusts similarly seems to involve the over-growth of other thalli or the preemption of space. As with other plants, access to space means access to resources and thus competitive success. For a crustose lichen competitive ability must involve rapid growth rate, the ability to prevent other lichens from colonising its own thallus, and the ability to successfully counteract any allelopathic chemicals released by other lichens. The release of chemicals by lichens is a relatively unexplored and potentially important aspect of their competitive interactions (Lawrey 1986).

Objectives of this study

The focus of this study is to investigate pattern in the spatial distributions of lichens at Jonas Rockslide, Jasper National Park, Alberta, and to relate the pattern, if found, to underlying environmental gradients. An assessment will be made of the role of various biotic and abiotic processes in organising the species of this community, while recognising that conclusions cannot be definite without community manipulation. Questions to be asked are:

1) How many species are present in this community, and what are they?

2) How are the species in this community organised spatially?

3) What dynamic processes are occurring among the species of this community and why isn't the community dominated by the apparently competitively superior foliose species?

4) How can so many species coexist without competitive exclusion occurring?

5) Is it possible to estimate the effects of competition in this community?

Their answers will contribute to our understanding of plant community processes in general. In addition, a detailed study of a diverse lichen community such as this will greatly contribute to our knowledge of the lichen flora of the Canadian Rocky Mountains.

Study Site

Description

The study site is a large rockslide in the Canadian Rocky Mountains. Jonas Rockslide is on Highway 93, 75km south of Jasper Townsite at $52^{o}26'$N, $117^{o}24'$W, in the Sunwapta river valley, on the west facing slope of Jonas Ridge (Figure 1.1). It is one of the largest rockslides in the Canadian Rocky Mountains, having dimensions of 3.5km length, 1km width and spanning from 1500m to 2200m in altitude (Cruden 1976). It is composed of two separate, but adjacent rockslides, thought to be of similar ages, one to the south of the other. The northern rockslide is the larger in area (although thought to be of less mass) (Bruce 1978), and when it fell, crossed to the opposite side of the valley, so that the Sunwapta river now runs through the lower part of the rockslide (Figure 1.2). The age of the rockslide has been suggested as 95 years by Bruce (1978) based on the lack of mention of the rockslide by explorers who passed through the Sunwapta River valley prior to 1893. Presumably, it was thought to have been of sufficient obstruction to travellers to have merited comment. However there are sufficient silty deposits at the rivers edge for an easily used animal track to be present, and if the explorers had taken this route they would not have been hindered by the rockslide. Lichenometric evidence, (presented in Chapter 3) suggests that the site is at least 500 years old and may be much older. In addition, the general level of species diversity (over 100 saxicolous lichen species) suggests a community much older than 95 years. An approximate age for the rockslide is important in understanding community processes. It is assumed that all the exposed rock surfaces have been exposed for the same length of time. This assumption is reasonable despite the fact that there would have been exposed rock surfaces before the rockface fell because the surface area to volume ratio of the failed mass that created the rockslide is very small, and therefore the chances of sampling a rockface that had been exposed prior to the rockslide are minute.

The rockslide is composed of one rock type, a honey-coloured quartzite sandstone. The rock is non-calcareous, except for a small portion of rocks that are occasionally flooded at the rivers edge which may have a thin silty calcareous deposit. The rock has split into large, angular boulders, and many of the exposed rockfaces are flat, having little microtopographic relief (Figures 1.2 & 1.3). An average boulder size is perhaps 2m x 2m x 1m. Individual rockfaces make ideal sampling surfaces, as they are so flat and factors such as slope and aspect are constant over the whole rockface. The rockslide debris presents rockfaces of a variety of aspects and slopes.

The rockslide is in the subalpine zone (Holland and Coen 1983), and has an average annual temperature of 0°C. Rainfall is 793mm annually, as measured at the Sunwapta Warden Station, 3km from the rockslide (Holland & Coen 1983). Tree cover at the site is low, approximately 20% over the rockslide as a whole; saxicolous lichens are the dominant plants.

Study Site Suitability

A number of factors make this site highly suitable for a study of pattern in a saxicolus lichen community:

1) The single rock type eliminates substrate diversity as a source of microhabitat complexity.

2) The flat rockfaces are suitable for grid sampling and variables such as aspect and slope are constant over the whole rocksurface.

3) The range of orientation of rockfaces allows the assessment of the importance of environmental factors such as slope and aspect in the ecology of saxicolous lichens.

4) The rockslide spans 700m altitude, allowing an assessment of the importance of altitude at one site.

5) Lichens are the dominant plants and the species diversity high.

6) The site is readily accessible for research.

7) It is in a National Park, and thus will be preserved for future studies. The rockslide itself is rarely visited by tourists, and is largely undisturbed. It is in a relatively unpolluted environment.

Bibliography

Aarssen, L. W. (1983) Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. American Naturalist, 122: 707-731.

Alpert, P. (1985) Distribution quantified by microtopography in an assemblage of saxicolous mosses. Vegetatio, 64: 131-139.

Armstrong, R. A. (1986) Competition between three lichen species using a factorial experimental design. New Phytologist, 104: 637-641.

Armstrong, R. A. (1982) Competition between three saxicolous species of Parmelia (lichens). New Phytologist, 90: 67-72.

Armstrong, R. A. (1981) Field experiments on the dispersal, establishment and colonisation of lichens on a slate rock surface. Environmental and Experimental Botany, 21: 115-120.

Armstrong, R. A. (1978) The colonisation of a slate rocksurface by a lichen. New Phytologist, 81: 85-88.

Armstrong, R. A. (1974) The descriptive ecology of saxicolous lichens in an area of south Merionethshire, Wales. Journal of Ecology, 62: 33-45.

Bender, E. A., Case, T. J. & Gilpin, M. E. (1984) Perturbation experiments in community ecology: theory and practice. Ecology, 65: 1-13.

Bertness, M. D. & Ellison, A. M. (1987) Determinants of pattern in a New England salt marsh plant community. Ecological Monographs, 57: 129-147.

Bruce, I. (1978) The Field estimation of shear strength on rock discontinuities. Ph.D. thesis, Department of Civil Engineering, University of Alberta.

Coxson, D. S. & Kershaw, K. A. (1983a) The ecology of Rhizocarpon superficiale. I. The rock surface boundary-layer microclimate. Canadian Journal of Botany, 61: 3009-3018.

Coxson, D. S. & Kershaw, K. A. (1983b) The ecology of Rhizocarpon superficiale. II. The seasonal response of net photosynthesis & respiration to temperature, moisture and light. Canadian Journal of Botany, 61: 3019-3030.

Creveld, M. (1981) Epilithic lichen communities in the alpine zone of southern Norway. Bibliotheca Lichenologica. J. Cramer. Fl.9490 Vaduz.

Cruden, D. M. (1976) Major rock slides in the Rockies. Canadian Geotechnical Journal, 13: 8-20.

Egan, R. S. (1987) A fifth checklist of the lichen-forming, lichenicolous & allied fungi of the continental United States and Canada. The Bryologist, 90: 77-173.

Fowler, N. (1981) Competition & coexistence in a North Carolina grassland. II. The effects of experimental removal of species. Journal of Ecology, 69: 843-854.

Fowler, N. & Antonovics, J. (1981) Competition & Coexistence in a North Carolina grassland. I. Patterns in undisturbed vegetation. Journal of Ecology, 69: 825-841.

Gauslaa, Y. (1984) Heat resistance and energy budget in different Scandinavian plants. Holarctic Ecology, 7: 1-78.

Grime, J. P. (1979) Plant Strategies and Vegetation Processes. John Wiley and Sons. Chichester, New York, Brisbane, Toronto.

Grubb, P. J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews, 52: 107-145.

Hale M. E., Jr. (1956) Studies on lichen growth rate and succession. Bulletin of the Torrey Botanical Club, 86: 126-129.

Harper, J. L. (1977) Population biology of plants. Academic Press, London, New York, San Fransisco.

Hawksworth, D. L. & Chater, A. O. (1979) Dynamism and equilibrium in a saxicolous lichen mosaic. Lichenologist, 11: 75-80.

Holland, W. D. & Coen, G. M. (1983) Ecological (Biophysical) land classification of Banff & Jasper National Parks. Volume II. Soil & vegetation resources. Alberta Institute of Pedology & Environment Canada.

Kappen, L. (1973) Response to extreme environments In "The Lichens" edited by V. Ahmadjian & M. E. Hale, Jr. pp 311-380. Academic Press, New York .

Kershaw, K. A. (1985) Physiological Ecology of Lichens. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Kershaw, K. A. (1983) The thermal operating-environment of a lichen. Lichenologist, 15: 191-207.

Kershaw, K. A. (1974) Studies on lichen-dominated systems. XII. The ecological significance of thallus colour. Canadian Journal of Botany, 53: 660-667.

Kershaw, K. A. & Watson, S. (1983) The control of seasonal rates of net photosynthesis by moisture, light and temperature in Parmelia disjuncta Erichs. The Bryologist, 86: 31-43.

Larson, D. W. (1980) Patterns of species distribution in an Umbilicaria dominated comuunity. Canadian Journal of Botany, 58: 1269-1279.

Larson, D. W. & Carey, C. K. (1987) Phenotypic variation within 'individual' lichen thalli. American Journal of Botany, 73: 214-223.

Larson, D. W. & Kershaw, K. A. (1975) Studies on lichen-dominated sytems XI. Lichen-heath and winter snow cover. Canadian Journal of Botany, 53: 621-626.

Lawrey, J. D. (1986) Biological role of lichen substances. The Bryologist, 89: 111-122.

Lawrey, J. D. (1981) Evidence for competitive release in simplified saxicolous lichen communities. American Journal of Botany, 68: 1066-1073.

Mahdi, A. & Law R. (1987) On the spatial organisation of plant species in a limestone grassland community. Journal of Ecology, 75: 459-476.

MacFarlane, J. D. & Kershaw, K. A. (1980) Physiological-environmental interactions in lichens. XI. Thermal stress and lichen ecology. New Phytologist, 84: 669-685.

McKay, C. P. & Friedmann, E. I. (1985) The cryptoendolithic microbial environment in the antarctic cold desert: temperature variations in nature. Polar Biology, 4: 19-25.

Oksanen, J. (1984) Interspecific contact and association in sand dune vegetation dominated by bryophytes and lichens. Annales Botanici Fennici, 21: 189-199.

Ott, S. (1987) Sexual reproduction & developmental adaptations in Xanthoria parietina. Nordic Journal of Botany, 7: 219-228.

Pentecost, A. (1980) Aspects of competition in saxicolous lichen communities. Lichenologist, 12: 135-144.

Pentecost, A. (1979) Aspect and slope preferences in a saxicolous lichen community. Lichenologist, 11: 81-83.

Sebens, K. P. (1986) Spatial relationships among encrusting marine organisms in the New England subtidal zone. Ecological Monographs, 56: 73-96.

Thomson, J. W. (1982) Lichen vegetation and ecological patterns in the high arctic. Journal of the Hattori Botanical Laboratory, 53: 361-364.

Turkington, R. A., Cavers, P. B. & Aarssen, L. W. (1977) Neighbour relationships in grass-legume communities. I. Interspecific contacts in four grassland communities near London, Ontario. Canadian Journal of Botany, 55: 2701-2711.

Turkington, R. & Harper, J. L. (1979) The growth, distribution and neighbour relationships of Trifolium repens in a permanent pasture. I. Ordination, pattern and contact. Journal of Ecology, 67: 201-218.

Watson, M. A. (1980) Patterns of habitat occupation in mosses - relevance to considerations of the niche. Bulletin of the Torrey Botanical Club, 107: 346-372.

Watt, A. S. (1947) Pattern and process in the plant community. Journal of Ecology, 35: 1-22.

Weber, W. A. (1962) Environmental modification and the taxonomy of crustose lichens. Svensk Botanisk Tidskrift, 56: 293-333.

Werner, P. A. (1979) Competition and coexistence of similar species. Chapter 12 in Topics in plant population biology. pp 287-312 Edited by Solbrig, O. T., Jain, S., Johnson, G. R., & Raven, P. H. Columbia University Press, New York

Wilson, S. D. & Keddy P. A. (1986) Species competitive ability & position along a natural stress/disturbance gradient. Ecology, 67: 1236-1242.

Yarranton, G. A. (1966) A plotless method of sampling vegetation. Journal of Ecology, 54: 229-237.

Yarranton, G. A. and Green, W. G. E. (1966) The distributional pattern of crustose lichens on limestone cliffs at Rattlesnake point, Ontario. The Bryologist, 69: 450-461.

Table 1.1: Definitions of words and concepts used in Chapter 1 and throughout the thesis.

Abiotic environmental factors: Those factors in the environment which are not determined by organisms or as a direct result of the effects of organisms.

Aspect: The compass direction towards which an object (rockface) faces.

Biotic environmental factors: Those factors in the environment arising from the effects of organisms.

Boundary layer conditions: The microclimatic conditions achieved at the surface/air boundary of an object (*e.g.* rock surface). Characterised by steep temperature and humidity gradients due to a thin layer of still air at the objects surface and the radiation absorption/re-radiation properties of the object.

Colonisation: Arrival & establishment of propagules on the rock surface.

Community: In this thesis the word community refers to the saxicolous lichens growing on the whole rockslide.

Competition: The interaction between two lichens (or other organisms) arising from the requirement of both for the same resource.

Ecophysiology: The interaction between a plant's physiology and its environment.

Individual: A single thallus. (N.B. A thallus may not represent a single genotype (Larson & Carey 1987)).

Interaction: An effect on one lichen caused by the presence of another. May be negative (*e.g.* competition) or positive (*e.g.* nutrient enhancement).

Microclimate: Local abiotic climatic factors, acting at a minutely differentiated scale. For instance, the microclimate one millimetre above the rocksurface may differ from that at the surface.

Microenvironment: As above, but also including the effects of biotic factors and edaphic factors such as substrate composition.

Microhabitat: Those specific microlocations where a particular organism lives.

Niche: Those parts of environmental gradients which are (= realised niche) or could be (= fundamental niche) occupied by a particular species. In a descriptive study such as this only realised niches can be assessed.

Niche separation: The difference between two species in their realised niches. In this context the phrase is not meant to imply a causative process.

Organisation: The arrangement of organisms with respect to space, time and each other arising from non-stochastic processes acting in the community.

Pattern: The arrangement of individuals in the community with respect to space, time and each other, that is to some extent predictable.

Population: All thalli belonging to a single species present at Jonas Rockslide.

Process: A causal agent in community organisation acting directly at the level of the individual organism (*e.g.* competition).

Recruitment: The establishment of new thalli in an existing population.

Stress: The effects on an organism of sub-optimal environmental conditions.

Slope: The inclination of a surface from the horizontal.

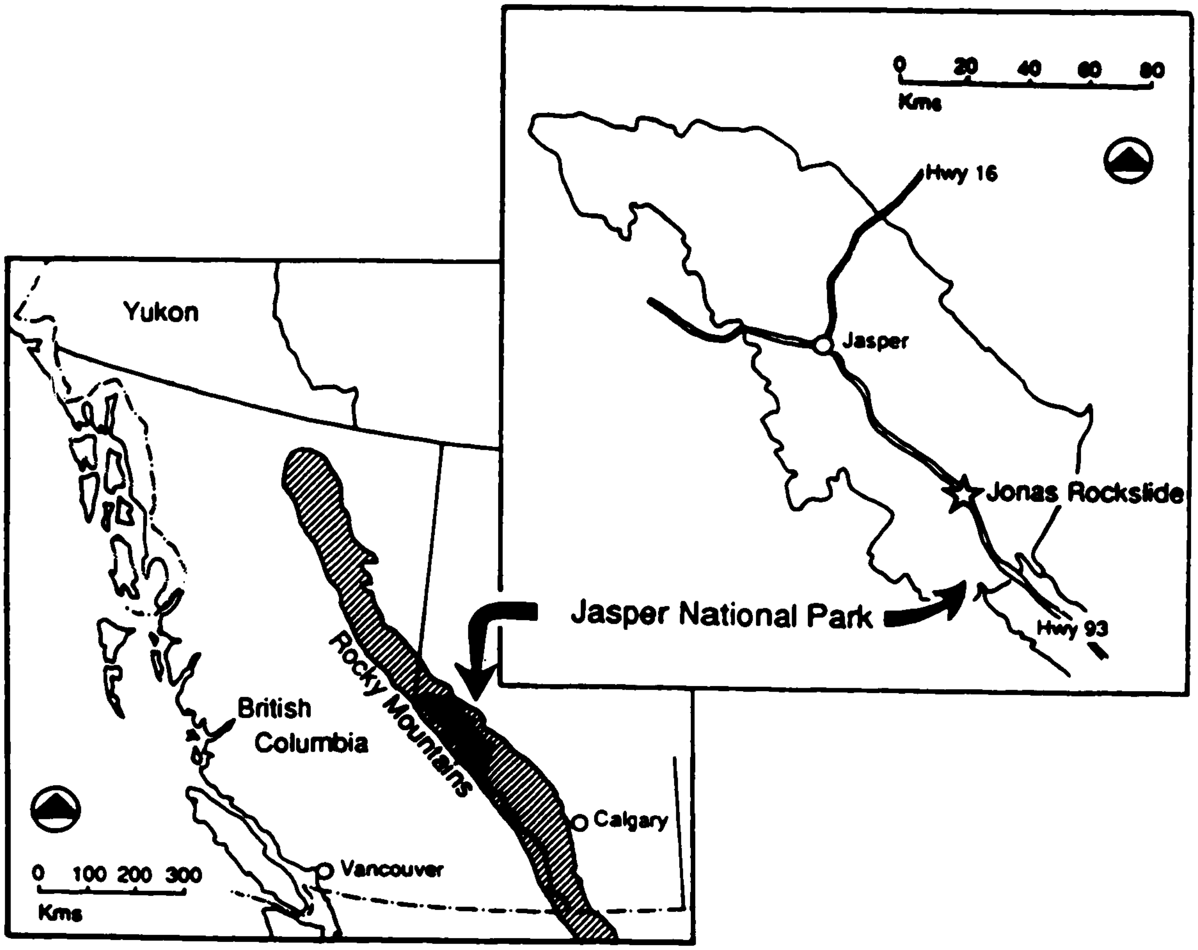

Figure 1.1: Location of Jonas Rockslide.

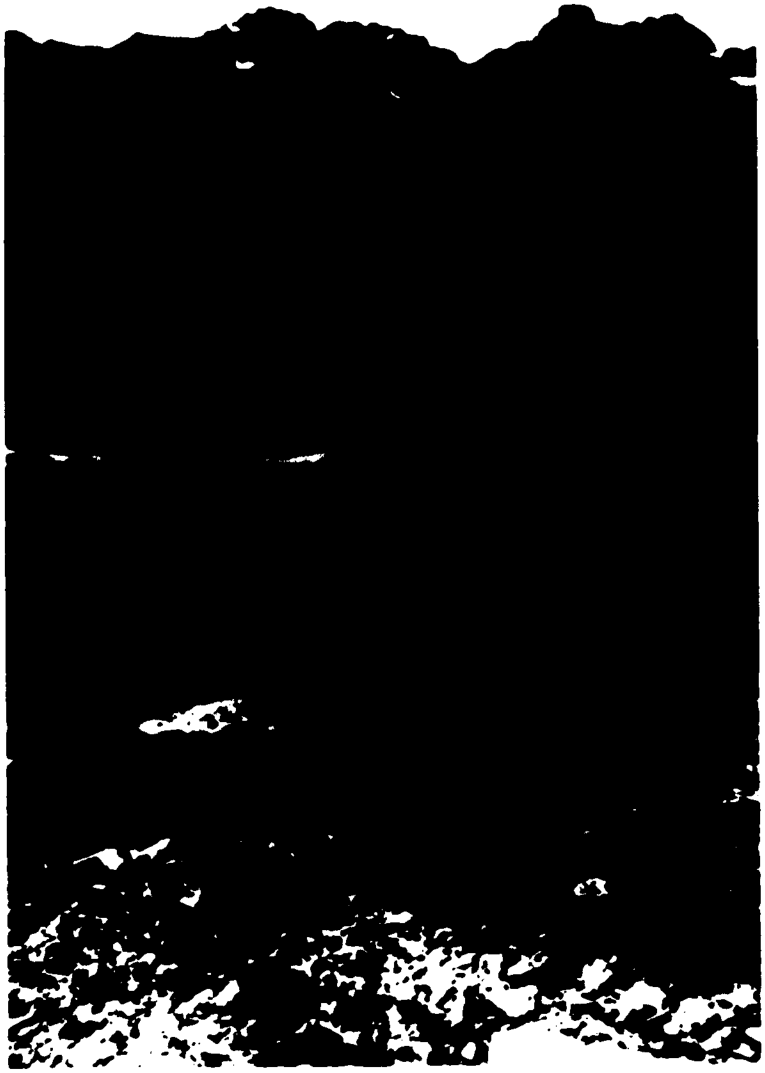

Figure 1.2: View of Jonas Rockslide looking down from Jonas Ridge to the Sunwapta River and Highway 93 below.

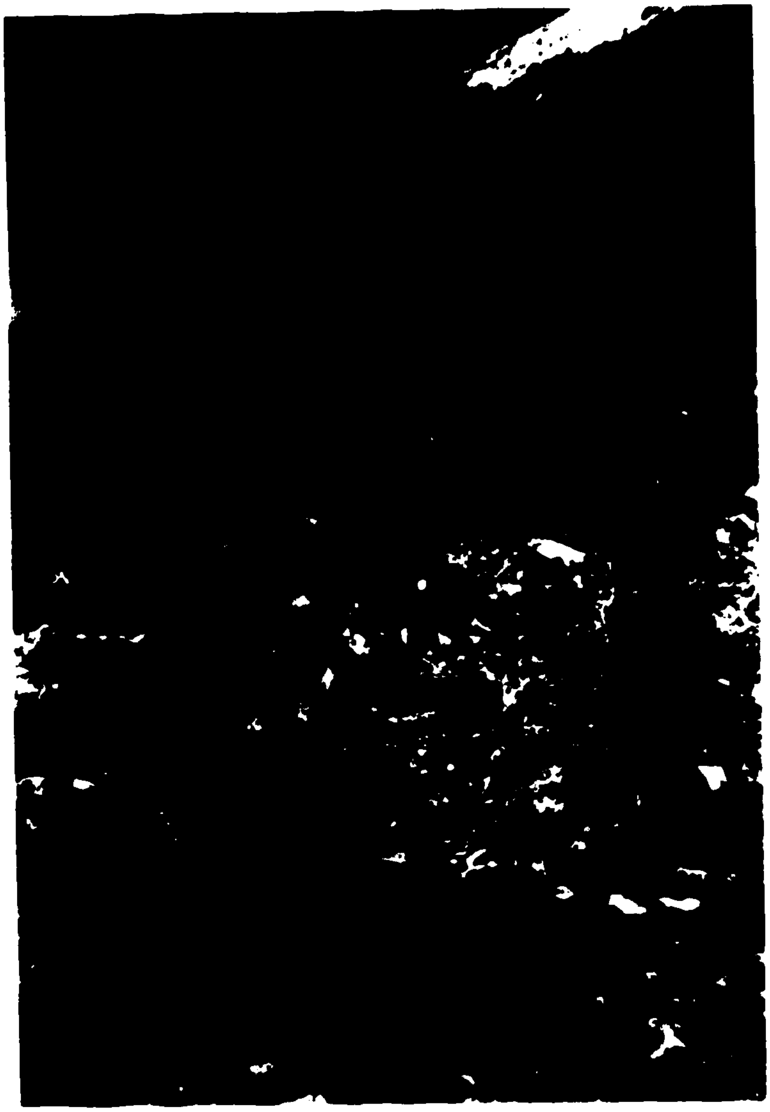

Figure 1.3: View across Jonas Rockslide looking north-east.

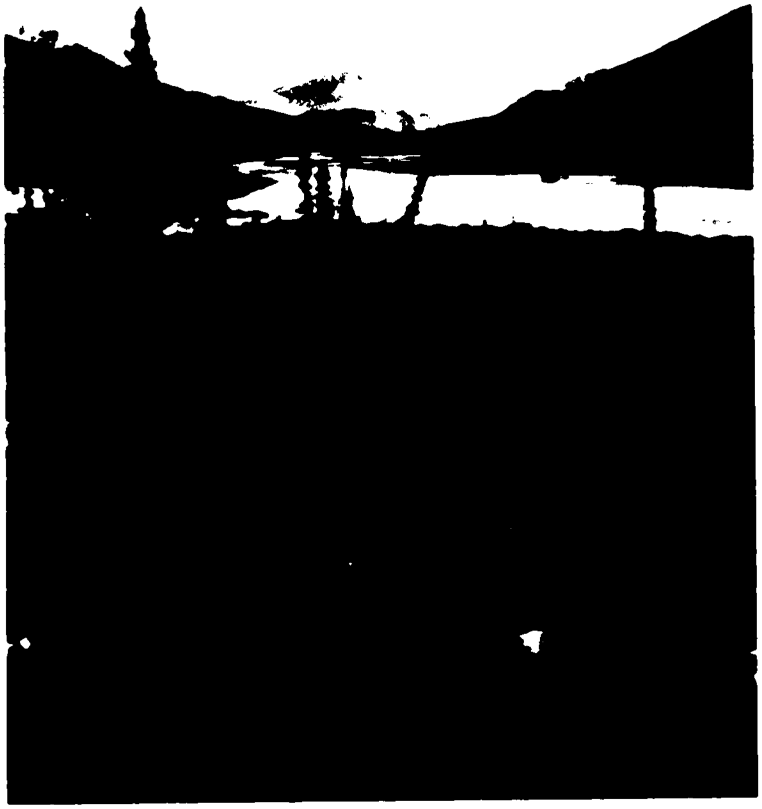

Figure 1.4: View from Jonas Rockslide at the Sunwapta River looking south.

II. THE SAXICOLOUS LICHEN FLORA OF JONAS ROCKSLIDE [1]

Introduction

The lichens discussed here were collected during a study investigating the spatial patterning of saxicolous lichens at Jonas Rockslide, Jasper National Park, Alberta. Although the initial interest of the study was in quantitative aspects of the ecology of this community, it soon became clear that the lichen flora is of interest in its own right, as a number of unusual species were recorded.

There is a surprising lack of published information concerning the lichen flora of the Canadian Rocky Mountains. The microlichens have been particularly little studied, and Jasper National Park less well studied than adjacent Banff National Park. Imshaug (1953) in his study of alpine macrolichens unfortunately did not reach as far north as Jasper National Park. See (1978) collected macrolichens in areas adjacent to Jasper National Park, as did Skorepa (Skorepa & Vitt 1976) who also collected microlichens. Bird (Bird & Marsh 1973a & b) collected extensively in Alberta, including the Rockies, but mainly in the southern parts.

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[1] A version of this chapter has been accepted for publication in THE BRYOLOGIST as John, E. A. The Saxicolous Lichen Flora of Jonas Rockslide, Jasper National Park, Alberta.

Many lichens were collected during the Biophysical Surveys of Banff and Jasper National Parks (Holland & Coen 1983), and although many new species were added to the lists for these areas, the collections were far from complete.

Jonas Rockslide was chosen for study because of its rich lichen flora and ease of access, however there are no previous collections known from this site. This is the only major rockslide of quartzite sandstone known from the Canadian Rockies (Cruden 1976), but as rocks of the Gog Quartzite group appear in many parts of the Eastern Main Ranges of the Canadian Rockies and also in the Purcell and Selkirk ranges to the West (Cook 1975), the lichen assemblage discussed here is likely to occur elsewhere.

It has long been recognised that lichens can be extremely sensitive to microclimate, and may have very specific microhabitat requirements. This is at least in part due to their small size, their intimate relationship with their substrate and relative lack of regulatory mechanisms for the control of water loss and temperature. It is likely to be particularly true of saxicolous lichens in an exposed habitat. The rock fluctuates greatly in temperature as it absorbs and loses radiant energy, and there is little opportunity for water retention by the substrate, so that large, rapid fluctuations in water regime also occur. The rockslide can be considered as a series of microhabitats, and the flora will be presented in this context.

Study Site and Methods

Study site

The rockslide is in the eastern main ranges of the Canadian Rocky Mountains, 75 kilometres south of Jasper, Alberta, on Highway 93, at 52° 24'N, 117° 24'W (Figure 1.1). It is on the eastern side of the Sunwapta River Valley and spans altitudinally from 1500m where it crosses the river to 2200m. It is approximately 1km wide. The rockslide is composed solely of quartzite sandstone, however at the river's edge the rocks may have a superficial calcareous silty deposit. The boulders of which the rockslide is composed are large, with an estimated average size of 2m x 1m x 1m, and the rock rubble is quite deep, in places extending to several metres.

The area receives an average of 793mm rain annually, and has a mean annual temperature of 0°C (Holland & Coen 1983). The age of the rockslide is not definitely known; there is no historical record of it before 1893 (Bruce 1978), but the sizes of lichen thalli at the site suggest that it is between 500 and 1000 years old. Tree cover is low on the rockslide; overall less than 20%, although in a few areas it is well developed. *Picea engelmannii* Parry is present on the lower slopes and *Pinus albicaulis* Englm. occurs on the upper slopes.

Methods

Only the saxicolous lichens, or those growing on moss over rock are discussed here; the list would be much longer if terricolous, corticolous and lignicolous lichens were included.

Percent cover estimates are available for some lichens; these cover values were obtained during quantitative sampling procedures (Chapter IV). Rockfaces were sampled using a grid of points, and the species of lichen at each grid point recorded. Lichens were identified using a dissecting microscope, and if neccessary spot test chemicals were applied by micropipette in the field, and apothecia were collected for later laboratory examination. Sampled rockfaces fulfilled the criteria that they be larger than 1m x 1m in area, of limited microtopographic relief, and not directly sheltered by other rockfaces or trees. Thus not all microhabitats at the site were sampled in this way, and although lichens were collected from microhabitats excluded by these criteria no cover estimates are available for these lichens. Voucher specimins were collected for all species reported in this chapter. These are deposited in ALTA, and a second set placed in CANL.

Results

One hundred and six species of saxicolous lichens or lichens growing on mosses over rock were found at Jonas Rockslide. These are listed in Table 2.1, as is the cover value for each lichen estimated from the grid sampling.

Overall lichen cover at the rockslide is 87%. Of this 47% is crustose, 15% foliose (excluding umbilicate), 9% umbilicate, 7% fruticose and 6% the filamentous lichen *Spilonema revertens*. Less than 1% of the sampled rock surfaces were occupied by moss. Because some thalli were sterile or otherwise unidentifiable, the figures in Table 2.1 do not add up to 87%.

Some general effects of the exposed habitat deserve mention. A darker colour of thallus and apothecia than is usually the case elsewhere is frequently observed. An example is Bellamerea alpina, which in less exposed habitats produces a white to pale grey thallus with brown apothecia. In exposed positions it often has a dark grey thallus and black apothecia. On the other hand a greater degree of pruinosity may be seen. At this site the areoles of Lecidea paupercula often have a thick white pruinose covering. Both these examples are possible adaptations to a high radiation environment, on the one hand to absorb at the cortex and on the other to reflect radiation that could possibly be damaging to the more sensitive algal cells beneath.

Another effect related to exposure is the erosion and depauperisation of thalli, particularly foliose forms. Older parts of thalli may be eroded by abrasive wind action, leaving small patches of young lobes which may not exhibit characteristics of the species, such as soredia, that would develop in older parts of the thallus. The effects of the environment on the morphology of lichen thalli have previously been discussed by Weber (1962).

Microhabitats

In the following discussion of microhabitats it should be remembered that Jonas Rockslide as a whole is a very exposed site, and that terms such as 'more' or 'less' exposed are used in this context. The least exposed sites at Jonas Rockslide might be considered highly exposed in another situation.

A number of microhabitats can be distinguished. A letter code is listed beside each category, which is used to categorise each species in the species list.

Crevices and overhangs (co)

Typical of crevices between rocks and overhangs are *Acarospora chlorophana* and *Haematomma lapponicum*, both brightly coloured lichens. Lichen cover is generally low (< 10%). Also present are sterile crusts and leprous lichens. This microhabitat is characterised by low light and temperatures, with precipitation only received via run-off.

Exposed edges (ee)

The flora of exposed rock edges is distinctive, with a number of species largely restricted to this microhabitat. Examples are *Rhizocarpon superficiale*, *Umbilicaria lambii*, *Sporastatia testudinea* and *Dimelaena oreina*. Exposed margins of rocks are likely to be snow free in winter and wind cooled in the summer. They are also likely to dry out rapidly after summer rain.

Rockface centres on rocks of low slope (rc)

Characteristic of this microhabitat is *Rhizocarpon bolanderi*. The centres of rockfaces with an inclination of less than 60° are likely to be snow covered in the winter, and to have high radiation input in the summer. Boundary layer effects are more important in the centres of rockfaces, and the rock surface may reach temperatures of 30°C to 40°C in summer.

Steep rock surfaces (st)

Steep rockfaces tend to receive less radiation than those with a shallower slope, especially if north facing (due to the angle of the sun's rays). They also tend to be drier as precipitation received is less and run-off faster. Snow is not retained. Characteristic of these microhabitats are *Rhizocarpon eupetraeum* and *Umbilicaria vellea*.

Sheltered rock surfaces (sh)

This category includes rocks sheltered by other rocks or by trees, and the lower parts of rockfaces. These places probably receive little incoming radiation, but tend to be more mesic than the previous microhabitat. Snow cover is deep and of long duration. Species found here include *Rhizocarpon polycarpon* and *Cetraria hepatizon*.

Riverside Rocks (rr)

Rocks that are periodically flooded by the Sunwapta river have a superficial calcareous deposit of silt, and have a distinct flora, including *Staurothele clopima* and *Lecidella stigmatea*.

Generalists (ge)

There is a group of species whose microhabitat tolerances seem broad, and are found in all except the extremes of the microhabitats listed above. These include *Rhizocarpon grande*, *Umbilicaria torrefacta* and *Aspicilia cinerea*.

Lichen epiphytes/parasites (le)

A small number of species are frequently epiphytic on other lichens. These include *Lepraria neglecta* and *Spilonema revertens*.

Moss epiphytes (me)

A number of species seem only to grow on living or dead moss. These include *Buellia papillosa* and *Leprocaulon subalbicans*.

New surfaces (ns)

Rocks that have recently been upturned, for instance at the roadside, have a distinct flora including such species as *Xanthoria elegans*.

Notes on species of special taxonomic or distributional interest

Arctoparmelia subcentrifuga. This is a rare lichen (Hale 1986) but is relatively common at Jonas Rockslide. It is also known from British Columbia (Noble *et*. *al*. 1987). It has a black lower cortex and a rugose upper cortex. Its lobes are broader than those of *A*. *centrifuga*.

Aspicilia cinerea. The K+ red reaction of this species seems somewhat variable at this site, ranging from an instant and bright reaction to a slow reaction which turns from yellow to orange and finally red after several minutes. The more rapid reaction seems to be correlated with a paler thallus. The morphology of this species is also very variable, ranging from areolate to verruculose. My collections of *Aspicilia cinerea* may well consist of more than one species.

Bellamerea alpina. The apothecia of this species are usually described as being brown (e. g. Ozenda & Clauzade 1970), but are black at Jonas Rockslide, except in particularly sheltered specimens. However the distinctive K+ red and I+ black reactions of its thallus confirm this lichen.

Buellia lacteoidea. The medulla has a C+ pale pink reaction not usually associated with this species.

Caloplaca epithallina. This epiphytic or parasitic lichen was found on Schereria tenebrosa, Spilonema revertens and Dimelaena oreina. Its bright red apothecia occur in small scattered [illegible].

Lecanora frustulosa. The apothecia of specimens from Jonas Rockslide are highly stipitate, giving the appearence of a minute fruticose lichen.

Lecidea paupercula. The distinction between this species and L. atrobrunnea depends on the colour of the hypothecium and thickness of the thallus and hymenium (Thomson 1979), otherwise they are quite difficult to distinguish. L. paupercula has a dark hypothecium and a high hymenium (100µ +), and the areoles are more dispersed than L. atrobrunnea. It is reported as having a K+ yellow reaction in the medulla (Thomson 1979), however this was not found. L. atrobrunnea is much more frequently reported than L. paupercula, however it is quite rare at Jonas Rockslide.

Melanelia stygia. Two forms of this species occur at Jonas Rockslide. One is the 'classic' convex form with narrow, finger like lobes. More common is a concave form with broader lobes. The PD+ orange reaction and laminal distribution of pseudocyphellae confirm that both are M. stygia.

Phylliscum demangionii. This normally rare lichen is not uncommon at Jonas Rockslide, growing scattered amongst other lichens, however the tiny, umbilicate squamules are only visible under a dissecting microscope. It is often growing amongst areoles of Rhizocarpon bolanderi, a co-occurence also noted by Gelting in Greenland (Gelting 1954). Its North American distribution appears to be disjunct between the west and the east. As it is such a tiny lichen and easily missed, it may well be more common than is presently realised.

The brown squamules are 1mm to 2mm in diameter at Jonas Rockslide, (although reported as larger elsewhere (Noble 1982)) and are studded with the ostioles of the sunken apothecia. The cortex is red in cross-section. The spores are oval, 10μm x 7μm and 16 per ascus.

Polychidium muscicola. No apotheciate specimens are known from Jonas Rockslide. however it exhibits the dichotomous branching pattern characteristic of P. muscicola (Thomson 1986).

Rhizocarpon alpicola. This species was, until recently, not known from North America. However, specimens have now also been reported from British Columbia (Noble et. al. 1987). It is very common in Europe (Runemark 1956). Its distribution at Jonas Rockslide seems very local, only one patch is known, but it is common at that sampling station. The specimens appear old and have very few apothecia, which is reported as a characteristic of this species (Runemark 1956). The medulla is I- and K-. The spores are 1-septate.

R. bolanderi. The interesting disjunct distribution of this lichen has been discussed by Brodo and Alstrupp (1981). It is only known from Greenland, Europe and Western North America. At Jonas Rockslide it is the most common lichen, covering nearly 9% of exposed rock surfaces, although not previously reported from Jasper National Park. It forms large diffuse patches, its areoles mingling with those of other lichens. It is easily confused with two other common saxicolous lichens, *Lecidea atrobrunnea* and *Rhizocarpon geminatum*. *L. atrobrunnea* also has shiny brown areoles, large black apothecia and a distinct black hypothallus. However the areoles of *R. bolanderi* are always concave with a dark rim while those of *L. atrobrunnea* are convex and have a pale margin. *R. geminatum* has distinctive areoles (although they may also be brown) but in apothecial section has many features in common with *R. bolanderi*, for instance two large, dark, muriform spores.

R. eupetraeoides. The relatively low cover recorded for this species at Jonas Rockslide partly reflects the fact that it rarely occurs on the exposed rockfaces sampled. It forms very large patches of up to 80 cm which appear to be one thallus. It is not common in North America, but has possibly previously been mistaken for the superficially similar *R. geographicum*. The medulla is I+ black and K+ yellow becoming red. The spores are 1-septate, 25-30μm x 12-14μm.

Schaereria cinereorufa. Specimens of this genus can be easily recognised in apothecial section by their cylindrical asci and lax paraphyses (Clauzade & Roux 1985). *S. cinereorufa* has only been found growing among mosses at Jonas Rockslide, but is usually reported as being saxicolous (*e.g.* see Creveld 1981). Due to its muscicolous habit it is not easily found at Jonas Rockslide, although several collections of it have been made. Its thallus consists of small brown squamules, on which are the black apothecia. It is rarely recorded in North America.

S. tenebrosa. A distinctive C+ red medullary reaction distinguishes this otherwise non-descript grey lichen. Its apothecia are uncommon and scattered among the areoles, and may show a pseudolecanorine margin. The thallus is often highly dispersed, with rock appearing between the areoles. This species is common at Jonas Rockslide on exposed rock edges, yet has not often been recorded elsewhere.

Spilonema revertens. The tiny black filaments of this species were commonly found growing on and among other lichens. It is probably an under-recorded lichen in North America. It was only rarely found to be apotheciate and some of the records may have consisted of unlichenised *Stigonema*.

General Discussion

The large number of interesting and unusual records from this single site partly reflects the degree of lichenological under-exploration of this area of the Rocky Mountains. In addition, the nature of the study involved inspecting the rock surfaces with a dissecting microscope, and careful identification of every sampled thallus. Thus, minute lichens such as *Phylliscum demangionii* were found, and individual thalli of lichens such as *Rhizocarpon alpicola* were identified, whereas they could easily have been dismissed as thalli of some other *Rhizocarpon*. The known distributions of many of the microlichens are probably a small portion of their actual distributions, and the need for more collection of these species is paramount.

Summary

One hundred and six species of saxicolous lichens are reported from a [illegible]ite sandstone rockslide in the Canadian Rocky Mountains at Jasper National Park, Alberta. A number of rare species are present, including *Phylliscum demangionii*, *Rhizocarpon alpicola* and *Arctoparmelia subcentrifuga*. The site is considered as a number of microhabitats and most lichens are found to be microhabitat specific. It is concluded that the lichen flora of the Canadian Rockies is highly understudied.

Bibliography

Bird, C. D. and Marsh, A. H. (1973a) Phytogeography and ecology of the lichen family Umbilicariaceae in southwestern Alberta. Canadian Journal of Botany, 51: 2169-2175.

Bird, C. D. and Marsh, A. H. (1973b) Parmeliaceae in southwestern Alberta. Canadian Journal of Botany, 51: 261-288

Brodo, I. M. & Alstrup, V. (1981) The lichen Bryoria subdivergens (Dahl) Brodo & D. Hawksw. in Greenland and North America. The Bryologist, 81: 229-235.

Bruce, I. (1978) The field estimation of shear strength on rock discontinuities. Ph.D. Thesis, Department of Civil Engineering, University of Alberta.

Clauzade, G. & Roux C. (1985) Likenoj de Okcidenta Europo. Ilustrita determinlibro. Bulletin de la Societe Botanique du Centre-ouest. Nouvelle serie, Numero Speciale: 7.

Cook, D. G. (1975) Structural style influenced by lithofacies, Rocky Mountain main ranges, Alberta - British Columbia. Geological Survey of Canada, Dept. Energy, Mines and Resources. Bull. No. 233.

Creveld, M. (1981) Epilithic lichen communities in the alpine zone of southern Norway. Bibliotecha Lichenologica, 17. J. Cramer. Fl.9490 Vaduz.

Cruden, D. M. (1976) Major rock slides in the Rockies. Canadian Geotechnical Journal, 13: 8-20

Egan, R. S. (1987) A fifth checklist of the lichen-forming, lichenicolous & allied fungi of the continental United States and Canada. The Bryologist, 90: 77-173.

Gelting, P. (1954) The Rhizocarpon species with peltate areoles occurring in Europe and North America. Svensk Botanisk Tidsskrift, 51: 71-92.

Hale, M. E. Jr. (1986) Arctoparmelia - a new genus in the Parmeliaceae (Ascomycotina). Mycotaxon, 25: 251-254.

Holland, W. D. & Coen, G. M. (1983) Ecological (Biophysical) Land classification of Banff and Jasper National Parks. Volume II. Soil & Vegetation Resources. Alberta Institute of Pedology.

Imshaug, H. A. (1957) Alpine lichens of the Western United States and adjacent Canada. I. The macrolichens. The Bryologist, 60: 177-272.

Noble, W. J. (1982) The lichens of the coastal Douglas-fir dry Subzone of British Columbia. Ph. D. Thesis, University of British Columbia.

Noble, W. J., Ahti, T., Otto, G. F. & Brodo, I. M. (1987) A second checklist and bibliography of the lichens and allied fungi of British Columbia. Syllogeus, No. 61, National Museums of Canada, Ottawa.

Ozenda P. & Clauzade, G. (1970) Les lichens. Etude biologique et flore illustree. Masson et Cie., Paris.

Runemark, H. (1956) Studies in Rhizocarpon. I. Taxonomy of the yellow species in Europe. Opera Botanica, 2: 1-152.

See, M. G. (1978) Alpine macrolichen vegetation in the Canadian Cordillera of Alberta and the Yukon. Ph.D. thesis, University of Alberta.

Skorepa, A. C. & Vitt, D. H. (1976) A quantitative study of epiphytic lichen vegetation in relation to SO_2 pollution in western Alberta. Information report NOR-X-161. Northern Forest Research Centre, Edmonton Alberta.

Thomson, J. W. (1984) American Arctic Lichens. 1. The Macrolichens. Columbia University Press, New York.

Thomson, J. W. (1979) Lichens of the Alaskan Arctic Slope. University of Toronto Press, Toronto.

Thomson, J. W. (1967) Notes on Rhizocarpon in the Arctic. Nova Hedwigia, 14: 421-481.

Weber, W. A. (1962) Environmental modification & the taxonomy of crustose lichens. Svensk Botanisk Tidskrift, 56: 293-333.

Table 2.1: List of saxicolous lichens known from Jonas rockslide including those growing on moss over rock. Nomenclature and abbreviated authority names follow Egan (1987), and a complete list of synonyms can be found in that publication. Some recently used synonyms are given at the end of the Table. Percent cover estimates were arrived at during grid sampling described in the methods. Those species without a cover value did not occur in a sampling grid. Microhabitats are described in the text. Abbreviations are as follows: co = crevices and overhangs; ee = exposed edges; rc = rockface centres on rocks of low slope; st = steep rock surfaces; sh = sheltered rock surfaces; rr = riverside rocks; ge = generalists; le = lichen epiphytes/parasites; me = moss epiphytes; ns = new surfaces.

Species	Percent cover on sampled rockfaces	Micro-habitat
Acarospora fuscata (Nyl.) Arnold	.04	rc
A. cervina Massal. var. *glaucocarpa* (Whalenb.) Körber		rr
Arctoparmelia centrifuga (L.) Hale	.31	st
A. incurva (Pers.) Hale	.06	st
A. subcentrifuga (Oxner) Hale	.18	st
Arthrorhaphis alpina (Schaerer) R. Sant.		co
Aspicilia caesiocinerea (Malbr.) Arnold	.27	rc
A. cinerea (L.) Körber	.06	ge
Bellemerea alpina (Sommerf.) Clauz. & Roux	21	rr/sh
B. cinereorufescens (Ach.) Clauz. & Roux	.96	rc/rr

Table 2.1: (continued)

Species	Percent cover on sampled rockfaces	Micro-habitat
Brodoa oroarctica (Krog) Goward	.29	ee
Bryoria sp.		rc
Buellia lacteoidea B. de Lesd.	.37	ee
B. papillata (Sommerf.) Tuck.	.02	me
Caloplaca cerina (Hedwig) Th. Fr.		co
C. epithallina Lynge		le
C. holocarpa (Hoffm.) Wade		ns
C. stillicidiorum (Vahl) Lynge		le
C. tetraspora (Nyl.) Olivier		le/me
Candelariella vitellina (Hoffm.) Müll. Arg.	.09	rc/le/me
Cetraria hepatizon (Ach.) Vainio	1.29	sh
Cladonia phyllophora Hoffm.		rc
C. pyxidata (L.) Hoffm.	.17	rc
Dimelaena oreina (Ach.) Norman	.08	ee
Diploschistes scruposus (Schreber) Norman	.06	sh
Haematomma lapponicum Räsänen		co
Hypogymnia austerodes (Nyl.) Räsänen	.01	sh
Lasallia pensylvanica (Hoffm.) Llano		sh
Lecanora cenisea Ach.	.08	sh
L. frustulosa (Dickson) Ach.	.08	rc
L. intricata (Ach.) Ach.	.17	sh
L. polytropa (Hoffm.) Rabenh.	.01	ge

Table 2.1: (continued)

Species	Percent cover on sampled rockfaces	Micro-habitat
L. rupicola (L.) Zahlbr.		sh
Lecidea atrobrunnea (Ramond) Schaerer		ee
L. auriculata Th. Fr.	.29	ge
L. confluens (Weber) Ach.	.09	ge
L. lapicida (Ach.) Ach.	.03	ge
L. lapicida f. *ochracea*		rc/sh
L. lithophila (Ach.) Ach.		ge
L. paupercula Th. Fr.	1.70	ee
L. plana (Lahm) Nyl.		ge
L. tessellata Florke.	.04	ge
Lecidella carpathica Körber	.37	sh
L. stigmatea (Ach.) Hertel & Leuck.	.06	rr
Lepraria neglecta (Nyl.) Lettau	1.05	le
Leprocaulon subalbicans (Lamb) Lamb & Ward	.05	me
Melanelia granulosa (Lynge) Essl.	2.12	ge
M. panniformis (Nyl.) Essl.	.35	st
M. sorediata (Ach.) Goward & Ahti	3.48	ge
M. stygia (L.) Essl.	3.00	ge
Ochrolechia androgyna (Hoffm.) Arn.		co
Orphniospora moriopsis (Massal.) D.Hawks.	1.13	ee
Parmelia omphalodes (L.) Ach.	.25	sh
P. saxatilis (L.) Ach.	.12	sh

Table 2.1: (continued)

Species	Percent cover on sampled rockfaces	Micro-habitat
Phylliscum demangionii (Moug.& Mont.) Nyl.		rc
Phaeophyscia endococcinea (Körber) Moberg	.01	rc
P. sciastra (Ach.) Moberg	.49	rc
Physcia caesia (Hoffm.) Furnr.	.03	sh
P. phaea (Tuck.) Thomson		sh
Physconia muscigena (Ach.) Poelt		sh
Polychidium muscicola (Sw.) S.Gray		me
Porpidia crustulata (Ach.) Hertel & Knoph	.02	ge
P. flavocaerulescens (Hornem.) Hertel & Schwab		rc
P. macrocarpa (DC.) Hertel & Schwab		ge
Protoparmalia badia (Hoffm.) Hafelner	.02	sh
Pseudephebe minuscula (Arnold) Brodo & D.Hawks	1.91	ee
P. pubescens (L.) M. Choisy	5.01	ee
Rhizocarpon alpicola (Anzi) Rabenh.	.11	sh
R. badioatrum (Sprengel) Th. Fr.		sh
R. bolanderi (Tuck.) Herre	8.94	rc
R. disporum (Hepp) Müll. Arg.	2.35 **	rc
R. eupetraeoides (Nyl.) Blomb. & Forss.	.18	sh
R. eupetraeum (Nyl.) Arnold	1.18	st
R. geminatum Körber		rc
R. geographicum (L.) DC.	2.11	sh
R. grande (Flotow) Arnold	2.39	ge

Table 2.1: (continued)

Species	Percent cover on sampled rockfaces	Micro-habitat
R. macrosporum Räsänen		sh
R. polycarpum (Hepp) Th. Fr.	.45	sh
R. riparium Räsänen	.04	sh
R. superficiale (Schaerer) Vainio	1.49	ee
Rhizoplaca chrysoleuca (Sm.) Zopf	.06	ee
R. melanophthalma (DC.) Leuck. & Poelt	.31	ee
Rinodina turfacea (Wahlenb.) Korber	.18	rc/le/me
Schaereria cinereorufa (Schaerer) Th. Fr.	.04	rc
S. tenebrosa (Flotow) Hertel & Poelt	2.02	ee
Spilonema revertens Nyl.	5.87	rc/ee
Sporastatia polyspora (Nyl.) Grumm.		re
S. testudinea (Ach.) Mass.	.05	re
Staurothele clopima (Ach.) Th. Fr.	.17	rr
Tuckermannopsis pinastri (Scop.) Hale		sh
Umbilicaria cylindrica (L.) Duby		st
U. deusta (L.) Baumg.	.07	st
U. hyperborea (Ach.) Hoffm.	1.95	ge
U. lambii Imsh.	1.29	re
U. phaea Tuck.		sh
U. polyphylla (L.) Baumg.	.02	st
U. proboscidea (L.) Schrader		st
U. rigida (Du Rietz) Frey		st

Table 2.1: (continued)

Species	Percent cover on sampled rockfaces	Micro-habitat
U. torrefacta (Lightf.) Schrader	5.59	ge
U. vellea (L.) Ach.	.27	st
Verrucaria muralis Ach.		nr
Xanthoparmelia taractica (Krempelh.) Hale		sh
Xanthoria candelaria (L.) Th. Fr.		nr
X. elegans (Link) Th. Fr.		nr

** This value also includes specimens of Rhizocarpon geminatum

Recently used synonyms

Aspicilia alpina(Sommerf.)Arnold = Bellemerea alpina(Sommerf.)Clauz. & Roux

A. cinereorufescens(Ach.)Massal. = Bellemerea cinereorufescens(Ach.)Clauz. & Roux

Buellia moriopsis(Massal.)Th.Fr. = Orphniospora moriopsis(Massal.)D. Hawksw.

Cetraria pinastri(Scop.)Gray = Tuckermannopsis pinastri(Scop.)Hale

Huilia crustulata(Ach.)Hertel = Porpidia crustulata(Ach.)Hertel & Knoph

H. flavocaerulescens(Hornem.)Hertel = Porpidia flavocaerulescens(Hornem.) Hertel & Schwab

H. macrocarpa(DC. in Lam. & DC.)Hertel = Porpidia macrocarpa(DC. in Lam. & DC.) Hertel & Schwab

Hypogymnia oroarctica Krog = Brodoa oroarctica(Krog) Goward

Table 2.1: (continued)

Lecanora *badia*(Hoffm.)Ach. = *Protoparmelia* *badia*(Hoffm.)Haffelner
L. *chrysoleuca*(Sm.)Ach. = *Rhizoplaca* *chrysoleuca*(Sm.)Zopf
L. *melanopthalma*(DC. *in* Lam. & DC.)Ramond = *Rhizoplaca* *melanopthalma*(DC.*in* Lam. & DC.) Leuck & Poelt
Lecidea *cinereorufa* Schaerer = *Schaereria* *cinereorufa*(Schaerer)Th. Fr.
L. *tenebrosa* Flotow = *Schaereria* *tenebrosa*(Flotow) Hertel & Poelt
Orphniospora *atrata*(Sm.)Poelt = *O.* *moriopsis*(Massal.)D. Hawksw.
Parmelia *disjuncta* Erichsen = *Melanelia* *granulosa*(Lynge)Esslinger
P. *panniformis*(Nyl.)Vainio = *Melanelia* *paniformis*(Nyl.)Esslinger
P. *sorediosa* Almb. = *Melanelia* *sorediata*(Ach.)Goward & Ahti
P. *sorediata*(Ach.)Th. Fr. = *Melanelia* *sorediata*(Ach.)Goward & Ahti
P. *stygia*(L.)Ach. = *Melanelia* *stygia*(L.)Essl.
Xanthoparmelia *centrifuga*(L.)Hale = *Arctoparmelia* *centrifuga*(L.)Hale
X. *incurva*(Pers.)Hale = *Arctoparmelia* *incurva*(Pers.)Hale
X. *subcentrifuga*(Oxner)Hale = *Arctoparmelia* *subcentrifuga*(Oxner)Hale

III. NOTE ON THE SIZES OF LARGEST THALLI OF THREE SPECIES OF RHIZOCARPON (SUBGENUS RHIZOCARPON) AT JONAS ROCKSLIDE [2]

Lichens in the genus Rhizocarpon, subgenus Rhizocarpon, (those with yellow-green thalli) have been used for three decades in lichenometry. This technique uses the sizes of the largest thalli present to date surfaces on which they are growing. A local lichen growth curve is usually established first, from lichens growing on surfaces of known age (Beschel 1961, Innes 1985).

The subgenus Rhizocarpon is a large one, with 30 species known from Europe (Clauzade & Roux 1985) and 18 species from North America (Egan 1987). Many of these cannot be easily distinguished in the field. Microscopic examination of reproductive structures is almost always essential for identification to species. As several species of yellow-green Rhizocarpon are likely to occur together at any one site, and there is no reason to suppose they will grow at the same rate, construction of mono-specific growth curves is essential. Although some work has compared the growth rates of different subgenus Rhizocarpon species (Calkin & Ellis 1980) much lichenometric work has been done by workers without a background in lichen taxonomy, and individual thalli are not normally identified to species (Innes 1985).

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2. A version of this chapter is submitted for publication to ARCTIC AND ALPINE RESEARCH, as John, E. A. Note on the sizes of largest thalli of three species of Rhizocarpon (subgenus Rhizocarpon) at a rockslide in the Canadian Rocky Mountains.

Thallus sizes of three species of *Rhizocarpon* were compared during an investigation of saxicolous lichen ecology at Jonas Rockslide in the Rocky Mountains at Jasper National Park, Alberta (52° 26'N 117° 24'W, altitude 500m - 2200m). The rockslide is a large one, three km in length and one km wide, formed of quartzite sandstone blocks. Its geology has been discussed by Bruce (1978) & Cruden (1976). The large rockslide is composed of two smaller slides, which occurred side by side, forming a contiguous area of rubble (Figure 3.1). These are referred to as the north and south slides. Bruce (1978) suggested that both slides occurred between 1885 and 1893. However, as this conclusion was based on the absence of historical evidence to the contrary, it is open to reassessment.

Six species of yellow-green *Rhizocarpon*, have been identified from Jonas Rockslide. Of these *Rhizocarpon geographicum* (L.) DC., *R. superficiale* (Schaerer.) Vainio, and *R. eupetraeoides* (Nyl.) Blomb. & Forss. are the commonest, occurring with frequencies of 2.1%, 1.5% and 0.2% respectively on exposed rockfaces, as determined during extensive sampling of the lichen flora of rockfaces using a grid sampling system (Chapter 4). These species were found to have distinct microhabitat requirements. *R. superficiale* is largely restricted to very exposed microhabitats, such as the edges and upper parts of rockfaces. *R. geographicum* is also common in more exposed microhabitats, but is not restricted to them, whereas *R. eupetraeoides* is more frequent in sheltered microhabitats, such as lower parts of rockfaces and on sheltered boulders.

In order to compare largest thallus sizes for these three species, and concurrently estimate the age of the rockslide, three areas [illegible] the rockslide were surveyed for thalli (Figure 3.1). Each area [illegible] approximately 150m x 150m. Two of the three areas were located on the northerly slide, 100m apart in altitude and 200m apart in horizontal distance. The third area was located on the south slide. The areas were thought to be similar microclimatically, however the south slide area was the most exposed, and the upper north slide the least exposed. In each area the largest thalli of each of the three species were located and measured. The diameter of the largest circle inscribable on the thallus was recorded (Innes 1985). Although we had considerable experience of these species and their field characteristics, confirmation of identification was made by laboratory examination of apothecia collected from each thallus measured, and by chemical tests performed in the field. The chemicals used were Metzler's reagent (I), 10% KOH solution (K) and $Ca(OCl)_2$ as bleach (C), chemicals used routinely in lichenology. Chemicals were applied with micropipettes to minute portions of thallus medullary tissue and colour changes observed. Only those thalli whose identification could be confirmed in the laboratory were included in the results.

The five largest thalli of each species were used and a mean calculated from their diameters, as recommended by Innes (1985) for lichenometric studies. The largest thallus was omitted from the analysis if it was more than 20% larger than the next largest thallus for that species (Calkin & Ellis 1980). The results are shown in Table 3.1. There are considerable differences between thallus sizes, both between species, and at different sites for the same species. A modification of Friedman's test (Conover 1980, p307) was used to test for significant differences in concordance between the species. Due to the absence of *Rhizocarpon eupetraeoides* from the lower north slide site, two comparisons were made, one between *R. superficiale* and *R. geographicum* at all three sites and one between all three species at the south site and the upper north slide site.

In both cases the differences between species are significant ($p < .001$). This contrasts with the findings of Calkin & Ellis (1980) who suggested that for thalli of less than 150mm diameter there was no significant difference between species in the subgenus *Rhizocarpon*.

For both *Rhizocarpon geographicum* and *R. superficiale*, differences between sizes on the two north slide sites are less than between north and south slides, which, according to lichenometric theory, suggests that the two slides are of different ages. However,differences between lichen sizes at the two sites are inconsistent, as *R. superficiale* thalli are larger on the south slide and the other two species have larger thalli on the north slide. Thus the evidence as to which slide is the older is conflicting. It would seem that environmental differences between the slides, or some other factors, have been more important than any effects of age in determining lichen thallus sizes. It is possible that there is no significant difference in age between the two slides. As the south slide is the most exposed the more rapid growth rate of *R. superficiale* at this site could be species and site specific due to optimal microhabitat conditions.

In order to estimate the overall age of the rockslide from this information a local lichen growth curve is needed. Other studies from around the world have shown that *Rhizocarpon geographicum* (*sensu lato*) grows at rates varying from 2mm to 90mm per century during the initial rapid growth phase, and 2mm to 30mm per century thereafter, depending largely on climate (Webber and Andrews 1973). The closest study is that from Mount Edith Cavell, 80km north at an elevation of 2400m (Luckman 1977). *R. geographicum* thalli from that site were estimated to grow at 11mm per century. If the *R. geographicum* thalli at Jonas Rockslide approximate this rate then the rockslide must be at least 800 - 900 years old. However, Jonas Rockslide undoubtedly has a different microclimate than the Edith Cavell site, and growth rates could be slower or faster. In addition, as they form part of a closed lichen community competition may have slowed or stopped growth. Thus, an estimate that the rockslide is between 500 and 1000 years old seems reasonable.

Three conclusions can be drawn from this study:

1) On a single aged substrate there are significant differences in largest thallus sizes between lichens of different species from the genus *Rhizocarpon* subgenus *Rhizocarpon*.

2) These species perform very differently in response to differences in environment.

3) Jonas Rockslide is likely to be at least 500 years old, possibly much older, and is certainly older than the 100 years suggested by Bruce (1978).

Summary

The largest thallus sizes of three species of *Rhizocarpon*, subgenus *Rhizocarpon* growing at a single site are significantly different. In addition each species appears to respond differently to local changes in microclimate. Jonas Rockslide, Alberta, Canada is estimated to be at least 500 years old, rather than the 100 suggested by other researchers.

Bibliography

Beschel, R. E. (1961) Dating rock surfaces by lichen growth and its application to glaciology and physiography (lichenometry). In G. O. Raasch (ed.), Geology of the Arctic. Vol. 2, University of Toronto Press, Toronto: 1044-1062.

Bruce, I. (1978) Field Estimation of shear strength on rock discontinuities. PhD thesis, Department of Civil Engineering, University of Alberta.

Calkin, P. E. & Ellis, J. M. (1980) A lichenometric dating curve & its application to Holocene glacier studies in the Central Brooks Range, Alasksa. Arctic and Alpine Research, 12: 245-264.

Conover, W. J. (1980) Practical Nonparametric Statistics. 2nd Edition. John Wiley and Sons, New York, Chichester, Brisbane, Toronto.

Cruden, D. M. (1976) Major rockslides in the Rockies. Canadian Geotechnical Journal, 13: 8-20.

Egan, R. S. (1987) A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. The Bryologist, 90: 77-173.

Innes, J. L. (1985) Lichenometry. Progress in Physical Geography, 9: 187-254.

Luckman, B. H. (1977) Lichenometric dating of holocene moraines at Mount Edith Cavell, Jasper, Alberta. Canadian Journal of Earth Sciences, 14: 1809-1822.

Webber, P. J. & Andrews, J. T. (1973) Lichenometry: a commentary. Arctic and Alpine Research, 5: 295-302.

Table 3.1: Sizes of 5 largest thalli for 3 species of Rhizocarpon (subgenus Rhizocarpon) at three sites on Jonas Rockslide. Measurements are in mm. s = standard deviation.

slide area	Rhizocarpon superficiale	Rhizocarpon geographicum	Rhizocarpon eupetraeum
upper north	168	98	272
	112	85	262
	100	92	303
	147	86	265
	120	110	246
	mean = 129.4	mean = 94.2	mean = 269.6
	s = 27.6	s = 10.25	s = 20.9
lower north	171	124	not present
	180	105	
	168	84	
	109	116	
	121	69	
	mean = 149.5	mean = 99.6	
	s = 32.35	s = 22.7	
south	219	62	94
	205	108	147
	183	92	110
	177	107	225
	167	61	60
	mean = 190.2	mean = 86	mean = 127.2
	s = 21.29	s = 23.25	s = 62.99

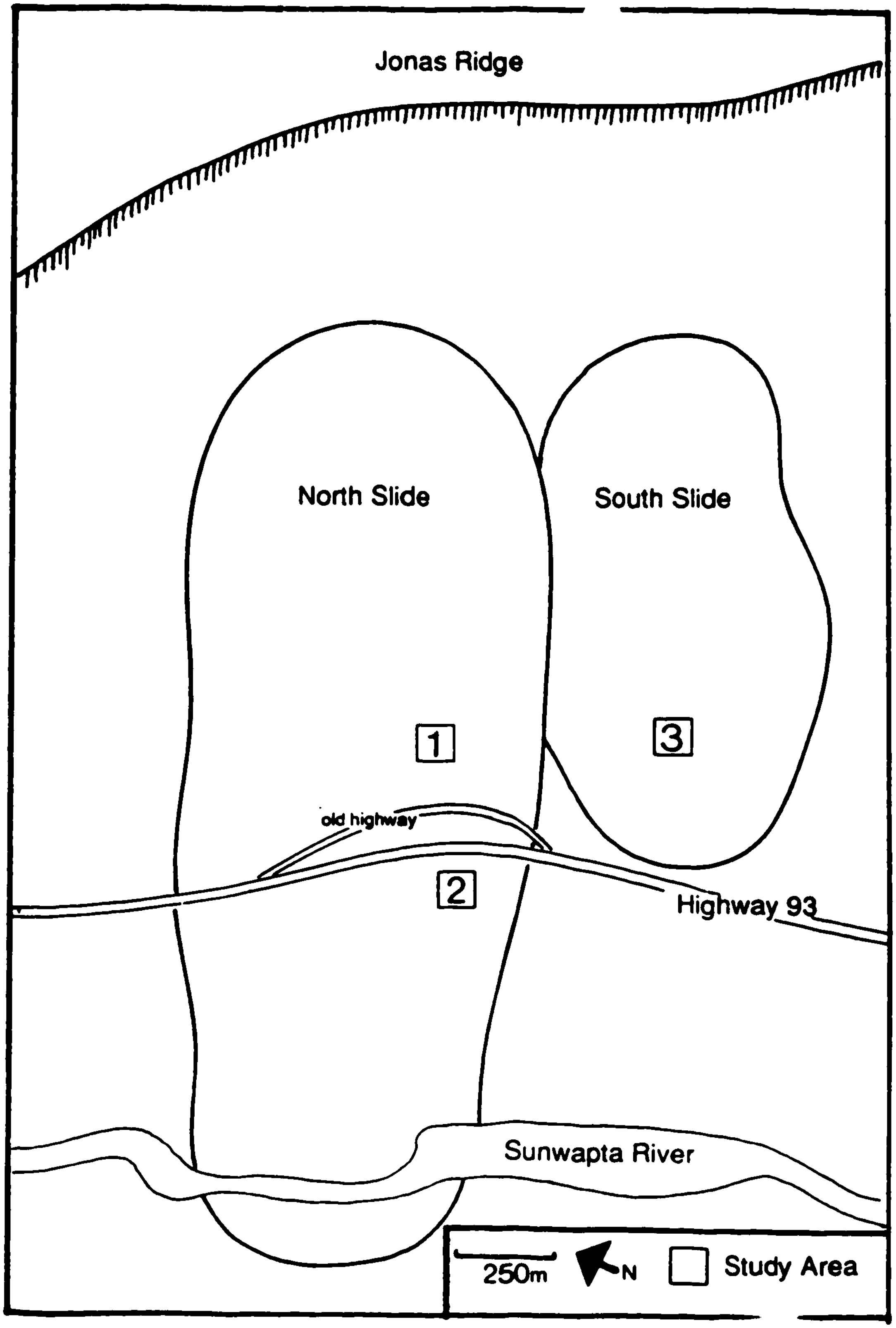


Figure 3.1: Sketch map of Jonas Rockslide, showing location of three areas searched for largest lichen thalli.

IV. FINE SCALE PATTERNING OF SPECIES DISTRIBUTIONS IN THE SAXICOLOUS LICHEN COMMUNITY AT JONAS ROCKSLIDE [3]

Introduction

The study of pattern in a plant community is an important first step in the elucidation of the processes organising that community (Watt 1947). In most plant communities even the description of pattern is highly complex and requires a spatially multi-dimensional study. This study investigates pattern in an exposed sub-alpine saxicolous lichen community which is structurally simple, with most interactions occurring within a few millimetres of the rock surface. Although foliose, fruticose and crustose growth forms coexist and may overlap one another, the vertical range is small and the pattern can be effectively studied in two dimensions. Thus, such a community offers an excellent chance to study pattern in its least complicated form, and at a scale relevant to the members of the community - that of the individual plant (Harper 1977).

However, the difficult taxonomy of lichens, particularly crustose species, and their inconspicuous growth form, has meant there are few studies of saxicolous lichen distribution at the scale of the individual thallus. Identification of species is difficult in the field, and many congenerics are distinguishable only by laboratory techniques.

3. A version of this chapter will be submitted for publication to HOLARCTIC ECOLOGY as John, E. A. Fine-scale patterning of species distributions in a saxicolus lichen community at Jonas Rockslide.

This chapter examines the spatial distribution of lichens on single rockfaces, and relates this to microenvironmental and community variables. The sensitivity of lichen and bryophyte distributions to microenvironment is well documented (*e.g.* Alpert 1985, McCarthy 1982, Flock 1978), and is probably due to their small size and lack of mechanisms for controlling water loss and heat. Previous studies of saxicolous lichen communities have examined the correlation of lichen distributions with whole rocksurface variables such as aspect and slope (Armstrong 1974, Pentecost 1979, Kappen & Redon 1984, Larson 1980), but have not examined the smaller scale of microhabitat differentiation.

One purpose of this study is to relate spatial pattern to biotic and abiotic variables at the scale of a single rockface, therefore a number of abiotic variables are measured. The intention was not to achieve an exhaustive description of microhabitat parameters, but rather to examine the kinds and sources of variation which could affect plant distribution. Saxicolous lichens have previously been found to be sensitive to the depth and duration of snow cover (*e.g.* Flock 1978), light (*e.g.* Kershaw & MacFarlane 1980), moisture availability (*e.g.* Larson 1980), temperature (*e.g.* Coxson & Kershaw 1983a, MacFarlane & Kershaw 1980) and substrate characteristics (Armstrong 1974).

Jonas Rockslide is particularly suitable for a study of intra-rockface patterning, because many of the rockfaces are flat, with little variation in microtopography, so that the complexities of microenvironment are reduced. A modification of Yarranton's point method of plotless sampling (Yarranton 1966) has been used previously in the fine scale study of plant communities (Turkington & Harper 1979), and is also used here.

Jonas Rockslide supports a diverse plant community containing over a hundred species of lichens living on the same substrate. The sizes of lichen thalli indicate that this community of slow growing plants has existed for at least 500 years, and there have certainly been interactions amongst its members in that time, such as those observed in a similar community by Hawksworth & Chater (1979). The question arises as to how so many species can persist together, without competitive exclusion, if they are sharing the same resources. One explanation of their coexistance is niche separation, where each species has different ecological requirements. Of this theory, Grubb (1977) says "most botanists find difficulty in understanding how all the species in a species rich plant community can possibly occupy different niches". A largely crustose saxicolous community (that is relatively undifferentiated, both morphologically and phenologically) would appear to exemplify this difficulty. By studying pattern one can determine whether niche differentiation is present, and thus further our understanding of the organisation of this plant community.

The objectives of this chapter are:

1. To report whether, at the scale of the individual rockface, non-random distributions can be found among the species present.

2. To relate simple microenvironmental measurements to these distributions.

3. To form hypotheses about the causes of pattern in this community.

Study site and methods

Study site

The field work was conducted at a large rockslide (52° 26'N, 117° 24'W) in Jasper National Park, Alberta, Canada. The rockslide is situated on Highway 93, 75km south of Jasper Townsite (Figure 1.1). The rockslide is composed of honey coloured quartzite sandstone (Bruce 1978), forming blocks of a range of sizes, but commonly up to 3m x 3m x 1m. There are many flat rockfaces. Jonas Rockslide is considered one of the major rockslides of the Canadian Rocky Mountains (Cruden 1976). It ranges from 1500m to 2200m in elevation, which places it in the subalpine, and is 3.5km long and 1km wide. The average annual temperature at that elevation is 0°C and average annual precipitation over the period 1971 to 1980 was 793mm as recorded at Sunwapta Wardens' Station, 3km from the rockslide (Holland & Coen 1983). It is on a southwest facing slope in the eastern main ranges of the Rocky Mountains. The rockslide is believed to have fallen at least 500 years ago, based on lichenometric evidence (Chapter 3).

The dominant plants at the site are saxicolous lichens, which cover 87% of exposed rock surfaces. One hundred and six species of saxicolous lichens have been recorded at Jonas Rockslide, of which nineteen have a cover value greater than 1% (Chapter 1). Tree cover (*Picea engelmanii* on the lower slopes and Pinus albicaulis on the upper slopes) is sparse, and trees are absent from 80% of the rockslide area.

Methods

Single rockfaces were sampled at intervals along six altitudinal transects. At each sampling station the three nearest suitable rockfaces were selected, based solely on the criteria that they should be flat, exposed, at least 1m x 1m in area and have a slope angle of less than 90° due to the difficulties of sampling overhanging rockfaces. Each rockface was sampled with a grid of points in which the rows were 10cm apart and the columns 20cm apart, so that the smallest sampled rockfaces had at least fifty sampling points. Figure 4.1 illustrates the sampling design. The columns ran parallel to the line of steepest slope of the rockface, but otherwise grids were positioned randomly on the rockface and did not start at a specified corner or edge. The grid points were located using a tape measure and a small pointed piece of tape was applied to the rock surface to indicate the precise sampling position.

At each point the species or genus of lichen present was determined with the aid of a portable dissecting microscope. When identification was possible only to genus in the field, apothecia were collected for laboratory dissection and chemical tests were made on minute portions of the thallus in the field. The chemicals used were Metzler's reagent (I), 10% potassium hydroxide solution (K), and calcium hypochlorite, as found in household bleach (C), chemicals used routinely in lichen identification (Dobson 1981). Only the genus was recorded for those thalli without apothecia, when this was possible. If no plant was present at the sample point, uncolonised rock was recorded. A total of 12,424 points were sampled on 128 rockfaces.

To analyse species distribution on specific parts of the rockface, the grid points for each rockface were classified in one of two categories, based on three sets of criteria (Figure 4.1):

1 Upper or lower portion of the rockface

2 Edge (within 20cm of the edge of the rockface) or non-edge grid points

3 Southerly or northerly portion of the rockface

For each species, the frequency with which it was found at grid points in each category over all 128 rockfaces, was compared with its expected frequency based on a null hypothesis of random distribution over the rockface. Using this null hypothesis, the expected proportion of a species' occurrences in each category is the proportion of all grid points in that category. The observed and expected proportions for each analysis for each species were compared using a log-likelihood ratio test (G-test, Sokal & Rohlf (1981)).

This analysis was repeated with the rocks divided into those of high (>100m above the Sunwapta River) and low altitude, in order to assess the effects of altitude on the distribution of lichens on individual rockfaces.

In a further analysis, the points on each rock were placed in one of eight combinations of the three categories described above, so that an assessment could be made of the probability of finding a species in a position that is, for instance, upper, edge and southerly (Figure 4.1). Expected values for each species in each category were calculated from the total proportion of all points in that category. The G-test was again used to assess the significance of the results, by summing the log-likelihood ratio over all eight categories.

To evaluate possible differences in microenvironment at different parts of the rockface, a series of microenvironmental investigations were made. A site visit to investigate snow cover was made on 19 and 20 February 1987. The depth of snow cover on rockfaces of different slope and aspect was noted, as was the presence and position of snow-free areas on rockfaces.

Temperature differentiation on one rockface was investigated using a CR5 micrologger (Campbell Scientific) in October 1987. The rockface on which the measurements were made had an aspect of 141° (facing south-east), a slope of 25° from the horizontal, and had no parts shaded from direct sunshine. Its dimensions were approximately 1.2m x 1.5m. Thirty thermocouples were attached to the rockface in five locations. Copper-constantan thermocouple wire with diameter 0.2mm was attached to lichen free rock surface using a clear silicon glue. The five locations were; within 1cm, 10cm and 30cm of the upper edge of the rockface, at the centre of the rockface and within 10cm of the lower edge of the rockface. The six thermocouple readings from each location were averaged to give a mean for that part of the rockface. Readings were made at 10 minute intervals from sunrise to sunset and every three hours during the night from 17-21 October 1987. Concordance of the means for each location was tested using Friedman's test (Conover 1980).

Results

Species Distributions

The discussion of results is restricted to the twenty-three species with over fifty records. These are listed in Table 4.1. The spatial microhabitat distributions for these species are shown in Figure 4.2. The bars represent the proportion of all occurrences of each species in each of the three microhabitat analyses. They can be compared with the expected value for each analysis. The species are ordered according to the probability of their being found on the upper part of the rockface. The sample size for each species is shown. Small samples decrease the sensitivity of the statistical test. Uncolonised rock is also included.

Sixteen of the twenty-three species show a non-random distribution with respect to at least one of the three microhabitat categories, and ten show non-randomness in two or three categories. Others appear randomly distributed with respect to these microhabitat variables. Those that do respond fall into one of two broad groups, referred to as 'upper rockface' species and 'lower rockface' species. The delimitation of these three groups is described in Figure 4.2. Upper rockface species are more often found on rockface edges and the more southerly parts of rockfaces, whereas lower rockface species are infrequently on rockface margins and more often on northerly parts of rocks. In no case is a species significantly likely ($p < 0.05$) to be found most frequently in categories found at these two extremes (Figure 4.2). For instance, no upper rockface species has a significant probability of being found more frequently on northerly parts of rocks. However, within each of these groups there is a range of responses.

The comparison of distributions at high and low altitude is shown in Table 4.2. The proportion of times a species was found on the edge of a rockface is compared at high and low altitudes, as is the proportion of times a species occurred on the upper part of a rockface. There is a trend for a species to be found more often on the edges of a rockface or on the upper portion of a rockface at low altitude than at high altitude. Thus, at high altitude, 'upper rockface species' are likely to have less extreme distributions and be found less often at the edges and upper parts, whereas 'lower rockface species' are more likely to be restricted to the lower and inner portions of the rockface. These generalisations are not true in all cases, but are true for the majority. Eighteen out of 24 species are more often on the edges at low altitude than at high, and 17 show increased probability of being found on the upper part of a rockface at low altitude.

In the combination analysis, six species were found to have distributions that were significantly different from expected ($p < 0.05$). Figure 4.3 shows the results for these species, expressed as number observed divided by number expected for each category. It should be remembered that although these species show a pattern that is significantly different from the expected over all eight categories, the numbers in each category may not differ greatly. One of the reasons that only six species show a significantly non-random result in this analysis is that the sample sizes become very low when divided into eight categories.

In general, these results reinforce those of the previous analysis, indicating that upper rockface species are also more frequent on edges and on southerly parts of rocks and that lower rockface species are overall less frequent on edges and southerly parts of rockfaces. However, there is also an indication that each of these microhabitat parameters can act separately in affecting a species' distribution. For instance, <u>Umbilicaria lambii</u> is most likely to be found on edges, whether upper, lower, north or south.

An example of the non-random distribution of lichens on a rockface can be seen in Figure 4.4.

<u>Microhabitat variables</u>

On 19 & 20 February 1987 the average snow depth on the 141 rockfaces examined at Jonas Rockslide was 24cm. However, parts of many rockfaces were free of snow, with a mean value of 82% snow cover, while 62% of rockfaces had some snow free areas, and 14% of rockfaces had either upper or lower edges exposed. On 50% of rockfaces the southernmost edge was exposed, and on 5% of rockfaces the northernmost edge was snow-free. Snow cover varied with rockface slope: steeper rockfaces having less snow and those steeper than 78^{o} having no snow. Rockface aspect had no clear effect; it interacts with a complex of factors including wind direction at time of snow deposition and radiation received at snow melt. Exposure is an important factor; exposed rockfaces and parts of rockfaces are likely to be snow-free. Although this survey was of necessity limited in scope, general conclusions can be drawn: snow-free areas occupy steeper rockfaces and occur on rockface edges, especially the most southerly and upper and lower edges. Horizontal rockfaces hold the deepest snow.

Figures 4.5a and 4.5b illustrate the temperature readings obtained from five areas of a single rockface over the same three hour period (10.00 hours to 13.00 hours) on two consecutive days. The weather on 17 October was sunny with a light northerly breeze, while on 18 October it was overcast and windless. The readings for 17 October are significantly concordant ($p < .001$) according to the Friedman test, whereas there is no significant concordance among the readings for 18 October.

Discussion

Microhabitat Variation

The temperature results suggest that temperature differences develop in a predictable way between parts of a rockface on sunny days. Under overcast skies these differences do not develop. On the sunny day, when air temperatures remained below 4°C, there was a 4°C difference between upper and lower edges on the same rockface. The regular and constant temperature increase from upper to lower edge may be due to the greater exposure to wind cooling of the upper parts of the rockface seen on this day. Parts of the rockface only 9cm apart show constant differences in microclimate (see lower two lines in Figure 4.5a). On sunny summer days these differences would be greater. For instance, in a study at an alpine location in adjacent Banff National Park, temperatures of 45°C were recorded for parts of a rock exposed to sun but sheltered from breezes, compared to 32°C when not sheltered from air currents (Coxson & Kershaw 1983a). As illustrated by Coxson & Kershaw's results, temperature at the rock surface can be dramatically different from the prevailing air temperature.

The combined effects of temperature differences and air currents will affect other microhabitat variables at the rock surface. Drying will occur at varying rates depending on the combined effects of air movement and temperature. The centre of a rockface has a better defined boundary layer of still air at its surface than the edges (Oke 1978). This would act to slow convective cooling and affect water loss. Rock surfaces on which water remains weather more rapidly than those from which it is rapidly lost. The importance of these results is that they illustrate that microenvironmental differences exist between parts of the same rockface.

Relation of species distributions to microhabitat variation

The spatial patterns in lichen distribution can be related to microenvironment. The microhabitat shared by the species in each of the two broad response groups has certain features in common. The upper, edge and southerly portions of rockfaces are the most exposed and therefore most likely to be free of snow in winter and exposed to air currents in summer. The lower, inner and northerly parts of rockfaces have longer periods of snow cover and will be less exposed to cooling and drying currents in summer. Evidence that a gradient of 'degree of exposure' is operating comes also from the comparison of the results obtained at high and low altitudes (Table 4.2). The fact that upper edge species are less restricted to upper edge habitats at high altitude than at low altitudes supports this hypothesis, as the higher parts of the rockslide are the most exposed. However, the results of the combination analysis indicate that the effects of being on the edge of a rockface are not necessarily the same as those of being in the south or upper portion of a rockface (Figure 4.3).

It is a reasonable hypothesis that each group of lichens will share certain ecophysiological adaptations to its spatially defined microhabitat. The upper rockface species have no snow cover and have to withstand harsh winter conditions such as fluctuating temperatures and wind driven abrasive particles, yet in mild winter weather they are in a position to photosynthesise as rocks and lichen thalli absorb radiation and cause snow melt around the rock edges, as observed in April 1987. Some lichens are able to photosynthesise at low temperatures (Kershaw 1985) and it is possible that they do most of their photosynthesis in spring and autumn when temperatures at the rock surface are just above 0°C and thalli are likely to be moist. In summer the upper rockface lichens are air cooled and unlikely to reach the high temperatures of sheltered parts of the rockface.

The most 'extreme' of the upper rockface lichens is *Rhizocarpon superficiale*, whose ecophysiology was studied by Coxson and Kershaw (1983a & b). It was found to photosynthesize optimally between 1°C and 14°C. An experiment in which dry thalli were subjected to temperatures of up to 45°C (a temperature that can be reached by a sheltered rockface in summer (Coxson & Kershaw 1983a)) showed that thalli subsequently showed reduced photosynthesis when incubated at 14°C, indicating that stress had occurred at the higher temperature (Coxson & Kershaw 1983b). No physiological data is available for any other upper rockface species, but lack of resistance to higher temperatures may be a factor common to all.

Another ecophysiological characteristic of 'upper rock lichens' may be intolerance of lengthy snow cover. Flock (1978) found snow cover to be correlated with lichen distributions, and lichenologists have traditionally distinguished between chionophobic and chionophilic lichens, based on their broad field distributions (Gaussla 1984, Creveld 1981).

Those species which showed random distribution among the spatial microhabitat categories are either tolerant of the full range of microenvironmental conditions encountered, or avoid the extremes of microenvironment. As an example of the latter, Coxson & Kershaw (1983a) found that on a day when saxicolous crustose lichen thalli temperatures reached 31°C, the temperature of an *Umbilicaria kraschenínnikovii* thallus at the same site did not rise above 15°C. An umbilicate lichen is only attached to the rock by a small umbilicus (or strand) and the rest of the thallus may be 1mm to 2mm above the surface. The temperature gradient above the rocksurface is extremely steep (Kershaw 1983), due to a thin boundary layer and an umbilicate or foliose lichen may avoid the extreme temperatures of [illegible] surface. The two common umbilicate *Umbilicaria* species at Jonas Rockslide are in the "random distribution" microhabitat category. *Umbilicaria lambii* is in the upper rockface group but has an adpressed pseudo-crustose growth form (Imshaug 1957).

Melanelia granulosa (Lynge) Essl. is also in the "random distribution" category. Studies of its physiology (under the name *Parmelia disjuncta* Erichsen) have shown that it can withstand temperatures of 45°C without loss of photosynthetic capacity (Kershaw & Watson 1983). This supports the hypothesis that temperature tolerance is a determinant of lichen distribution, as this lichen is found on all parts of the rockface.

The lower rockface species may be intolerant of exposed positions and must be tolerant of the higher temperatures reached at the centre of a rockface. In the winter they are covered by a thick layer of snow, which lasts until late in the spring. This may select for lichens able to photosynthesize at low light intensities as light penetrates the snow. No physiological studies of any species in this group have been published.

Hypotheses about ecophysiological tolerance are potentially testable under experimental conditions. If supporting evidence is not found then other hypotheses to explain niche differentiation must be adopted, such as weaker competitive ability of certain lichens restricting their distribution. The apparently narrow ecological tolerances of some of these lichens contrasts with the findings of Armstrong (1974) who concluded that saxicolous lichens have broad tolerances. This difference may be explained by the fact that he was studying whole rockfaces, without addressing intra-rockface variation.

Importance of thallus colour and morphology

The morphology and colour of each of the lichens studied in this analysis is shown in Table 4.1. The importance of lichen thallus colour and morphology and its relation to ecology and physiology has been investigated by Gaussla (1984) and Kershaw (1974). Gaussla found that, in general, dark lichens reflected less radiation in both the visible and infra-red regions, compared to pale lichens and Kershaw found that a white thallus painted black reached higher temperatures than an unpainted thallus of the same species. It is suggested that the abundance of dark lichens in extremely cold and exposed climates is due to their ability to absorb radiant energy and maintain a temperature higher than that of air or substrate. Under snow cover thin enough for light to penetrate the lichens absorb radiation and melt the snow from below, creating a sheltered microenvironment, potentially suitable for photosynthesis at low temperatures (Larson & Kershaw 1975). Most of the commonest foliose lichens at Jonas Rockslide are dark in colour, and most of them do not show strong distribution patterns at this scale of investigation. The exception is Arctoparmelia centrifuga which is pale green and is found most often on the upper parts of rocks.

It may be more important for foliose lichens to be dark than for crustose lichens, as the crusts are within the substrate boundary layer, and are warmed as the substrate heats up. The common crusts at Jonas Rockslide range in colour from yellow to pale grey to black. Few crusts do not show a distinct distribution pattern. Due to their intimate substrate contact, crustose lichens are likely to experience the microenvironmental extremes of the substrate and thus could be expected to exhibit stronger microhabitat preferences than foliose lichens. The most prominent crustose genus is Rhizocarpon, and this exhibits clear microhabitat differences between the subgenera Rhizocarpon (yellow-green thallus) and Phaeothallus (grey thallus). The yellow-green species tend to be found in more exposed positions than the grey species. It has been suggested that the yellow pigments reflect ultra-violet radiation (Gaussla 1984), which could be important for a plant exposed to strong insolation.

Niche differentiation

These results show distinct spatial distribution patterns, amongst lichens, at the scale of individual rockfaces, and this can be related to putative microenvironmental differences. The microhabitat categories analysed in this study are very crude ones and ignore many possibilities for microhabitat distinction that may be important to the individual lichens. For instance, lichens may depend on minute features in surface topography for establishment (Armstrong 1981). The "plants' eye view" (Turkington & Harper 1979) of the rockface is that it is a much more heterogeneous environment than it initially appears to the ecologist. However, even at the level of this study in which the microhabitats are not fully or precisely characterised, we can see that many of the species are occupying different niches. This indicates that the resources of the habitat are shared amongst the species such that they are not all in direct competition.

The progression from a knowledge of pattern in an ecosystem [illegible] understanding of the processes causing that pattern is a difficu[illegible], requiring manipulation of the system. A system in which the organisms may only grow at 11mm (in diameter) per century (Luckman 1977) is not a suitable one. However patterns can lend support to hypotheses about processes. This study has shown that this community is highly organised even at the intra-rockface scale. The organisation can be related to inferred environmental variables such as temperature and snow cover, but this does not indicate the mechanism of organisation.

During the initial stages of colonisation lichen propagules are likely to land at random all over the rockface. Unfortunately little is known of lichen establishment, which is a complex process involving two organisms, but at some point during establishment distribution patterns are determined that correlate with microhabitat. Whether this occurs because of ecophysiological intolerances alone, or as a result of differential competition is unknown. In some other plant communities growing on an environmental gradient, it has been found experimentally that competition is more severe on some parts of the gradient than others (i.e. there are preferred areas in which many species grow well), and less able competitors are restricted to the extremes of their fundamental niche (Wilson & Keddy 1986, Bertness & Ellison 1987). On the other hand, it is possible that in a stressful environment such as this one, biotic interactions are unimportant in community organisation compared to the interactions of each species with its abiotic environment. This was suggested to be the case for a saxicolous moss community (Alpert 1985).

In this structurally simple plant community, competition between crustose lichens will be only for space on the rockface, although foliose lichens have the ability to overtop other lichens and compete three dimensionally. In this respect, it is worth noting that at Jonas Rockslide uncolonised rock is apparently randomly distributed with respect to the microhabitat categories 'edge' and 'upper' and has a tendency to be less frequent on northern parts of rocks (Figure 4.2). Thus for the two most important microhabitat categories controlling plant distribution, the amount of uncolonised rock is equally distributed, implying that competition for space does not differ according to microhabitat. However, it is possible that rock currently uncolonised is for some reason uncolonisable. Eighty-eight percent of the surface area of rockfaces is colonised and some parts of all rockfaces are very densely colonised, with thalli intermingling, and it is unlikely that competition is not occurring. It is possible that competition is at least in part responsible for the niche differentiation seen here.

Summary

1. Distinct patterns of species distribution within individual rockfaces are found in a saxicolous lichen community growing on an exposed rockslide in the Canadian Rockies.

2. A grid system is used for sampling individual rockfaces and the likelihood of finding a species on particular parts of the rockface is analysed.

3. Lichens can be divided into three broad groups: those which are distributed apparently at random over the rockfaces, those which are more likely to occur on upper, outer and southerly portions of the rockfaces and those which are found more often on lower, inner and northerly portions of the rockfaces. The species investigated are approximately evenly distributed among these three groups.

4. Simple microclimatic measurements allow lichen distributions to be related to microenvironmental characteristics of each part of a rockface. The upper rockface surfaces are often snow-free in winter and may be wind-cooled in summer. The lower rockface group probably experience deeper and more persistent snow cover and may reach potentially stressful high temperatures on sunny summer days.

5. It is hypothesised that lichen distributions are at least in part explained by ecophysiological adaptations to their particular microhabitat, while recognising that competition may also play a role in community organisation.

Bibliography

Alpert, P. (1985) Distribution quantified by microtopography in an assemblage of saxicolous mosses. Vegetatio, 64: 131-139.

Armstrong, R. A. (1981) Field experiments on the dispersal, establishment and colonisation of lichens on a slate rock surface. Environmental and Experimental Botany, 21: 115-120.

Armstrong, R. A. (1974) The descriptive ecology of saxicolous lichens in an area of south Merionethshire, Wales. Journal of Ecology, 62: 33-45.

Bertness, M. D. & Ellison, A. M. (1987) Determinants of pattern in a New England salt marsh plant community. Ecological Monographs, 57: 129-147.

Bruce, I. (1978) The Field estimation of shear strength on rock discontinuities. Ph.D. thesis, Department of Civil Engineering, University of Alberta.

Conover, W. J. (1980) Practical Nonparametric Statistics. 2nd Edition. John Wiley & Sons. New York, Chichester, Brisbane, Toronto.

Coxson, D. S. & Kershaw, K. A. (1983a) The ecology of *Rhizocarpon superficiale*. I. The rock surface boundary-layer microclimate. Canadian Journal of Botany, 61: 3009-3018.

Coxson, D. S. & Kershaw, K. A. (1983b) The ecology of *Rhizocarpon superficiale*. II. The seasonal response of net photosynthesis & respiration to temperature, moisture and light. Canadian Journal of Botany, 61: 3019-3030.

Creveld, M. (1981) Epilithic lichen communities in the alpine zone of southern Norway. Bibliotheca Lichenologica. J. Cramer. Fl.9490 Vaduz.

Cruden, D. M. (1976) Major rock slides in the Rockies. Canadian Geotechnical Journal, 13: 8-20.

Dobson, F. (1981) Lichens. An illustrated guide. The Richmond Publishing Co. Ltd., Richmond, U.K.

Flock, J. W. (1978) Lichen-bryophyte distribution along a snow-cover soil-moisture gradient, Niwot Ridge, Colorado. Arctic and Alpine Research, 10: 31-47.

Gauslaa, Y. (1984) Heat resistance and energy budget in different Scandinavian plants. Holarctic Ecology, 7: 1-78.

Grubb, P. J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews, 52: 107-145.

Harper, J. L. (1977) Population biology of plants. Academic Press, London, New York, San Fransisco.

Hawksworth, D. L. & Chater, A. O. (1979) Dynamism and equilibrium in a saxicolous lichen mosaic. Lichenologist, 11: 75-80.

Holland, W. D. & Coen, G. M. (1983) Ecological (Biophysical) land classification of Banff & Jasper National Parks. Volume II. Soil & vegetation resources. Alberta Institute of Pedology & Environment Canada.

Kappen, L. & Redon, J. (1984) Microclimate influencing the lichen vegetation on different aspects of a coastal rock in the Maritime Antarctic. Instituto Antarctico Chileno (INACH), Serie Cientifica, 31: 53-65.

Kershaw, K. A. (1985) Physiological Ecology of Lichens. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Kershaw, K. A. (1983) The thermal-operating environment of a lichen. Lichenologist, 15: 191-207.

Kershaw, K. A. (1974) Studies on lichen-dominated systems. XII. The ecological significance of thallus colour. Canadian Journal of Botany, 53: 660-667.

Kershaw, K. A. & MacFarlane, J. D. (1980) Physiological-environmental interactions in lichens. X. Light as an ecological factor. New Phytologist, 84: 687-702.

Kershaw, K. A. & Watson, S. (1983) The control of seasonal rates of net photosynthesis by moisture, light and temperature in Parmelia disjuncta Erichs. The Bryologist, 86: 31-43.

Larson, D. W. (1980) Patterns of species distribution in an Umbilicaria dominated community. Canadian Journal of Botany, 58: 1269-1279.

Larson, D. W. & Kershaw, K. A. (1975) Studies on lichen-dominated sytems. XI. Lichen-heath and winter snow cover. Canadian Journal of Botany, 53: 621-626.

Luckman, B. H. (1977) Lichenometric dating of holocene moraines at Mount Edith Cavell, Jasper, Alberta. Canadian Journal of Earth Sciences,14: 1809-1822.

MacFarlane, J. D. & Kershaw, K. A. (1980) Physiological-environmental interactions in lichens. XI. Thermal stress & lichen ecology. New Phytologist, 84: 669-685.

McCarthy, P. M. (1982) Microclimate and a maritime lichen cleft community. Lichenologist, 14: 195-197.

Pentecost, A. (1979) Aspect and slope preferences in a saxicolous lichen community. Lichenologist, 11: 81-83.

Sokal, R. R. & Rohlf, F. J. (1981) Biometry. The Principles and Practice of Statistics in Biological Research. 2nd Edition. W. H. Freeman & Company, New York.

Turkington, R. & Harper, J. L. (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. Journal of Ecology, 67: 201-218.

Watt, A. S. (1947) Pattern and process in the plant community. Journal of Ecology, 35: 1-22.

Wilson, S. D. & Keddy P. A. (1986) Species competitive ability & position along a natural stress/disturbance gradient. Ecology, 67: 1236-1242.

Yarranton, G. A. (1966) A plotless method of sampling vegetation. Journal of Ecology, 54: 229-237.

Table 4.1: Growth form and colour of species discussed in Chapter 4. Nomenclature follows Egan (1987).

Species code	Species Name	Growth Form	Colour
Ar.c.	*Arctoparmelia centrifuga* (L.) Hale	Foliose	Yellow-green
A.c.	*Aspicilia cinerea* (L.) Körber	Crustose	Grey
B.c.	*Bellemerea cinereorufescens* (Ach.) Clauz. & Roux	"	"
C.h.	*Cetraria hepatizon* (Ach.) Vainio	Foliose	Black
G.a.	*Grimmia affinis* Hornsch.	Moss	Dark green
L.p.	*Lecidea paupercula* Th. Fr.	Crustose	Brown/black
Lp.n.	*Lepraria neglecta* (Nyl.) Lettau	Leprose	White
M.g.	*Melanelia granulosa* (Lynge) Essl.	Foliose	Brown/black
M.o.	*M. sorediata* (Ach.) Goward & Ahti	"	"
M.s.	*M. stygia* (L.) Essl.	"	"
O.m.	*Orphniospora moriopsis* (Massal.) D.Hawks.	Crustose	Grey/black
Ph.s.	*Phaeophyscia sciastra* (Ach.) Moberg	Foliose	Grey
P.m.	*Pseudephebe minuscula* (Arnold) Brodo & D. Hawks.	Fruticose-adpressed	Black
P.p.	*P. pubescens* (L.) M. Choisy	"	"

Table 4.1: (continued)

Species code	Species Name	Growth Form	Colour
R.b.	*Rhizocarpon bolanderi* (Tuck.) Herre	Crustose	Brown
R.d.	*R. disporum* (Hepp) Mill. Arg.	"	Grey
R.e.	*R. eupetraeum* (Nyl.) Arnold	"	"
R.g.	*R. geographicum* (L.) DC.	"	Yellow-green
R.r.	*R. grande* (Flotow) Arnold	"	Grey
R.p.	*R. polycarpum* (Hepp) Th. Fr.	"	"
R.s.	*R. superficiale* (Schaerer) Vainio	"	Yellow-green
S.t.	*Schaereria tenebrosa* (Flotow) Hertel & Poelt	"	Grey
S.r.	*Spilonema revertens* Nyl.	Filamentous	Black
U.h.	*Umbilicaria hyperborea* (Ach.) Hoffm.	Umbilicate-foliose	"
U.l.	*U. lambii* Imsh.	Crust-like foliose	"
U.t.	*U. torrefacta* (Lightf.) Schrader	Umbilicate-foliose	"
U.r.	Uncolonised rock		

Table 4.2: Comparison of microhabitat preferences at high (>100m above the Sunwapta River) and low altitudes. Full species names can be found in Table 4.1. Species are listed in the same order as they appear in Figure 4.2, for easy comparison. Stars are used to indicate the degree of significance of the deviation of the observed number of occurrences of a species in a particular category from the expected value shown at the end of the table. The G-test was used (Sokal & Rohlf 1981). (* p< 5%, ** p< 1%, *** p< .01%)

species	sample size		proportion of records on upper part of rockface		proportion of records on edge of rockface	
	high	low	high	low	high	low
R.s.	132	53	.71***	.77***	.65***	.83***
L.p.	82	129	.69**	.65***	.65**	.61**
U.l.	101	59	.58*	.66**	.72***	.73*
Ar.c.	7	46	.43	.65*	.43	.52
S.t.	160	91	.54	.64**	.57**	.59**
O.m.	92	48	.51	.69**	.62**	.5
P.p.	323	299	.49	.62***	.55**	.61***
R.g.	105	157	.55	.55	.46	.58**
M.s.	204	169	.53	.56	.52	.46
P.m.	133	104	.50	.54	.50	.70**
R.r.	154	143	.47	.56	.40	.47
U.t.	344	350	.47	.55	.44	.50
M.g.	127	136	.43	.59*	.47	.47
U.h.	138	104	.46	.55	.41	.49

Table 4.2: continued.

species	sample size		proportion of records on upper part of rockface		proportion of records on edge of rockface	
	high	low	high	low	high	low
M.o.	219	214	.45	.55	.43	.46
R.e.	81	66	.43	.58	.55	.48
U.r.	575	1001	.48	.49	.48	.48
R.d.	99	193	.41	.49	.27	.45
A.c.	328	301	.44	.46	.45	.45
R.b.	270	841	.37**	.37***	.45	.41***
G.a.	18	52	.50	.31**	.39	.54
S.r.	228	501	.32***	.35***	.31***	.35***
B.c.	27	92	.37	.34**	.52	.41
Lp.n.	72	59	.29**	.37	.36*	.51
Ph.s.	0	61		.33*		.33*
C.h.	67	94	.33*	.30*	.48	.53
R.p.	24	32	.21**	.25**	.37	.44
totals (expected values)	5204	7220	.464	.487	.479	.478

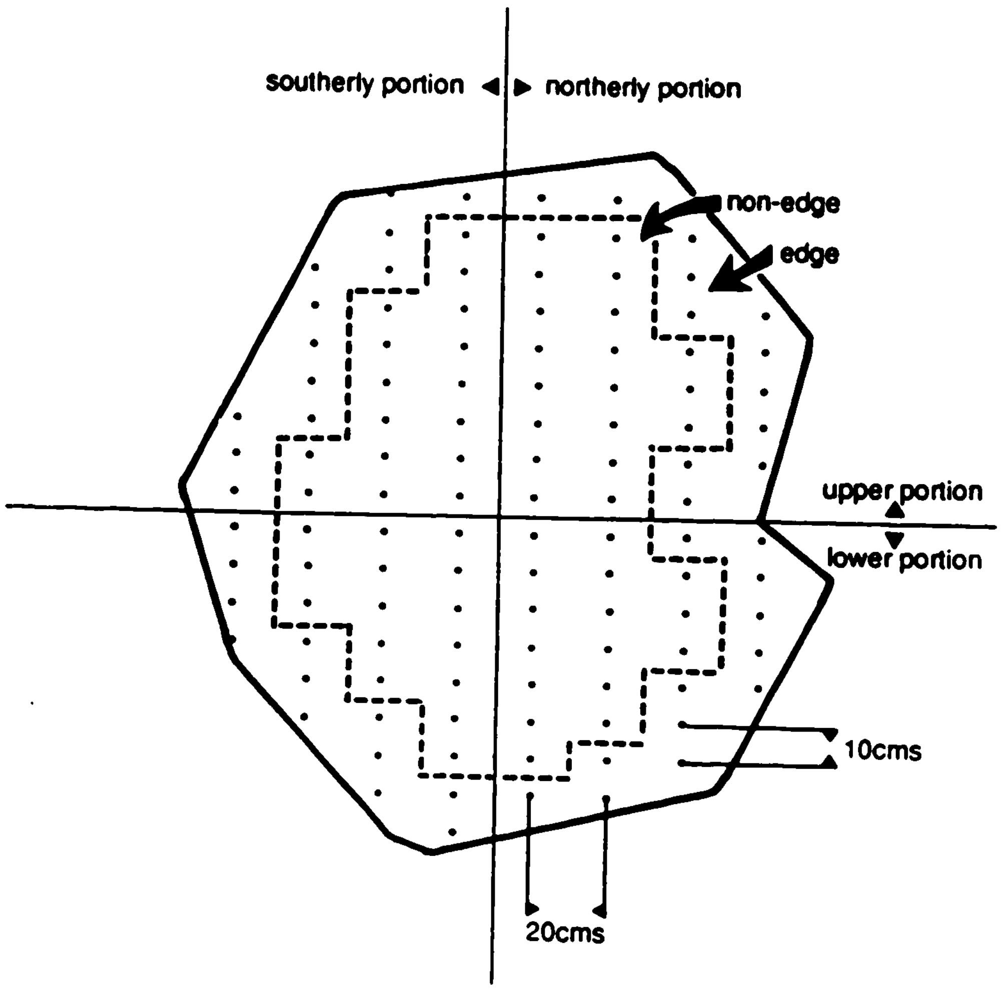
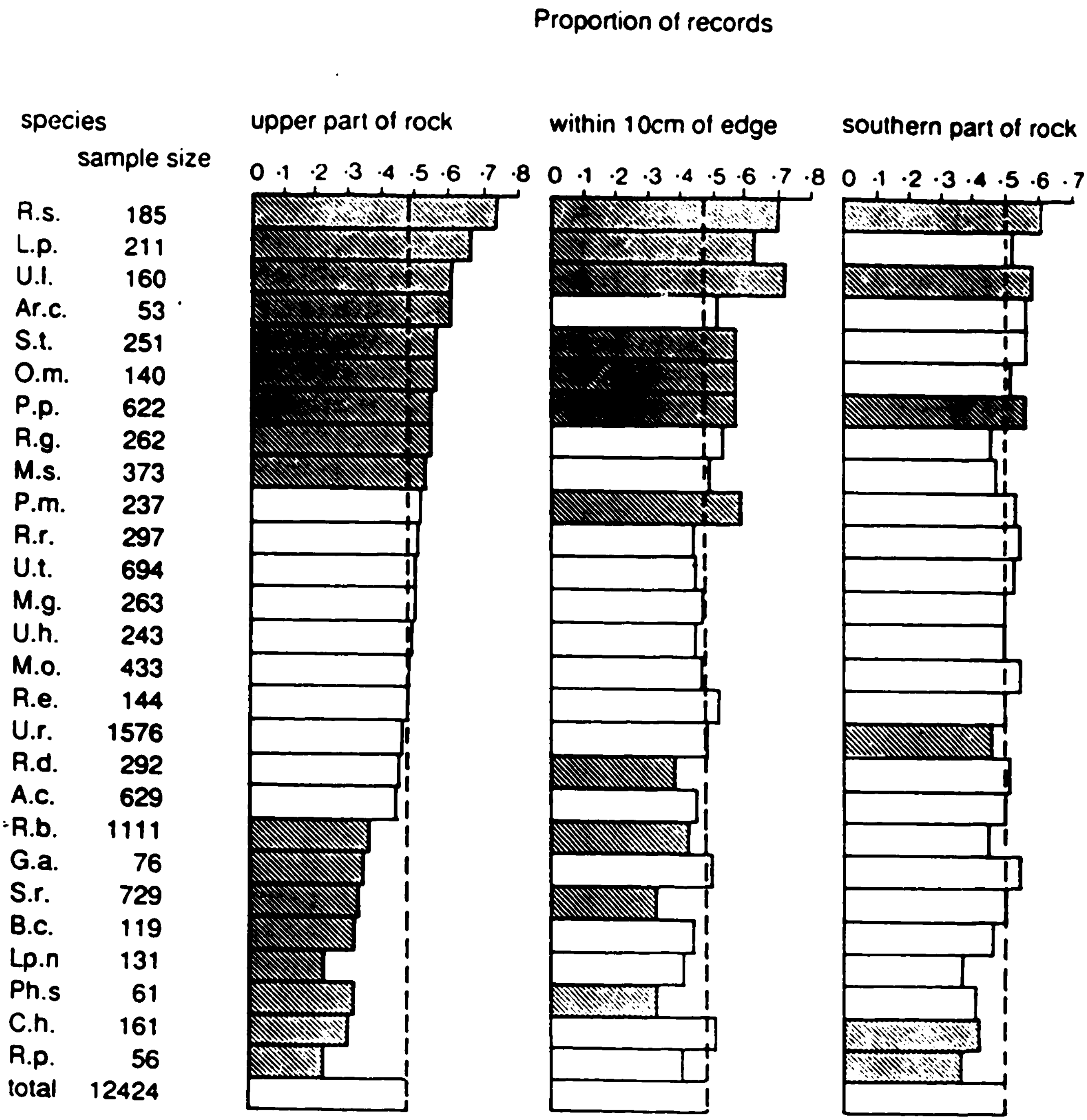
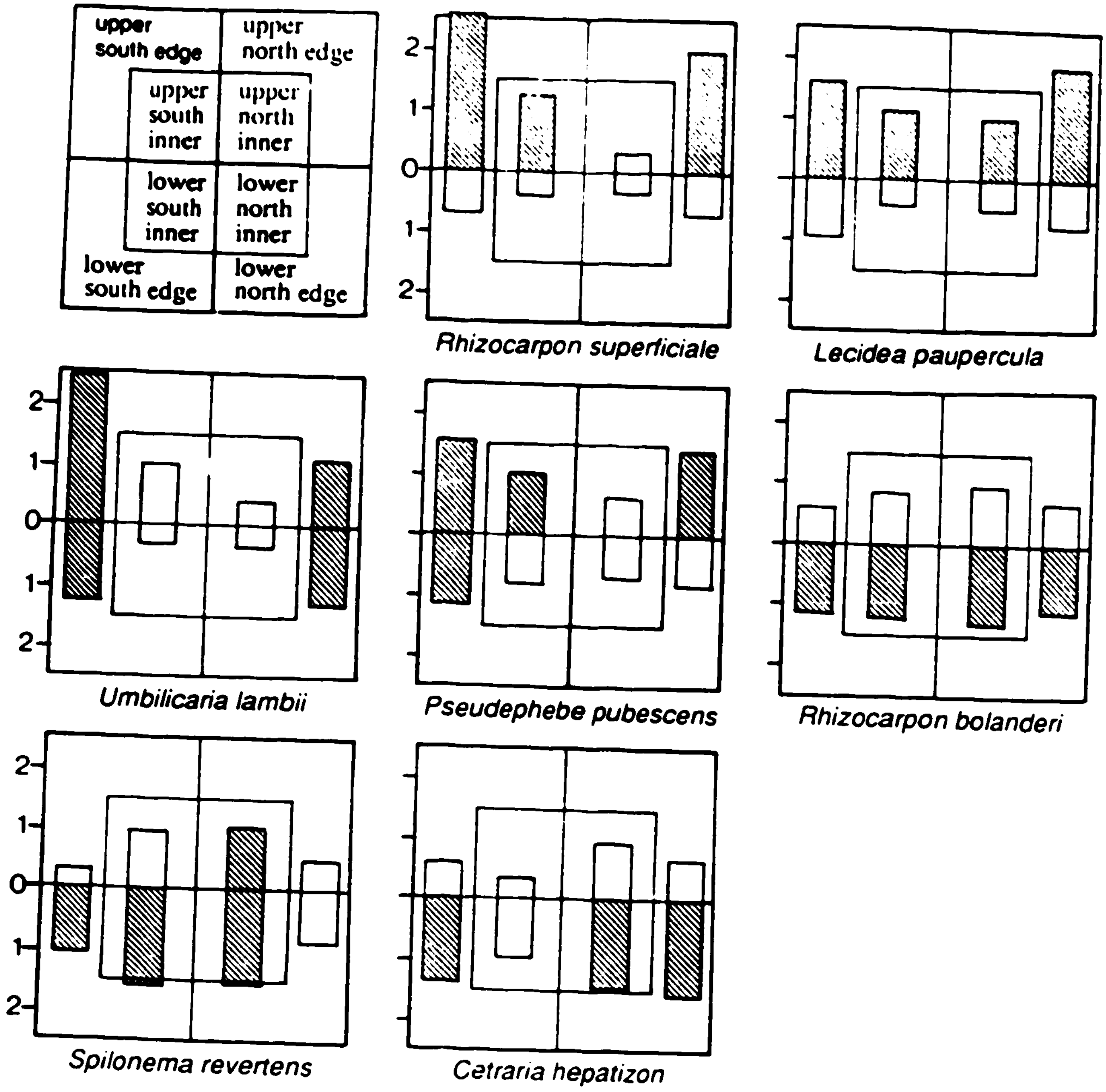


Figure 4.1: Sampling design for an individual rockface. The grid of dots represents the sampling grid. This rockface faces east, thus its southerly portion is shown on its right.

Figure 4.2: Microhabitat preferences of all species with greater than 50 records. The first column contains the species code and the second column shows the sample size for each species. Full species names can be found in Table 4.1. On the basis of this diagram the species can be divided into three groups. The first ten species are refered to as 'upper rockface species' and the the final eight species are the 'lower rockface' group. The central group of species are the 'random distribution' group. Shaded bars are those whose statistical probability of occurring by chance is less than 5%.


Proportion of records
species
sample size
upper part of rock
within 10cm of edge
southern part of rock
0 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8
0 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8
0 ·1 ·2 ·3 ·4 ·5 ·6 ·7
R.s. 185
L.p. 211
U.l. 160
Ar.c. 53
S.t. 251
O.m. 140
P.p. 622
R.g. 262
M.s. 373
P.m. 237
R.r. 297
U.t. 694
M.g. 263
U.h. 243
M.o. 433
R.e. 144
U.r. 1576
R.d. 292
A.c. 629
R.b. 1111
G.a. 76
S.r. 729
B.c. 119
Lp.n 131
Ph.s 61
C.h. 161
R.p. 56
total 12424



Rhizocarpon superficiale

Lecidea paupercula

Umbilicaria lambii

Pseudephebe pubescens

Rhizocarpon bolanderi

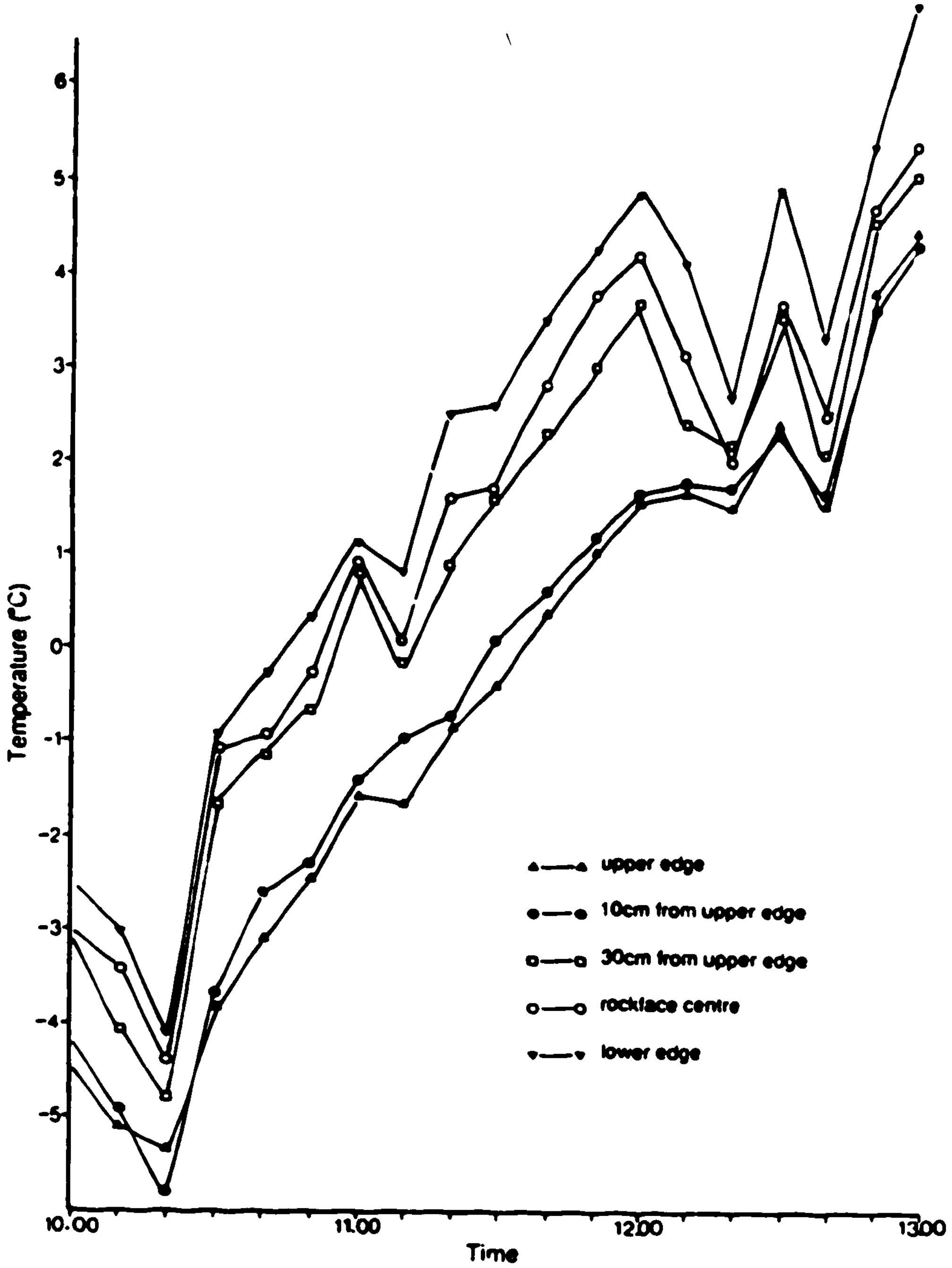
Spilonema revertens

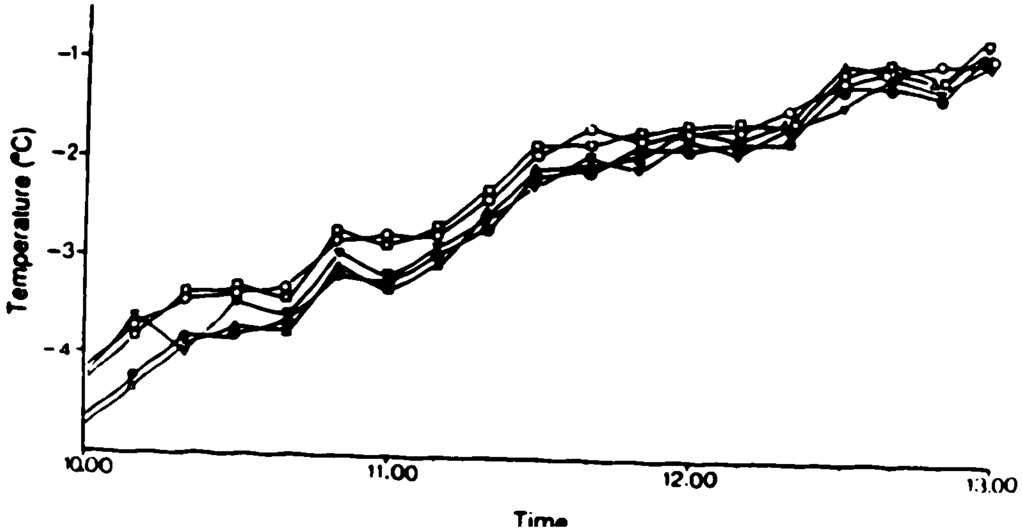
Cetraria hepatizon

Figure 4.3: Diagramatic representation of the distributions of seven species within rockfaces. The bars show observed / expected ratio for each part of the rockface. Where the observed value is greater than the expected the bar is shaded. Species illustrated are those where a log-likelihood ratio test indicated a probability value of less than 5% over all eight categories. Individual bars may not differ significantly from expected. The sample size for each lichen is shown in Table 4.1.

Figure 4.4: Rockface showing non-random lichen distributions. It can be seen that the yellow green thalli of *Rhizocarpon superficiale* are predominately around the upper edge of the rockface.

Figure 4.5: Temperature readings from 5 parts of a rockface on two consecutive days over a four hour period. a) 17 October 1987, a sunny day. b) 18 October, overcast. Each area was sampled with 5 thermocouples, and the mean of these readings is shown.


Temperature (°C)
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
10.00
11.00
12.00
13.00
Time
upper edge
10cm from upper edge
30cm from upper edge
rockface centre
lower edge


Temperature (°C)
-1
-2
-3
-4
10.00
11.00
12.00
13.00
Time

V. ENVIRONMENTAL CORRELATES OF SPECIES DISTRIBUTIONS IN THE SAXICOLOUS LICHEN COMMUNITY AT JONAS ROCKSLIDE. [4]

Introduction

The biotic and abiotic factors responsible for the organisation of plant communities, and the nature of that organisation, have long been the concern of plant ecologists. This chapter reports part of a study of the environmental correlates of spatial pattern amongst the lichens of a saxicolous lichen community at Jonas Rockslide in Jasper National Park, Alberta. The pattern of lichen distribution over individual rockfaces at this site has been described elsewhere and it was shown that each rockface consists of a number of microenvironments, amongst which lichen species are not evenly distributed (Chapter IV). The rockslide community, containing over a hundred species, was found to show spatial organisation at the scale of the individual rockface.

However a number of environmental factors act at the scale of the whole rockface in conjunction with the within individual rockface factors, and are likely to be important determinants of species distribution patterns. The role of such factors as rockface aspect, inclination from the horizontal and degree of exposure, must be studied at this larger

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4. A version of this chapter will be submitted for publication to VEGETATIO as John, E. A. Environmental correlates of species distributions in a saxicolous lichen community at Jonas Rockslide, Jasper National Park, Alberta.

scale. The ways in which species distributions are correlated with these variables will provide further information about the organisation of this community.

Jonas Rockslide is particularly suitable for a study of the correlations of environmental factors and species distributions in a saxicolous lichen community. Despite the large species diversity the community is structurally simple, as the plants are restricted to within a few millimetres of the rock surface. The rock surfaces themselves are often flat, reducing the structural complexity of the microenvironment to measureable levels, and there is only one rock type at the site.

In the absence of shading, slope and aspect determine the amount of direct solar radiation received on a rockface. Gates (1956) provides a method for calculating radiation input to a flat surface, and the relationship of slope and aspect to insolation received at latitude 52^{0} N is shown in Figure 5.1. Slope angle also has an effect on the rate of precipitation deposition and retention on the rock surface. In the absence of strong winds, horizontal surfaces are likely to receive more rain or snow than steeply sloping surfaces, and retain it for longer, thus affecting moisture available to plants growing there. In addition, surfaces which retain water weather more rapidly, affecting the texture and quality of the rock. Exposure, here defined as absence of shelter from sun or wind, will affect radiation and precipitation received and air currents reaching the rock surface, in turn determining temperature and rate of drying at the rock surface. In this study, these and other factors will be related to the pattern of lichen distributions.

Other workers have studied saxicolous lichen communities at this scale, comparing lichen distributions on whole rocksurfaces with different environmental characteristics. Larson (1980), Armstrong (1974), Pentecost (1979) and Yarranton (1966) found that slope was a factor controlling at least some lichen distributions in each of the communities they studied. Kappen & Redon (1984) found that aspect profoundly affected the lichens in a maritime antarctic saxicolous community and that this effect was related to moisture conditions. Orwin (1972) also found aspect to be important, but related this to degree of shelter from abrasive winds, as well as moisture conditions. Armstrong (1974) and Pentecost (1979) also found that aspect had a lesser, but important role in controlling species distributions. Experiments by Armstrong (1975) showed that lichen growth rates changed when transplanted to rocks of different aspect. Light intensity was correlated with lichen distributions by Lawrey (1981) and Armstrong (1974). Larson (1980) found that 'exposure' could be related to lichen distributions and Flock (1978) correlated some saxicolous lichen distributions to a 'snow-cover-soil-moisture gradient'. Armstrong (1974) also found that rock porosity and microtopography were important determinants of the micro-environment at the rock surface.

In this study the correlation of environmental parameters with species distributions will be determined using a canonical correlation analysis.

Study site and methods

Study site

The field work was conducted at a large rockslide ($52^{\circ}26'$N, $117^{\circ}24'$W) in Jasper National Park Alberta, Canada. The rockslide is situated on Highway 93, 75km south of Jasper Townsite (Figure 1.1) and is composed of pink quartzite sandstone (Bruce 1978), forming blocks of a range of sizes, but commonly up to 3m x 3m x 1m. There are many flat rockfaces. Jonas Rockslide is considered one of the major rockslides of the Canadian Rockies (Cruden 1976). It ranges from 1500m to 2200m in elevation, which places it in the subalpine, and is 3.5km long and 1km wide. The average annual temperature at that elevation is 0°C & average annual precipitation over the period 1971 to 1980 was 793mm as recorded at the Sunwapta warden station, 3km from the rockslide (Holland & Coen 1983). It is on a southwest facing slope in the Eastern Main Ranges. The rockslide is believed to have fallen at least 500 years ago, based on lichenometric evidence (Chapter III).

The dominant plants at the site are saxicolous lichens, which cover 87% of exposed rock surfaces. 100 species of saxicolous lichens have been recorded at Jonas Rockslide, of which 19 have a cover value greater than 1%. Trees cover less than 20% of the area of the rockslide. Picea engelmannii is present on the lower slopes and Pinus albicaulis occurs on the upper parts of the rockslide.

Methods

Rockfaces were sampled along three parallel elevational transects on the rockslide. Transects were started at positions where there was a clear view along the vertical axis of the rockslide and where there was easy access to the rockslide. They were run parallel to the direction of maximum altitudinal variation. The first sampling station was 90m from the start of the transect and others at 90m intervals thereafter. The range of elevation was from the Sunwapta River (1500m) to the maximum height of safe travel on the rockslide (2200m). Eighty-four rockfaces were sampled. At each sampling station elevation was measured using an altimeter. A bench mark where Highway 93 crosses the rockslide was used as a reference point at the start and finish of each transect to correct for any pressure changes during the sampling period. Elevations are expressed as a relative value, with the river given the value 0.

At each sampling station the three nearest suitable rockfaces were selected for sampling, using only the criteria that they should be flat, larger than 1m x 1m in area, between 0° and 90° in slope angle and not closely sheltered by trees. Each rockface was sampled with a grid of points, after the plotless sampling method of Yarranton (1966). The columns of the grid were 20cm apart, and the rows 10cm apart, as shown in Figure 4.1. For details see Chapter IV. At each grid point the species of lichen present was identified with the aid of a portable dissecting microscope. Many lichen genera, particularly the crustose genera, contain species that are indistinguishable without detailed examination under a compound microscope and chemical testing. For these species apothecia were collected from fertile thalli & chemical tests were made on the thallus in the field. The chemicals used were $Ca(ClO)_2$ (C), as found in household bleach, Metzler's reagent (I), and 10% KOH solution (K). (The other commonly used lichenological chemical, PD, was not used in the field due to its carcinogenic properties.) The chemicals were applied with a micropipette (diameter 10u) to the thallus medulla after it had been exposed with a razor blade.

At each rockface environmental parameters were measured (Table 5.1). Aspect was measured with a compass, as the direction in which the rockface was facing, ranging from 0^{o} (magnetic north) to 360^{o}. It was later corrected for magnetic declination. An inclinometer was placed on a rigid meter ruler and the steepest slope angle of the rockface was measured, ranging from 0^{o} (horizontal) to 90^{o}. As the rockfaces chosen were all flat, the above variables do not vary appreciably over the rockface. The degree of weathering of the rockface surface was estimated, using a scale of 1 to 5. A value of 1 indicates absence of weathering; the rock does not chip when hit with a hammer, while 5 denotes a rock with a crumbly, flaky surface. The number of trees within a 30m radius was recorded. The rock colour was compared with a soil colour chart, and a value for each rock recorded in the field. These values were later ranked from light to dark and placed in one of five subjectively determined colour categories given values from 1 (pale) to 6 (dark red or purple).

Snow depth and % cover was measured on 142 rockfaces of varied aspect and slope in February 1987.

For the purposes of this study the amount of direct solar radiation received by a rock surface was modelled using equations found in Gates (1956) and Campbell (1977):

$$S\ (\text{sloped surface}) = S\ (\text{horizontal surface}) \times \cos(i)$$

where: $$S\ (\text{horizontal surface}) = Sp \times \sin\phi$$

$$\cos(i) = \cos\beta \cos(z) + \sin\beta \sin(z) \cos(a-\eta)$$

$$\sin\phi = \sin\lambda \sin\delta + \cos\lambda \cos\delta \cos(15t)$$

η=aspect of rock,measured from the south; λ=latitude; δ=solar declination; t=time from solar noon; z=zenith angle of the sun; a= azimuth of sun; β= slope of rock; S =direct beam solar radiation received

A number of simplifying assumptions were made. Shading by other rocks or trees was not accounted for. It was assumed that the duration of sunshine over the whole rock slide was the same (although it would tend to vary with position), and the model calculated radiation received between 8am & 7pm in the summer, and between 10am and 5pm at the equinox. Beam strength was assumed not to vary either diurnally or annually, and was given an arbitrary value. No attempt was made to include reflected or diffuse radiation.

As an estimate of total radiation received over the year for each rock, radiation input was calculated at half-hourly intervals for one day at the summer solstice and the equinox. The values for the half-hourly intervals were summed and the summer values added to twice the equinox values to obtain a radiation index for each rock. Winter values were not included because snow cover would prevent radiation from reaching most rock surfaces.

The size of each rockface studied was calculated from the number of grid points examined, and used as a further environmental variable.

Table 5.1 summarises all the environmental variables used and Table 5.2 shows the distribution of rocks amongst each of the environmental variables.

Analytical methods

To examine the relationships between the measured environmental variables and species distributions a canonical correspondence analysis was performed using the CANOCO program of Ter Braak (1987). The correspondence analysis option was used. This program is used to ordinate species amongst axes that are constrained to be linear combinations of the measured environmental variables, so that the relationship between species and environment can be clearly seen. The input matrix of environmental variables may contain both nominal and measured values. All variables are standardised by CANOCO during the analysis, so that they have mean of zero and standard deviation of one.

In order to include the effects of position on the rockface, each rockface was split into eight subsections for this analysis, and each subsection included as a sample plot. Eighty-five of the sampled rocks were used in this analysis resulting in 672 subplots (84 rockfaces X 8 subsections). Species abundances were expressed as number of occurrences per plot and were not transformed; they ranged from 0 to 14. The environmental variables for each subsection included the nominal variables 'top', indicating whether the subsection was from the upper or lower portion of the rockface, 'south', indicating whether it was on a northerly or southerly part of the rock and 'edge', indicating whether it was an outer or inner subsection. The division of a rockface into subsections is illustrated in figure 4.1. The other environmental variables of slope, sun (radiation received), altitude, weathering, colour and number of trees were the same for all 8 subsections of the rockface.

As with any ordination technique, the CANOCO programme makes certain assumptions about the way the species are distributed with respect to the environmental variables, in this case that the species curves are Gaussian and unimodal and that their optima fall within the range of the variables measured. However in a complex community such as this, a range of responses are likely to be seen amongst the species to their environment and these assumptions are unlikely to be true for all species. Thus, to help corroborate species environment relationships found using CANOCO, a non-parametric correlation coefficient, Spearman's rho, was calculated for each species with each environmental variable.

Results

Snow cover

On 18 & 19 February 1987 average snow depth over 141 studied rockfaces at Jonas Rockslide was 24cm. However, parts of many rockfaces were free of snow, with a mean value of 82% snow cover, while 62% of rockfaces had some snow free areas, and 14% of rockfaces had either upper or lower edges exposed. On 50% of rockfaces the southernmost edge was exposed, and on 5% of rockfaces the northernmost edge was snow free. Snow cover varied with rockface slope: steeper rockfaces having less snow and those steeper than 78^{o} having no snow. Rockface aspect had no clear effect; it affects a complex of factors including wind direction at time of snow deposition and radiation received at snow melt. Exposure is an important factor; exposed rockfaces and parts of rockfaces are likely to be snow free. Although this survey was of necessity limited in scope, general conclusions can be drawn, that would be applicable in unexceptional snow conditions. Snow free areas are steeper rockfaces and on rockface edges, especially the most southerly and upper and lower edges. Horizontal rockfaces hold the deepest snow.

Correlations between environmental variables

The matrix of correlations between environmental variables, as produced by CANOCO, is shown in Table 5.3. The values are Pearson correlation coefficients (Ter Braak 1987b). The environmental variables are shown to be largely independent, however there are three significant correlations. Slope and weathering show a negative correlation, and slope is also negatively correlated with radiation, this is because horizontal rocks receive radiation all day long. There is a negative relationship between trees and weathering.

Correlations between environmental variables and ordination axes

The first ordination axis has an eigenvalue of .12. Using a monte-carlo simulation technique available in CANOCO (Ter Braak 1987) with 99 simulations this result is shown to be significant at the .01 probability level. (A monte-carlo simulation allows an estimation of the probability that an eigenvalue could have been obtained by a random arrangement of species distributions with respect to the environmental variables.) Thus, although the eigenvalue seems low, it has a high level of statistical significance.

The matrix showing correlations between environmental variables and the ordination axes is shown in Table 5.4. It shows that altitude is the major determinant of axis 1 (eigenvalue 0.12), with slope, weathering and the nominal variables 'top' and 'edge' also correlated. Axis 2 (eigenvalue 0.07) is primarily determined by slope, with 'sun' and 'trees' also important. The third axis (eigenvalue 0.05) is correlated primarily with 'trees' and secondarily with rockface size. The final axis is the least important in explaining variation in species distributions (eigenvalue .04), and is correlated with altitude, size and 'sun'. Thus altitude and slope are the most important correlates of species distributions at Jonas Rockslide, with trees, sun, 'top', 'edge', weathering of intermediate importance and size and colour of little importance.

Species-environment bi-plot

The species environment bi-plot illustrates the species positions on the ordination axes, and the direction of maximum variation of each of the environmental variables in relation to each of the axes. The centroids of the nominal environmental variables ('top', 'edge' and 'south') are shown. The biplot allows easy assessment of the importance of each environmental variable in determining the position of each species on the ordination diagram.

The first four axes of the species-environment biplot account for 80.7% of the variation amongst species, as shown in Table 5.5, produced by the CANOCO program. The species-environment biplots for axes 1 & 2 and axes 1 & 3 are shown in Figures 5.2 & 5.3. This shows the species positions on these axes, with species of low weight (i.e. the rarer species in the community, occurring with a cover value of less than 0.5%) denoted by an open circle. The species at the edges of the ordination are usually low in weight, and had little influence in defining the axes. The direction of greatest variation in each environmental variable is superimposed as an arrow. The length of each arrow indicates the relative importance of that parameter in determining the axes. The size of the angle between the arrow of an environmental variable and an axis is an inverse measure of their correlation. As the environmental variables are standardised by this program all the environmental arrows pass through the origin of the ordination.

It is suggested (Ter Braak 1987) that the species can be ranked with respect to each environmental variable by projecting their positions onto the arrow of the environmental variable, using a line that is perpendicular to the arrow. This allows a direct comparison of the correlation of each environmental variable with the distribution of each species. Thus, for example, it can be seen that *Rhizocarpon eupetraeum* has a positive correlation with the variable slope, being found on steeper rocks, whereas *R. bolanderi* has a negative correlation with this variable.

A problem in the interpretation of the species-environment bi-plot is that each species has its position determined in relation to all the environmental variables and therefore its apparent relationship to one particular environmental variable may be somewhat misleading.

Comparison of species-environment biplot and non-parametric correlation coefficients

The results of the Spearmans' rho tests comparing species abundances with environmental variables is shown in Table 5.6. These results can be used to confirm a relationship between a species and a particular environmental variable that is indicated by the species-environment bi-plot. In general the two techniques produce results that are in close agreement. One case in which the results are different is the relationship between Umbilicaria lambii and sun. In the biplot it appears to have a strong positive correlation with 'sun' yet the non-parametric test indicates that there is no significant relationship. The position of this species in the biplot may have been determined by it's relationship to other environmental factors.

Discussion

Effects of environmental variables

Few of the measured environmental variables represent a simple environmental gradient; each of the characteristics measured have a role in controlling a number of primary determinants of species composition. For instance, slope not only affects water availability on the rock surface, but also affects incoming radiation, and winter light quality via depth of snow cover, among other factors. However, it is worth considering what the major effects of each of the measured environmental variables are.

Elevation undoubtedly represents a highly complex gradient. The upper parts of the rockslide are more exposed and temperatures are lower, on average. Wind speed increases with increasing altitude (Creveld 1981). Lichens low on the rockslide are in closer proximity to the Sunwapta River, which would not only increase humidity but during periodic floods leave a deposit of silt on the surface of the rocks. This deposit is calcareous, and so radically changes the lichen environment. However this only affects a very small proportion of the sampled rocks.

Increasing slope is associated with xerophytic and chionophobic species, as steeply inclined rocks recieve less precipitation (Creveld 1981) and retain less snow (see results). Species often found on rocks of low slope have a more mesic environment but may also need adaptations to heat stress of a high radiation environment. In addition, horizontal rocks are most prone to weathering (Table 5.3), presumably due to the retention of surface water (Creveld 1981), so that species growing there have a less stable substrate, providing opportunities for recolonisation, and possibly being more suitable for rapidly growing species.

A large number of trees around a rock provides shelter from sun and wind and alter the rock surface environment by litter deposition.

The variable 'sun' represents a simple gradient, representing only incoming direct beam radiation. However, its relative unimportance (compared to 'slope' and 'altitude') in determining species distributions is likely to be due to the fact that lichens can only photosynthesize when moist or in humid conditions, and have few water retention mechanisms. If the sun shines after rain, the rocks dry out in several minutes. Thus most photosynthesis occurs on overcast days, when radiation is diffuse. This variable will have an effect on species distributions via its effect on the temperature of dry rocks. Coxon & Kershaw (1983) showed that lichens can suffer heat stress when dry, at temperatures reached by a rock surface on a sunny day.

Rock colour is related to its chemical composition, and also its degree of weathering, but is not an important correlate of species distributions.

Rockface size has an effect on the microclimate at the rock surface. The larger its surface area, the less effect cooling 'edge effects' will have on the microclimate at the rockface centre.

The nominal variables, 'top', 'edge' and 'south' refer to position on the rockface, as shown in Figure 4.1. Upper parts of the rockface are more exposed, less likely to be shaded than lower parts and more likely to be snow free. Rockface edges are also more exposed, experience longer snow free periods and do not reach such high temperatures as inner parts of the rockface due to cooling air circulation caused by the higher windspeeds received by the edges of an object (Creveld 1981). Southerly parts of the rockface are more likely to be snow free than northerly parts due to greater insolation. Those species growing most frequently on top, edge and southerly portions of rockfaces are likely to be chionophobic and tolerant of exposed conditions.

Characterisation of species groupings

Table 5.7 shows the species names and their percent cover over all sampled rockfaces for all species included in this analysis.

As would be expected from the complex nature of the environmental gradients the species do not fall into obvious groups. However, examination of Figure 5.2 allows categorisation of species which agree well with field observations, and based on the first two ordination axes, loose species groupings can be identified, based on the correlations of their distributons with environmental variables. The first two axes together account for 53% of the variation in the data (Table 5.5).

In the lower left hand quadrant of the ordination is a group of species associated with rockfaces of low altitude, low slope, high amounts of incoming radiation and highly weathered rocks. The dominant species in this group, in terms of % cover, are Rhizocarpon bolanderi and Spilonema revertens. This group of species is tolerant of high temperatures as they are on rocks which receive high amounts of incoming radiation, however these are probably also the most mesic rocks. Thalli of species in this group are rarely discrete in shape, and often intermingle, which may be indicative of a highly competitive environment. This group is associated with the only two plants in this analysis that could be considered indicative of progressing succession; Grimmia affinis and Cladonia pyxidata. The fact that these rocks are more weathered and flatter has allowed some buildup of particulate matter, leading to a successional trend. Species from this group are rarely found around the edges or on the upper parts of rocks. At the far edge of this group on the ordination diagram are species only found very close to the river, Staurothele clopima and Bellamerea alpina.

The second group of species appears in the lower right corner of the ordination diagram. These are species positively correlated with slope, altitude and radiation. They are most often found on the upper and outer parts of a rock surface, thus are exposed and snow free in winter. Their exposed position may prevent them reaching the high temperatures of the previous group. Characteristic species of this group are Rhizocarpon superficiale, Pseudephebe pubescens and Umbilicaria lambii. Thalli of species in this group are often discrete and easily definable, except for those of Pseudephebe, which can grow over and among other thalli.

In the centre of the diagram is the third group of species, which are probably generalists with regard to the measured environmental factors. Using this technique it is hard to distinguish generalists from species whose optima coincide with the means of the environmental variables. However experience of their field distributions places them as widespread generalists. Typical are Rhizocarpon grande, Aspicilia cinerea and Umbilicaria torrefacta. The species in this group are also generalists with respect to microhabitat, being equally likely to be found on all parts of a rockface.

A fourth group is probably best characterised by Rhizocarpon eupetraeum. These species tend to be found on steeply sloping, higher elevation surfaces receiving little direct radiation. Their environment is probably xeric and snow free. Thalli of species in this group are often discrete and surrounded by uncolonised rock, suggesting that competition may be unimportant in these environments.

In the upper left quadrant is a very loose grouping of species associated with shady rocks that are less extreme in altitude and slope than the fourth group. They are more often found on lower parts of rocks than upper, and probably have a more mesic environment than the previous group. Cetraria hepatizon is characteristic of this group. Figure 5.3 shows the ordination obtained on axes 1 & 3. The third axes allows separation of the effects of environmental factors which vary in the same direction on axes 1 & 2. For instance the effects of trees and size of rock on species distributions can be separated by looking at axis 3. This separates species which may appear together in the first ordination diagram, for instance Cetraria hepatizon and Lecanora cenisea.

It is evident that this is a highly complex plant community, both in terms of the variation in environment within and between rockfaces and in terms of the large species diversity and the responses of individual species to their environment. Although it is clear that abiotic factors have an important role in the organisation of this community, biotic processes such as competition, are also involved. The distributions of individual species may not be determined solely by their ecophysiological tolerances to environmental conditions, but also in part by their competitive abilities. For instance, some species may be excluded from areas suitable for rapidly growing species by being unable to compete with them. Evidence that competition does occur among the species of a saxicolous lichen community has been supplied by other workers (Hawksworth & Chater 1979, Pentecost 1980), and indirect evidence that it can affect community composition is found in the studies of Lawrey (1981) and Yarranton & Green (1966). The role of such biotic factors cannot be assessed in the present study.

The first four axes of this ordination only explain 83 % of the variation in species distributions, thus some of the variation cannot be explained by a species environment bi-plot. It is possible that stochastic processes may also have a role to play, for instance in the initial colonisation of a rockface by a lichen, which depends on the presence of both algal and fungal propagules. It is also certain that some ecological factors important to lichen distributions have not been measured.

Summary

The importance of various abiotic environmental factors in determining species distributions in a saxicolous lichen community at Jonas Rockslide, Jasper National Park, Alberta is assessed using a canonical correspondence analysis. This technique allows ordination of species on axes determined by measured environmental variables. The variables found to be most highly correlated with species distributions are altitude on the rockslide, inclination from horizontal of the rockface (slope), and an estimate of direct beam radiation received by each rockface. These results are supported by the results of a non-parametric correlation test. These variables are thought to determine temperature and water availability at the rock surface. Using the first two ordination axes, species can be loosely divided into groups, based on shared responses to the measured environmental variables.

Bibliography

Armstrong, R. A. (1977) The response of lichen growth to transplantation to rock surfaces of different aspect. New Phytologist, 78: 473-478

Armstrong, R. A. (1974) The descriptive ecology of saxicolous lichens in an area of south Merionethshire, Wales. Journal of Ecology, 62: 33-46

Campbell, G. S. (1977) An introduction to environmental biophysics. Heidelberg Science Library. Springer-Verlag New York, Heidelberg, Berlin

Creveld, M. (1981) Epilithic lichen communities in the alpine zone of southern Norway. Bibliotheca Lichenologica. J. Cramer. Fl. 9460 Vaduz.

Flock, J. W. (1978) Lichen - bryophyte distribution along a snow-cover soil-moisture gradient, Niwot Ridge, Colorado. Arctic and Alpine Research, 10: 131-147

Gates, D. M. (1965) Radiant energy, its reciept and disposal. In Waggoner, P. E. (ed.) Agricultural Meteorology. Meterorological Monographs 6 NO.28American Meteorological Society Boston pp 1 - 26

Hawksworth, D. L. & Chater, A. O. (1979) Dynamism and equilibrium in a saxicolous lichen mosaic. Lichenologist, 11: 75-80

Holland, W. D. & Coen, G. M. (1983) Ecological (Biophysical) land classification of Banff & Jasper National Parks. Volume II Soil and vegetation resources.Alberta Institute of Pedology & Environment Canada

Kappen, L. & Redon, J. (1984) Microclimate influencing the lichen vegetation on different aspects of a coastal rock in the maritime Antarctic. Instituto Antarctico Chileno (INACH), Serie Cientifica, 31: 53-65

Lawrey, J. D. (1981) Evidence for competitive release in simplified saxicolous lichen communities. American Journal of Botany, 68: 1066-1073

Orwin, J. (1972) The effect of environment on assemblages of lichens growing on rock surfaces. New Zealand Journal of Botany, 10: 37-47

Pentecost, A. (1980a) Aspects of competition in saxicolous lichen communities. Lichenologist, 12: 135-144

Pentecost A. (1980) The lichens and bryophytes of rhyolite & pumice-tuff outcrops in Snowdonia, and some factors affecting their distribution. Journal of Ecology, 47: 371-413

Ter Braak, C. J. F. (1987) CANOCO - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO institute of applied Computer Science, Wageningen, The Netherlands.

Ter Braak, C. J. F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology, 67: 1167-1179

Yarranton, G. A. & Green, W. G. E. (1966) The distributional pattern of crustose lichens on limestone cliffs at Rattlesnake point, Ontario. Bryologist, 69: 450-461

Table 5.1: Environmental variables considered in the CANOCO analysis

variable	values taken	explanation
top	0 - 1	whether upper (1) or lower (0) part of rockface
edge	0 - 1	whether within 10 cm. of rockface edge (1) or not (0)
south	0 - 1	whether southerly (1) or northerly (0) part of rockface
slope	0 - 90	inclination from horizontal of rockface
alt	0 - 250	elevation above Sunwapta River in metres
size	50 - 200	size of whole rockface (number of sample points)
colour	1 - 5	colour of rockface; pale (1) to dark (5)
weath.	1 - 5	estimate of degree of weathering of rockface; slight (1) to extreme (5)
trees	1 - 20	number of trees within 30m radius of rockface
sun	1 - 300	estimate of direct beam solar radiation received by rockface

Table 5.2: Distributions of each of the environmental variables for the 84 rocks used in the CANOCO analysis of Chapter 5. See methods for details. For a summary for all 128 sampled rocks see Appendix 3.

A. Altitude.

Class range (m)	0-10	11-30	31-50	51-100	101-150	151-200	200-250
number of rocks	13	7	8	25	17	10	6

B. Slope.

Class range (o)	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-90
number of rocks	7	19	20	17	14	5	2	2

C. Aspect.

Class range (o)	0-44	45-89	90-134	135-179	180-224	225-269	270-314	315-359
number of rocks	6	10	5	18	15	15	3	12

D. Direct beam radiation.

Class range (arbitrary units)	0-40	41-80	81-120	121-160	161-200	201-240	240-280
number of rocks	3	4	6	16	24	28	5

E. Trees within 30m of rockface.

Class range (number of trees)	0	1-5	6-10	11-15	16+
number of rocks	17	40	11	9	8

Table 5.2: (continued)

F. Rock colour.

Class (1=pale, 6=dark)	1	2	3	4	5	6
number of rocks	9	7	9	14	29	17

G. Weathering of rock.

Class (1=little weathered)	1	2	3	4	5
number of rocks	20	48	10	7	0

H. Size.

Class (number of points on rock)	40-60	61-80	81-100	101-120	121-140	141-180
number of rocks	8	28	21	14	10	6

Table 5.3: Correlations between environmental variables. Values are Pearson correlation coefficients.

	top	edge	south	slope	alt	size	colour	weath	trees	sun
top	1.000									
edge	.008	1.000								
south	.015	-.016	1.000							
slope	-.004	.008	.014	1.000						
alt	-.013	-.005	.014	.180	1.000					
size	.015	-.107	.028	-.150	.041	1.000				
colour	-.008	.008	-.019	-.042	-.171	-.078	1.000			
weath	-.010	-.019	-.012	-.350	-.087	.148	.029	1.000		
trees	.015	-.009	.019	198	.239	-.003	.020	-.296	1.000	
sun	-.008	-.006	.032	-.299	.107	-.001	-.074	-.019	-.022	1.000

Table 5.4: Correlations of environmental variables with ordination axes. Values are Pearson correlation coefficients.

top	.2576	-.0835	.1926	.0889
edge	.2003	-.0927	.1377	.1098
south	.0801	-.0776	-.0342	.0146
slope	.2819	.3878	-.0028	.1552
altitude	.3557	.1168	.0616	-.2833
size	-.0452	.1335	-.2160	-.2248
colour	-.1857	-.1614	.1362	.0422
weather	-.2515	-.1260	-.1572	.0377
trees	-.1444	.3070	.3447	-.1518
sun	.0612	-.3296	.0124	-.2105
	species axis 1	species axis 2	species axis 3	species axis 4

Table 5.5: Percent variance accounted for by the first four axes of the species-environment bi-plot

axis	percent variance (cumulative)
1	34.9
2	54.3
3	68.4
4	80.7

Table 5.6: Results of Spearman's rho test comparing species distributions (number of occurrences) with environmental variables for 85 whole rock surfaces. Species occurring on over 15 rocks included. Values > .2138 significant at 5% level. Full species names are shown in Table 5.7

species	slope	alt	size	weath	tree	colour	sun
arc cen	.197	.104	.122	.062	-.130	-.074	-.220
asp cin	.350	.070	-.159	.420	.050	-.04	.123
cet hep	.097	.254	.177	.069	.248	-.096	-.206
led pau	-.041	-.020	-.146	.047	.081	-.020	-.080
ldl car	.020	-.180	.149	.118	-.217	-.056	.019
lep neg	-.159	.146	.276	.120	-.057	-.173	-.029
mel gra	.208	.284	.119	-.265	-.129	-.125	-.032
mel pan	.337	.228	.208	-.090	.190	-.299	-.154
mel sor	-.013	.271	.247	-.028	.184	-.170	.001
mel sty	.060	.424	.263	-.050	.183	-.187	-.022
orp mor	.249	.195	.121	-.163	-.194	-.157	-.073
pse min	-.156	-.041	.014	-.032	-.094	-.022	.393
pse pub	-.010	.213	-.096	-.107	-.308	-.012	.205
rhi bol	.303	.141	.080	.125	.184	-.164	.014
rhi dis	-.216	-.310	-.114	.049	-.266	-.151	.083
rhi eup	.378	.235	.152	-.101	.081	-.194	-.351
rhi geo	.010	-.108	-.068	.174	.128	.141	-.078
rhi gra	.028	.245	.030	-.002	-.016	.134	.072
rhi pol	-.219	-.090	.124	.239	-.247	-.050	-.256
rhi sup	.244	.027	-.243	-.144	-.060	.098	.182

Table 5.7 : Species included in the analysis in Chapter 5.

code	Species	% cover
arc cen	*Arctoparmelia centrifuga* (L.) Hale	.31
arc inc	*A. incurva* (Pers.) Hale	.06
arc sub	*A. subcentrifuga* (Oxner) Hale	.20
asp cae	*Aspicilia caesiocinerea* (Malbr.) Arnold	.27
asp cin	*A. cinerea* (L.) Korber	5.10
bel alp	*Bellemerea alpina* (Sommerf.) Clauz. & Roux	.21
bel cin	*B. cinereorufescens* (Ach.) Clauz. & Roux	.96
bro oro	*Brodoa oroarctica* (Krog) Goward	.29
bue lac	*Buellia lacteoidea* B. de Lesd.	.37
can vit	*Candelariella vitellina* (Hoffm.) Mull. Arg.	.10
cet hep	*Cetraria hepatizon* (Ach.) Vainio	1.30
cla pyx	*Cladonia pyxidata* (L.) Hoffm.	.17
dim ore	*Dimelaena oreina* (Ach.) Norman	.08
dip scr	*Diploschistes scruposus* (Schreber) Norman	.06
lec cen	*Lecanora cenisea* Ach.	.08
lec fru	*L. frustulosa* (Dickson) Ach.	.08
lec int	*L. intricata* (Ach.) Ach.	.17
led aur	*Lecidea auriculata* Th. Fr.	.29
led con	*L. confluens* (Weber) Ach.	.09
led pau	*L. paupercula* Th. Fr.	1.70
ldl car	*Lecidella carpathica* Korber	.37
ldl sti	*L. stigmatea* (Ach.) Hertel & Leuck.	.06
lep neg	*Lepraria neglecta* (Nyl.) Lettau	1.05

Table 5.7: (continued)

code	species	% cover
mel gra	*Melanelia granulosa* (Lynge) Essl.	2.12
mel pan	*M. panniformis* (Nyl.) Essl.	.35
mel sor	*M. sorediata* (Ach.) Goward & Ahti	3.48
mel sty	*M. stygia* (L.) Essl.	3.00
orp mor	*Orphniospora moriopsis* (Massal.) D.Hawks.	1.13
par omp	*Parmelia omphalodes* (L.) Ach.	.25
par sax	*P. saxatilis* (L.) Ach.	.12
pha sci	*Phaeophyscia sciastra* (Ach.) Moberg	.49
pse min	*Pseudephebe minuscula* (Arnold) Brodo & D. Hawks.	1.91
pse pub	*P. pubescens* (L.) M. Choisy	5.01
rhi alp	*Rhizocarpon alpicola* (Anzi) Rabenh.	.11
rhi bol	*R. bolanderi* (Tuck.) Herre	8.94
rhi dis	*R. disporum* (Naeg. *ex* Hepp) Mull. Arg.	2.35
rhi eud	*R. eupetraeoides* (Nyl.) Blomb. & Forss.	.18
rhi eup	*R. eupetraeum* (Nyl.) Arnold	1.18
rhi geo	*R. geographicum* (L.) DC.	2.11
rhi gra	*R. grande* (Flotow) Arnold	2.39
rhi pol	*R. polycarpum* (Hepp) Th. Fr.	.45
rhi sup	*R. superficiale* (Schaerer) Vainio	1.49
rhz chr	*Rhizoplaca chrysoleuca* (Sm.) Zopf	.06
rhz mel	*R. melanophthalma* (Lam. & DC.) Leuck. & Poelt	.31
rin tur	*Rinodina turfacea* (Wahlenb.) Korber	.18
sch ten	*Schaereria tenebrosa* (Flotow) Hertel & Poelt	2.02

Table 5.7: (contd.)

code	species	% cover
spi rev	*Spilonema* *revertens* Nyl.	5.87
sta clo	*Staurothele* *clopima* (Ach.) Th. Fr.	.17
umb deu	*Umbilicaria* *deusta* (L.) Baumg	.07
umb hyp	*U*. *hyperborea* (Ach.) Hoffm.	5.59
umb lam	*U*. *lambii* Imsh.	1.29
umb tor	*U*. *torrefacta* (Lightf.) Schrader	1.95
umb vel	*U*. *vellea* (L.) Ach.	.27

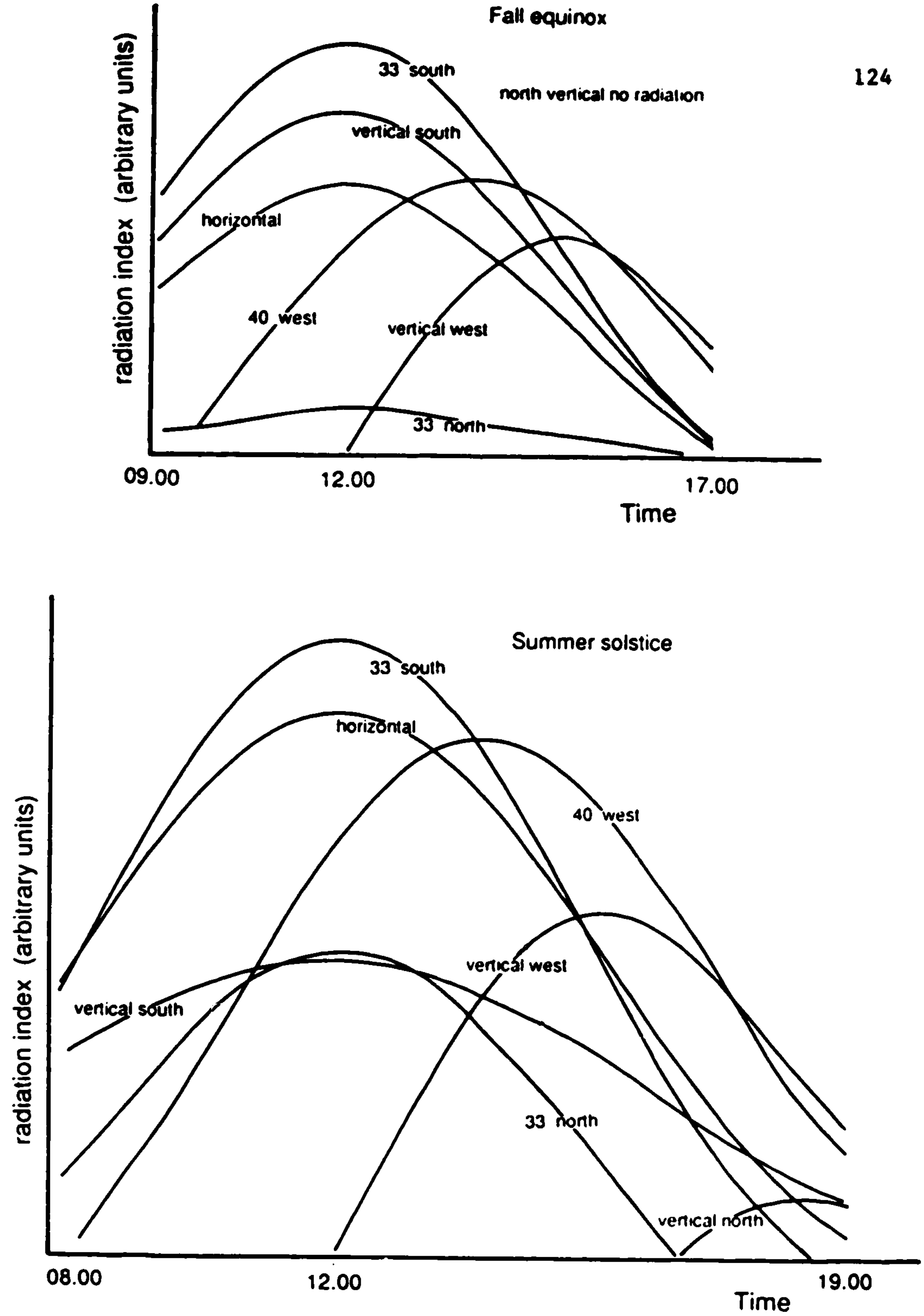
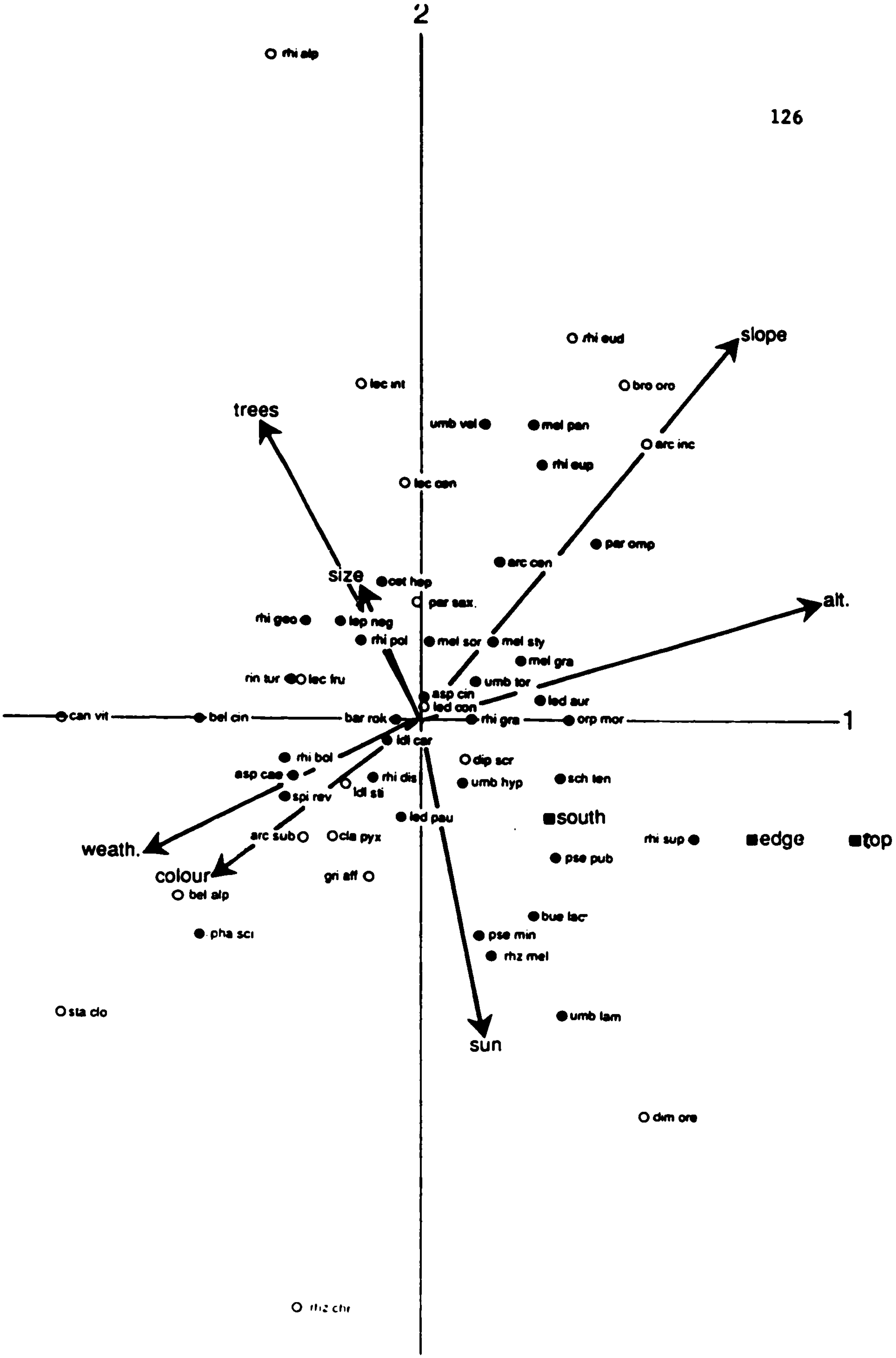


Figure 5.1: Relationship of slope and aspect of surface to direct solar radiation received per unit area at 52°N. Values are relative, therefore no units are given.

Figure 5.2: Species-environment bi-plot for axes 1 & 2 of CANOCO ordination. Species positions are shown by open or closed circles. Open circles denote species with a cover value of less than 0.2%, closed circles represent species with a greater cover value. Arrows represent the direction of maximum variation of the measured environmental variables and squares represent the centroid positions of nominal variables.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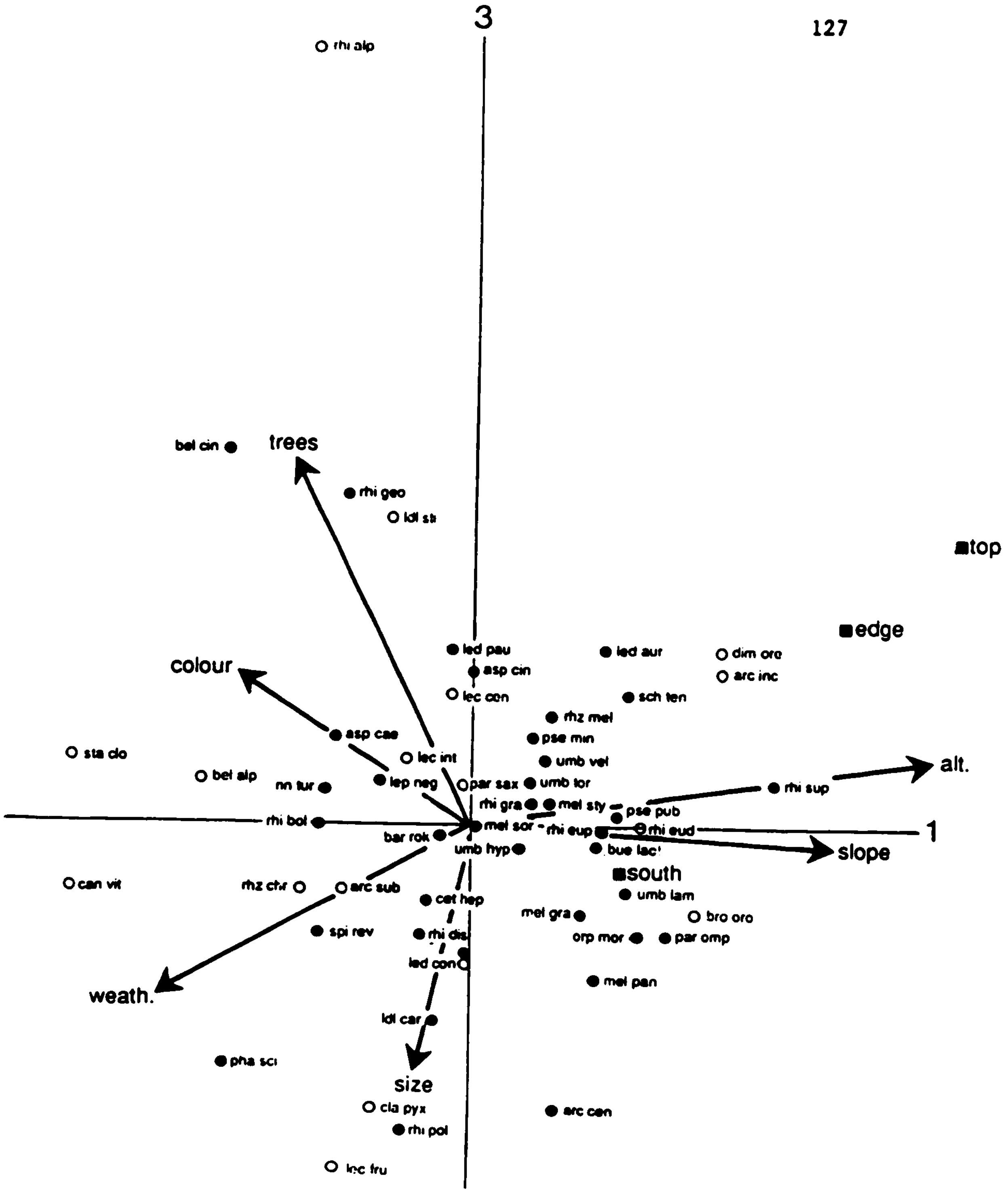

Figure 5.3: Species-environment bi-plot for axes 1 & 3 of CANOCO ordination. See legend to Figure 5.2 for explanation.

VI. AN ASSESSMENT OF THE ROLE OF BIOTIC INTERACTIONS AND DYNAMIC PROCESSES IN THE ORGANISATION OF SPECIES IN A SAXICOLOUS LICHEN COMMUNITY [5]

Introduction

As part of a community a plant occupies an environment composed of biotic and abiotic components, both of which must be assessed to gain a complete understanding of plant community organisation. Elsewhere (Chapters 4 & 5) an assessment was made of the role of abiotic factors in the organisation of a saxicolous lichen community at Jonas Rockslide, Jasper National Park, Alberta. Plant distributions were found to be related to microenvironmental factors at two scales; within, and between, rockfaces. This was hypothesised as being due, at least in part, to ecophysiological adaptation to specific niches. A canonical correlation analysis, CANOCO, (Ter Braak 1987) shows which species tend to occupy similar environmental positions on environmental gradients. The outcome of this ordination is shown in Figure 6.1 for the first two ordination axes. The species discussed in this chapter are listed in Table 6.1, and Table 6.2 shows the cover value for each lichen growth form at this site. There is little evidence of succession beyond a community dominated by crustose

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[5] A version of this chapter has been accepted for publication in THE CANADIAN JOURNAL OF BOTANY as John, E. A. An assessment of the role of biotic interactions and dynamic processes in the organisation of species in a saxicolous lichen community.

lichens except on those rockfaces which were flat or sheltered enough to allow the growth of species such as the fruticose lichen Cladonia pyxidata and the moss Grimmia affinis. These two plants are associated with lichens found on rocks of low slope, low altitude and high radiation input.

Recently, plant community ecologists have stressed the importance of working at the scale of the individual plant, at which, ultimately, community processes must occur. Using plotless techniques such as point sampling (Turkington & Harper 1979) and plant centered sampling (Mahdi & Law 1987) it has been shown that the potential importance of biotic interactions varies from community to community. In the current study, a point sampling technique is used in a nearest neighbour analysis to investigate associations at the scale of the individual thallus between lichens growing on a rockface.

In a community in which niche separation is important, associations may merely reflect shared realised niches, or indicate that biotic interactions such as competition and allelopathy are also important. By varying the scale of the association analysis, information is obtained about the scale at which niches are shared, and hypotheses about the nature of community processes can be addressed. For instance, Armstrong (1981) found that rain water run-off from a slate surface colonised by lichens contained viable propagules from the plants on the substrate. One would therefore expect lichen colonisation of a rockface to proceed downwards as propagules are washed away from a parent plant. This would lead to more intra-specific associations in a vertical direction than in a horizontal direction on the rockface.

One hypothesis for the role of phenolic lichen substances is that they are allelopathic and aid the lichen in competition with other lichens and plants. Such substances have been shown to inhibit the germination of lichen spores (Lawrey 1986). Evidence for such interactions could also be provided by association analyses at different scales.

It is of interest to look for evidence that dynamic processes are still occurring. The rockslide on which this community exists is thought to be at least 500 years old and it is plausible that a static equilibrium between the species present has been reached. The apparent absence of succession may be due to this, or it may indicate that cyclic successional processes are occurring on individual rocks (c.f. Watt 1947). Indirect evidence for or against continuing recruitment into lichen populations can be found in size class data for each species. Other workers have studied size class histograms from saxicolous lichen populations, using the assumption that thallus size is a measure of thallus age. Farrar (1974) found evidence for successional changes in the recruitment rates of two roof-top species. Innes (1986) studied two species populations that showed evidence of population aging through time, without continuous or recent recruitment.

Dynamic interactions between thalli have been observed in other saxicolous lichen communities (Hawksworth & Chater 1979, Hale 1956) and there is evidence that competition between saxicolous lichens does occur, even between effectively two dimensional crustose thalli. Lawrey (1981) found evidence that a pollution sensitive competitor had restricted the realised niche of another species in an unpolluted environment. Yarranton and Green (1966) found similar circumstantial evidence of competitive exclusion when examining slope preferences of saxicolous lichens. The experiments of Armstrong (1982, 1986) provide conclusive evidence that competition could have an effect on lichen community composition, and also indicate a mechanism by which species may coexist, in that a strong competitor in two species trials is weakened in three species trials. Hawksworth & Chater (1979) observed adjacent thalli over a time period, noting that some crustose thalli could overgrow others. Pentecost (1980) observed the interaction boundaries of saxicolous lichens and noted that the degree of competitive success of a species depended partly on the species of its competitor, and the nature of the contact between them. For instance some species were more competitive at 'window contacts' at the centre of a senescing thallus than at contacts at the growing edge of a thallus.

Evidence from field observations will be combined with that of the association analyses and thallus size data in an assessment of the role of biotic interactions in community processes at this site.

Study Site and Methods

Study site

Field work was conducted at Jonas Rockslide, a large rockslide in Jasper National Park Alberta, Canada. The rockslide is on Highway 93, 75km south of Jasper Townsite ($52^{o}26'N$, $117^{o}24'W$) (Figure 1.1) and is composed of honey coloured quartzite sandstone (Bruce 1978), forming blocks of a range of sizes, but commonly up to 3m x 3m x 1m. There are many flat rockfaces. Jonas Rockslide is considered one of the major rockslides of the Canadian Rockies (Cruden 1976). It ranges from 1500m to 2200m in elevation, which places it in the subalpine, and is 3.5km long and 1km wide. The average annual temperature at that elevation is 0^oC & average annual precipitation over the period 1971 to 1980 was 793mm as recorded at the Sunwapta warden station, 3km from the rockslide (Holland & Coen 1983). The rockslide is on a southwest facing slope in the Eastern Main Ranges and is believed to have formed at least 500 years ago, based on lichenometric evidence (Chapter 3)

The dominant plants at the site are saxicolous lichens, which cover 87% of exposed rock surfaces. Over 100 species of saxicolous lichens have been recorded at Jonas Rockslide, of which 19 have a cover value greater than 1%. Tree cover is sparse, trees being absent from 80% of the rockslide area. Picea engelmannii is the most common tree on the lower slopes, with Pinus albicaulis on the upper slopes of the rockslide.

Methods

Rockfaces were sampled along six parallel altitudinal transects on the rockslide, from the Sunwapta River (1500m) to the maximum height of safe travel on the rockslide (2200m). Transects were started at positions where there was a clear view along the vertical axis of the rockslide and where there was easy access to the rockslide. They were run parallel to the direction of maximum altitudinal variation. The first sampling station was 90m from the start of the transect and others at 90m intervals thereafter.

At each sampling station the three nearest suitable rockfaces were selected for sampling, using only the criteria that they should be of low microtopographic relief, larger than 1m x 1m in area, between 0° and 90° in slope angle and not closely sheltered by trees. Each rockface was sampled with a grid of points, after the plotless sampling method of Yarranton (1966). The columns of the grid were 20cm apart, and the rows 10cm apart (Figure 4.1). For details see Chapter 4. At each grid point the species of lichen present was identified with the aid of a portable dissecting microscope. Many lichen genera, especially among the crusts, contain species that are indistinguishable without detailed examination under a compound microscope and chemical testing. For these species apothecia were collected from fertile thalli and chemical tests were made on the thallus in the field. The chemicals used were Ca(ClO)2 (C), as found in household bleach, Metzlers reagent (I), and 10% KOH solution (K). They were applied with a micropipet (diameter 10 m) to the thallus medulla after it had been exposed with a razor blade.

At 25 of the rockfaces data were collected for a detailed 'nearest neighbour' analysis. At each point, in addition to the point species sampled by the grid, the species of lichen touching this lichen nearest to the sampling point was also recorded. Both were identified by the methods described above. Due to the difficulties of distinguishing individual thalli of some species, the next thallus of a different species was recorded. Uncolonised rock was treated as if it were another lichen species so that the tendency of a lichen species to have no contacting neighbours could also be assessed. During this analysis, thallus sizes were also measured. The longest and shortest diameter of each sampled thallus were recorded, and these were later averaged to give a 'mean diameter' for each thallus.

Association analyses

Association analyses were performed at a variety of size scales. For the 'nearest neighbour' analysis, only data from the 25 specially sampled rocks were used. For the other analyses, data from all rocks were pooled.

Nearest Neighbour Analysis

In this analysis, the expected value for each association was calculated recognising that the probability of a species being selected as a 'point' or a 'neighbour' are not the same. For the association of species i with species j the expected values of joint occurrences were calculated as:

$$E_n(J(i,j)) =(p(i_{pt}) \times p(j_{nn})) \times N_n + (p(j_{pt}) \times p(i_{nn})) \times N_n$$

where: $E_n(J(i,j))$ is the expected number of joint occurrences of species i and species j in the nearest neighbour analysis; $p(i_{pt})$ is the probability that species i is selected as a sampling point; $p(j_{nn})$ is the probability that species j is selected as the nearest neighbour of another lichen; N_n is the total number of point pairs included in the nearest neighbour analysis.

The association table prepared is an asymmetrical one in which all joint occurrences of the same two species are summed, irrespective of which is the point, and which the neighbour. It is recognised that this is not ideal (de Jong et. al. 1983), however it brings sample sizes into a manageable range.

Adjacent grid points analysis

Associations between lichens at adjacent grid points were also calculated, for both columns and rows. As columns were 20cm apart and rows 10cm apart, (see Figure 4.1) column associations (i.e. associations between lichens at adjacent points in the same column) were calculated at two scales, 10cm and 20cm. Thus there were three analyses in this section, one between adjacent row points, 20cm apart, one between adjacent column points at a spacing of 10cm and one between alternate column points, at a spacing of 20cm. In each of these analyses, points were only used once, to allow for an assumption of statistical independence. 'Expected' values for each association were calculated as:

$$E_a(J(i,j)) = n_a(i) \times n_a(j) / 2N_a$$

where $E_a(J(i,j))$ is the expected number of joint occurrences of species i and species j in each of the adjacent grid points analyses; $n_a(i)$ & $n_a(j)$ are the number of occurrences of species i & species j in the analysis, and N_a is the number of point comparisons in each analysis.

In the final association analysis, whole rockfaces were used as the sampling unit, and all the data from one grid pooled. In the above analyses uncolonised rock was treated as if it were a species, whereas it was not included in this analysis because it occurs on every rock. The number of occurrences of each pair of species on one rockface was compared to the expected value of joint occurrences, calculated approximately as:

$$E_r(J(i,j)) = n_r(i) \times n_r(j) / N_r$$

where $E_r(J(i,j))$ is the expected number of rocks on which species i and species j both occur; $n_r(i)$ & $n_r(j)$ are the number of rocks on which species i and j occur and N_r is the total number of rocks.

In all analyses, the significance of the results was assessed using the 'log-likelihood ratio test' ('G-test', Sokal & Rohlf 1981). A 2 x 2 contingency table was prepared for each pair of species and each of the cells was included in the calculation. A test value greater than 3.8 indicates a value significant at the 5% level.

In all the analyses, associations between species are designated as positive, when two species tend to occur together more often than expected at the 5% probability level (using a two-tailed test), as negative, when two species occur together significantly less often than expected or as non-significant, when the observed proportion of joint occurrences does not depart significantly from the expected value.

Thallus Sizes

Thallus diameters collected in the nearest neighbour analysis are used to calculate a mean and variance for each species, and a size class distribution for each species is also prepared. Only those thalli sampled as points (not those sampled as nearest neighbours) are included in order to avoid any sampling bias.

Results

In all the association analyses tables those associations shown to be statistically significant by the 'G' test (at the 5% level or less) are shown. Those cases where one of the expected values is less than 5 are shown if the G-test indicates that the result is significant at the 5% level or less, although the test is less reliable in this case (Sokal & Rohlf 1981). These are distinguished from those results that are statistically more reliable.

Nearest neighbour analysis

Table 6.3 shows the results of the nearest neighbour analysis. The sample size for each lichen in the analysis is also shown, as is the number of times each species was sampled as a point and as a 'neighbour'.

The results can most easily be considered if the species are divided into groups of similar morphology, as indicated in Table 6.3. Foliose lichens tend to have negative associations with uncolonised rock, and no significant relations between lichens except for the associations of *Umbilicaria torrefacta* and *Melanelia stygia* and between *M. granulosa* and *Spilonema revertens*. The latter is filamentous and may grow on *M. granulosa*.

Crustose lichens show some positive relationships with uncolonised rock, no statistically reliable associations with foliose lichens and mostly negative relations amongst each other. The only statistically reliable positive relationship amongst the crusts is that of *Rhizocarpon bolanderi* and *Bellamerea cinereorufescens*. *Spilonema revertens* tends to grow on and around other lichens and has a series of strong relationships with other lichens, four positive and four negative. There is often an asymmetry between the number of times a lichen is hit as a point and as a neighbour. A lichen which tends to grow on, and around, other lichens will be more often hit as a 'neighbour' than its cover value would suggest.

Adjacent grid points analysis

The results of these association analyses are shown in Tables 6.4, 6.5 and 6.6. Table 6.7 summarises these results. Those associations with an expected value of less than 5 are shown in the association tables, but not included for summation in Table 6.7. The number of point pairs compared in each analysis is given. Fewer significant associations would be expected in those analyses with fewer comparisons. In each analysis the number of significant associations is far greater than would be expected by chance. (Approximately 5% of the possible species pairs would be expected to show significant associations if the species were randomly distributed).

Each analysis shows more significant negative than positive associations. If inter-specific associations alone are considered then this trend is magnified; very few interspecific associations are positive. A number of species stand out as having more inter-specific associations than others; *Rhiozocarpon bolanderi*, *Pseudephebe pubescens*, *Spilonema revertens* and *Melanelia stygia*. The same species show a high number of associations in all analyses, and 19 of the species pairs show the same trend of association in all three analyses. In no case does a significant result in one analysis conflict with the result for the same species pair in another analysis.

There are a large number of intra-specific positive associations in the row and 10cm column analyses, but only *Umbilicaria torrefacta* and *Rhizocarpon disporum* show intraspecific negative results.

There are some associations with uncolonised rock, both negative and positive, among the crustose lichens at the 20cm scale. At 10cm only *Grimmia affinis* and *Lepraria neglecta* have negative relationships with bare rock.

Whole rock analysis

The results of this analysis are shown in Table 6.8. It shows that at this scale there are far more positive than negative relationships amongst species. A number of species stand out as having a large number of associations, both positive and negative, and these are not the same species as do so in the previous analysis. This is partly an artefact of sample size, as those species which occur on most rocks (such as *Rhizocarpon bolanderi* and *Spilonema revertens*) are unlikely to have a significant number of positive or negative associations. Species which have a large number of associations (twelve or more) are *Cetraria hepatizon*, *Melanelia stygia*, *M. granulosa*, *Pseudephebe pubescens*, *Lepraria neglecta*, *Rhizocarpon eupetraeum*, *R. grande*, and *Umbilicaria torrefacta*. Species with very few associations are *Rhizocarpon geographicum* and *R. disporum*.

Thallus sizes

Table 6.9 shows the mean and variance for the diameter of each lichen species as well as the number of samples on which this was based. Data for sterile thalli identified only to genus are also shown. The size class distributions for all species with a sample size greater than 20 in this analysis are shown in Figure 6.2. The size classes are not all of even spacing. In interpreting these results it is worth noting that immature thalli of some species are unlikely to be identified to species level, due to the absence of apothecia or other distinctive reproductive structures. Thus, the '*Rhizocarpon* sp. (grey)' category probably includes members of other species in that sub-genus (Phaeothallus) that have not yet developed apothecia. The same applies to the '*Rhizocarpon* sp. (yellow-green)' and '*Melanelia* sp.' Other species, such as *Rhizocarpon bolanderi* and *Lecidea paupercula* can be recognised from thallus characteristics alone, even as small thalli.

It should also be noted that the probability of sampling a thallus is related to its area, thus small thalli are likely to be under-represented in this analysis. A thallus of diameter 250mm has a surface area 10,000 times that of one with diameter 2.5mm. Using a random sampling technique, the probability of sampling a thallus would be in direct proportion to its area. As a grid sampling system is used here, this is not the case; for instance thalli have a probability of 1 of being sampled if they are larger than the grid spacing. Thus the chances of sampling a particular thallus are related to its area, but not in direct proportion.

Discussion

Nearest neighbour analysis

At this scale there is a clear difference in the relationships of crustose and foliose lichens to their immediate environment. The fact that crusts contact with uncolonised rock more frequently than their proportions in the community would suggest, whereas the foliose lichens 'sample' less uncolonised rock than expected, results from an important difference in the biology of these two growth forms. The only factor for which a crust can compete is space on the rock surface, and its success in intercepting resources such as light and water will depend solely on the amount of rocksurface it occupies. Colonisation of a crust is unlikely to be successful in a colonised area. It is possible that crustose lichens have contact avoidance mechanisms which slow or prevent growth in a 'no-contact' zone between adjacent thalli, possibly due to allelopathic substances. Field observations (no numerical data available) suggest that there is often a thin zone of uncolonised rock around thalli of certain species such as *Rhizocarpon eupetraeum* and *R. superficiale*. Those species with the most pronounced associations with uncolonised rock may have allelopathic properties, or, conversely, may be very weak competitors, unable to grow in the presence of other lichens. It is worth noting that '*Rhizocarpon* sp.' thalli have a high association with bare rock. This group may represent young colonisers, and they may be unable to persist in contact with other lichens.

The 'avoidance' of uncolonised rock by foliose lichens could be because bare rock presents an inhospitable microclimate for establishment and growth. When in direct contact, foliose lichens are clearly better competitors than crustose lichens, being able to overtop them and intercept light and moisture. Crustose lichens overtopped by foliose lichens usually appear dead or dying, as recognised by their loss of pigment and crumbling thalli. However, as foliose lichens only cover 25% of the rock surface area at Jonas Rockslide, some factor prevents their complete dominance. (See overall discussion).

Spilonema revertens is usually found growing on the thalli of other lichens. However it exhibits strong negative relationships, as well as positive relationships, implying an inability to colonise all species. This parallels the findings of Culberson *et.al*. (1977) who found that an epiphytic *Lepraria* species was only able to colonise one of two closely related Parmelia species. They suggested that this was due to the presence or absence of allelopathic chemicals in the Parmelia species. An alternative explanation in the current case is that S. revertens only colonises those lichens growing in suitable microenvironmental conditions, and is responding to microhabitat rather than species. However Aspicilia cinerea and Rhizocarpon grande have similar microhabitat requirements (see Figure 6.1), yet R. grande is not colonised and A. cinerea is.

The difference between the number of times a lichen is 'hit' as a point and as a neighbour may reflect fundamental differences between species in the way they grow and sample their environment. Those species more often hit as points have discrete thalli and probably experience relatively little of the surrounding environment, whereas those species hit more frequently as neighbours grow over and around other lichens and must make contacts with many other lichens.

Adjacent grid points analysis

The larger than 'expected' number of associations between species is not surprising given that species are not arranged randomly over the rockfaces, but exhibit correlations with microenvironmental variables. Most of the negative associations are between species with different reponses to microenvironment, and most of the positive associations are between species which appear close together in Figure 6.1.

This study provides no evidence for any allelopathic or inhibitory effects (as suggested by the nearest neighbour analysis) extending to the 10cm scale as at that scale there are no positive associations with bare rock. The fact that certain crustose lichens have negative associations with uncolonised rock at this scale, whereas they are positively associated with it at the nearest neighbour scale of analysis may be due to patchy lichen distribution. This is corroborated by the negative relationship of uncolonised rock with itself.

Responses do not differ greatly between the column and row association analyses indicating that there is no important role for the vertical distribution of propagules or chemical substances down the rockface as opposed to horizontally, at least at this scale. If propagules were being distributed downwards then more intra-specific associations would be expected vertically than horizontally, whereas a comparison of the row and column associations at the 20cm scale shows that the reverse is true. The sample sizes in these two analyses are not sufficiently different to explain this result. The larger number of intra-specific associations in the horizontal analysis may indicate that microenvironmental factors such as temperature and humidity do not change so rapidly across a rockface as down it.

The large number of intra-specific associations in both the 10cm column and row analyses may be indicative of a very local dispersal process, either via thallus fragmentation, diaspore or ascospore colonisation. The possibility that this result is due to two adjacent grid points sampling the same thallus can be eliminated for most species by studying the mean thallus diameter data. The average thallus size for all species is less than 100mm, and although the variability is very high the proportion of thalli greater than 100mm is very small, except for *Umbilicaria lambii* and *Bellamerea cinereorufescens*. These are the two species with an intra-specific association in the 20cm column analysis.

That many of the inter-specific relationships seen at this scale are between species in the same 'ecological grouping' may reflect ecophysiological responses to abiotic variables. This indicates that the scale at which microhabitats are shared is at least 20cm. However there is evidence that *Rhizocarpon bolanderi* ~~may have~~ has an important role in community organisation. At both the 10cm and 20cm scales of analysis it shows a large number of negative and positive relationships with other species. It has large spreading thalli that intermingle with other lichens and tend to occupy large areas of the rock surface, apparently excluding even otherwise very generalist species such as *Melanelia granulosa*. It tends to grow on well weathered rocks and these less stable substrates may be unsuitable for certain other lichens.

Whole rockface associations

Those species with large numbers of associations may be indicative of species with particularly specialised microhabitats at the whole rockface scale, so that other species either prefer or avoid them. Those species with few associations may be generalists or may have very specific within rockface requirements such that their distributions are not correlated with whole rockface variables.

Thallus sizes

In this discussion it will be assumed that a thallus' diameter is related to its age. This is a basic tenet in the use of lichens for dating surfaces, lichenometry, in which it has been shown that the size of the largest thallus on a substrate can be used as a measure of the age of that substrate. Presumably the largest thalli on a substrate have been able to grow close to their optimal rate and have not been compromised by competitive interactions with other lichens or suboptimal microhabitat conditions. However a thallus may be small because it is young or because it has grown very slowly, ceased growth altogether (due to competition or environmental sub-optimality) or because it is a portion of a larger thallus that became separated. However it will be assumed here that small thalli are more recent recruits to a species population than large thalli and that there is some correlation between size and age. Bearing in mind that large thalli are far more likely to be sampled than small thalli, it can be seen that vigorous recruitment is occurring in almost all species populations included in this analysis. However there is some variation in the rate of recruitment, with species such as *Lecidea paupercula*, *Umbilicaria lambii* and *Umbilicaria torrefacta* showing a relatively small proportion of thalli in the smaller size classes, and the group of grey *Rhizocarpon* species showing a higher proportion of thalli in the smaller classes, especially if thalli in the sterile grey *Rhizocarpon* category are considered as belonging to one of these species. Such rapid recruitment rates in a relatively old saxicolous lichen community contrast with the findings of Innes (1986) who found evidence that in the two populations he studied the average lichen size increased with community age and contained few small thalli. Possibly he had chosen species characteristic of early successional stages in that community, which were no longer in their period of maximum recruitment.

Differences in recruitment rate amongst current populations at Jonas Rockslide can be accounted for by two possible factors. As the rockslide is several hundred years old, it is possible that climatic changes in that time have adversely affected the recruitment rate of some species, while enhancing that of others. Alternatively, successional changes amongst the biota of the rockslide may have made recruitment less likely amongst certain species.

A high recruitment rate is presumably countered by death in old or young thalli. Death may be caused by senescence, competition with other thalli by overgrowth or possible allelopathic effects, poor environmental conditions leading to a non-compensatory photosynthetic rate and catastrophic events, such as breaking or scaping off of thalli, upturning of boulders, etc. Such factors will provide new sites for colonisation.

Overall discussion of community processes at Jonas Rockslide

Many of the positive and negative associations seen at all scales could be explained as shared responses to environmental conditions, as they seem to corroborate species-environment groupings. However this does not mean that biotic interations are not important in producing those groupings. Species positions along an environmental gradient may be determined by competition as well as by their ecophysiological optima. Evidence that this happens amongst saxicolous lichens comes from the findings of Lawrey (1981) and Yarranton and Green (1966). In a crowded community such as this, with 88% lichen cover, competition is likely to be important.

A few of the relationships seen between species can be related to specific biological interactions, for instance that between _Spilonema revertens_ and _Rhizocarpon bolanderi_. The former species seems unable to grow on uncolonised rock and is epiphytic on the thalli of other lichens, however it is unable to grow on the thalli of all other species. This difference may reflect the presence of allelopathic substances preventing the growth of S. revertens on all species. It would be to a host species' advantage to prevent epiphytic growth, as an epiphyte would intercept light and water resources.

That crustose lichen thalli are generally not amenable to colonisation by foliose lichens is evidenced by the large size and extreme age of some of the crustose lichen thalli. Prevention of thallus invasion may be an important role for phenolic lichen substances.

There is some evidence of a zone of inhibition around the thalli of crustose lichens, but there is no evidence that this extends to the 10cm scale. This presents an interesting contrast with those saxicolous lichen communities where a dense mosaic of touching thalli is formed (e.g. Hawksworth & Chater 1979). As foliose lichens have an obvious competitive advantage over crustose lichens, it is somewhat surprising that there is only 25 % cover by foliose lichens (see Table 6.2). In some areas quite large expanses of foliose thalli can be seen, apparently overgrowing crustose lichens. There must be some process preventing the complete overgrowth of crustose by foliose lichens. An explanation could be that foliose lichens are unable to grow in the most exposed microhabitats, as they are easily broken & eroded by wind abrasion. However it was noted in an Chapter 4 that many foliose lichens are generalists with respect to microhabitat. Often an expanding foliose lichen is represented only by the outer concentric ring of younger tissue, presumably because older tissue has been centrally abraded. Orwin (1971) and Webber (1966) have commented on the abrasive effects of wind and wind carried particles on lichen thalli. Perhaps such abrasive action keeps the cover of foliose lichens to relatively low levels. Another hypothesis for their low cover is that these species may have very specialised establishment requirements: this has not been investigated.

The high level of recruitment indicates that colonisation sites must be constantly available. The abrasion of foliose lichens mentioned above would expose areas suitable for recolonisation, and such areas can be seen to be being recolonised. Crustose thalli may also lose their older, central portions due to senescence or abrasion, providing 'windows' for recolonisation. Pentecost (1980) found that 'windows' provided opportunities for colonisation to species that would otherwise be uncompetitive. Death of thalli would also release colonisation sites. Flaking rock is another method by which colonisation sites become available.

The evidence, although circumstantial, suggests that this lichen community is highly dynamic. The importance of cyclic successional processes has been noted in other communities (Watt 1947). It is likely that cyclic patterns occur in the occupation of space on the rocksurface by various lichen species. This could explain why the apparently competitively superior foliose lichens do not dominate, if senescence and abrasion reduce the sizes of older thalli, creating spaces for recolonisation by other species.

The preliminary evidence seems to suggest that although biotic interactions obviously occur between the species in this community abiotic factors may also be important in community organisation. This could be a good example of a community made up largely of 'stress tolerators' (Grime 1979), in which the stressful nature of the environment means that biotic interactions are less important than in other plant communities, (although it should be remembered that conditions stressful to a vascular plant may not be stressful to a lichen, and *vice versa*). The exception to this may be found on those rockfaces where conditions allow the growth of species indicative of progressing succession, such as *Grimmia affinis* and *Cladonia pyxidata*. In these places competition must become of increasing importance, and species such as the apparently aggressive *Rhizocarpon bolanderi* seem to have an important role in community structure.

Summary

A saxicolous lichen community is examined for evidence of dynamic processes and biotic interactions amongst its members. Relationships amongst species are examined in a series of association analyses at three scales: a) the 'nearest neighbour' scale, i. e. associations between touching thalli, b) associations between thalli 10cm and 20cm apart, c) associations at the scale of the whole rockface. The nearest neighbour analysis reveals fundamental differences in the way crustose and foliose thalli 'sample' their environment; crustose lichens are most likely to have uncolonised rock as a nearest neighbour whereas foliose lichens are more likely to contact another thallus. Associations between species at the 10cm and 20cm scales are often negative, reflecting the degree of microhabitat specificity in this community, however intra-specific associations at the same scale are often positive, possibly indicating local dispersal processes. At the whole rock scale, there are many

positive associations indicating that even at this larger scale, microhabitat specificity is important. Thallus size distributions are also studied, and these indicate that recruitment into lichen populations is an ongoing process, based on the assumption that small thalli are younger than large thalli. There is little evidence of succession to a higher plant community over most of the rocks at this 500 year old site and it is hypothesised that cyclic successional processes maintain this dynamic and diverse community.

Bibliography

Armstrong, R. A. (1986) Competition between three lichen species using a factorial experimental design. New Phytologist, 104: 637-641.

Armstrong, R. A. (1982) Competition between three saxicolous species of *Parmelia* (lichens). New Phytologist, 90: 67-72.

Armstrong, R. A. (1981) Field experiments on the dispersal, establishment and colonisation of lichens on a slate rock surface. Environmental and Experimental Botany, 21: 115-120.

Bruce, I. (1978) The Field estimation of shear strength on rock discontinuities. Ph.D. thesis, Department of Civil Engineering, University of Alberta.

Cruden, D. M. (1976) Major rock slides in the Rockies. Canadian Geotechnical Journal, 13: 8-20.

Culberson, C. F., Culberson, W. L. and Johnson, A. (1977) Non random distribution of an epiphytic *Lepraria* on two species of *Parmelia*. The Bryologist, 80: 201-203.

Egan, R. S. (1987) A fifth checklist of the lichen-forming, lichenicolous & allied fungi of the continental United States and Canada. The Bryologist, 90: 77-173.

Farrar, J. F. (1974) A method for investigating lichen growth rates & succession. Lichenologist, 6: 151-155.

Grime, J. P. (1979) Plant Strategies and Vegetation Processes. John Wiley and Sons. Chichester, New York, Brisbane, Toronto.

Hale, M. E., Jr. (1956) Studies on lichen growth rate and succession. Bulletin of the Torrey Botanical Club, 86: 125-129.

Hawksworth, D. L. & Chater, A. O. (1979) Dynamism and equilibrium in a saxicolous lichen mosaic. Lichenologist, 11: 75-80.

Holland, W. D. & Coen, G. M. (1983) Ecological (Biophysical) land classification of Banff & Jasper National Parks. Volume II. Soil and vegetation resources. Alberta Institute of Pedology & Environment Canada.

Innes, J. L. (1986) The size-frequency distributions of the lichens *Sporastatia testudinea* and *Rhizocarpon alpicola* through time atStorbreen, South-west Norway. Journal of Biogeography, 13: 283-291.

De Jong, P., Aarssen, L. W. & Turkington, R. (1983) The use of contact sampling in studies of association in vegetation. Journal of Ecology, 71: 545-559.

Lawrey, J. D. (1986) Biological role of lichen substances. The Bryologist, 89: 111-122.

Lawrey, J. D. (1981) Evidence for competitive release in simplified saxicolous lichen communities. American Journal of Botany, 68: 1066-1073.

Mahdi, A. & Law, R. (1987) On the spatial organisation of plant species in a limestone grassland community. Journal of Ecology, 75: 459-476.

Orwin, J. (1972) The effect of environment on assemblages of lichens growing on rock surfaces. New Zealand Journal of Botany, 10: 37-47.

Pentecost, A. (1980) Aspects of competition in saxicolous lichen communities. Lichenologist, 12: 135-144.

Sokal, R. R. & Rohlf, F. J. (1981) Biometry. The Principles and Practice of Statistics in Biological Research. 2nd Edition. W. H. Freeman & Company, New York.

Ter Braak, C. J. F. (1987) CANOCO - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO Institute of Applied Computer Science, Wageningen, The Netherlands.

Turkington, R. & Harper, J. L. (1979) The growth, distribution and neighbour relations of Trifolium repens in a permanent pasture. I. Ordination, pattern and contact. Journal of Ecology, 67: 201-218.

Watt, A. S. (1947) Pattern and process in the plant community. Journal of Ecology, 35: 1-22.

Weber, W. A. (1962) Environmental modification and the taxonomy of crustose lichens. Svensk Botanisk Tidskrift, 56: 293-333.

Yarranton, G. A. (1966) A plotless method of sampling vegetation. Journal of Ecology, 54: 229-237.

Yarranton, G. A. & Green, W. G. E. (1966) The distributional pattern of crustose lichens on limestone cliffs at Rattlesnake point, Ontario. The Bryologist, 69: 450-461.

Table 6.1: Species included in analysis of Chapter 6 (nomenclature follows Egan (1987)

code	species	% cover
arc cen	*Arctoparmelia centrifuga* (L.) Hale	.3
asp cin	*Aspicilia cinerea* (L.) Körber	5.1
bel cin	*Bellemerea cinereorufescens* (Ach.) Clauz. & Roux	1.0
bue lac	*Buellia lacteoidea* B. de Lesd.	.4
cet hep	*Cetraria hepatizon* (Ach.) Vainio	1.3
cla pyx	*Cladonia pyxidata* (L.) Hoffm.	.2
led pau	*L. paupercula* Th. Fr.	1.7
lep neg	*Lepraria neglecta* (Nyl.) Lettau	1.1
mel gra	*Melanelia granulosa* (Lynge) Essl.	2.1
mel pan	*M. panniformis* (Nyl.) Essl.	.4
mel sor	*M. sorediata* (Ach.) Goward & Ahti	3.5
mel sty	*M. stygia* (L.) Essl.	3.0
orp mor	*Orphniospora moriopsis* (Massal.) D.Hawks.	1.1
pha sci	*Phaeophyscia sciastra* (Ach.) Moberg	.5
pse min	*Pseudephebe minuscula* (Arnold) Brodo & D. Hawks.	1.9
pse pub	*P. pubescens* (L.) M. Choisy	5.0

Table 6.1: continued

code	species	% cover
rhi bol	*Rhizocarpon bolanderi* (Tuck.) Herre	8.9
rhi dis	*R. disporum* (Hepp) Müll. Arg.	2.4
rhi eup	*R. eupetraeum* (Nyl.) Arnold	1.2
rhi geo	*R. geographicum* (L.) DC.	2.1
rhi gra	*R. grande* (Flotow) Arnold	2.4
rhi pol	*R. polycarpum* (Hepp) Th. Fr.	.5
rhi sup	*R. superficiale* (Schaerer) Vainio	1.5
rhi ugr	*R.* sp. (grey thallus)	5.5
rhi uyg	*R.* sp. (yellow-green thallus)	1.2
rhz mel	*Rhizoplaca melanophthalma* (DC.) Leuck. & Poelt	.3
sch ten	*Schaereria tenebrosa* (Flotow) Hertel & Poelt	2.0
spi rev	*Spilonema revertens* Nyl.	5.9
umb hyp	*Umbilicaria hyperborea* (Ach.) Hoffm.	5.6
umb lam	*U. lambii* Imsh.	1.3
umb tor	*U. torrefacta* (Lightf.) Schrader	1.9
unc rok	uncolonised rock	12.7
gri aff	*Grimmia affinis* Hoppe & Hornch. *ex.* Hornch.	

Table 6.2: Cover values for lichen growth forms at Jonas Rockslide

Growth form	% cover
crustose	47
umbilicate	9
other foliose	15
total foliose	24
fruticose	7
filamentous	6
total lichen cover	86

Table 6.3: Nearest neighbour association analysis.
Associations between contacting lichens

sample sizes

	tot	pt	nn		ur	ut	uh	ul	ms	mg	mo	ch	pp	pm	sr	ln	lp	cm	rg	re	rd	ru	rg	rs	ry	rb	ac	bc	st	ga
rock	822	326	496	unc rok																										
	188	113	75	umb tor																										
	76	51	25	umb hyp	=																									
foliose	41	29	12	umb lam																										
	137	73	64	mel sty	=	++																								
	71	34	37	mel gra																										
	91	44	47	mel sor	=																									
	66	40	26	cet hep	=																									
fruticose	227	101	126	pse pub			+	+		+		+																		
	55	31	24	pse min									-																	
filament.	421	160	261	spi rev						=			=																	
leprose	80	27	53	lep neg	=-				+			+																		
	89	48	41	led pau	+++										=-															
	36	22	14	cam mor							+																			
	117	70	47	rhi gra									++		=															
	53	35	18	rhi eup	+++				+						=															
	100	57	43	rhi dis	++				-					+																
crustose	261	132	129	rhi ugr	+++										++	-	=		=	-										
	123	63	60	rhi geo	++											-														
	37	23	14	rhi sup	++			+														-								
	67	31	36	rhi uye	+++										=															
	393	207	186	rhi bol	+++			-							+++		=		-	-				-						
	160	99	61	asp cin					+		+				+++		-					=			-					
	56	35	21	bel cin	++	-							-				+						+			++				
	82	51	31	sch ten									+		++															
moss	41	14	27	gri aff									-		-	+						-				-				

Legend: +,- G-test indicates p<0.05, but one of the expected values is less than 5, thus test is unreliable
++,= G-test indicates 0.05>p>0.001
+++,=- G-test indicates p<0.001
Full species names can be found in Table 6.1
tot = total number of times species sampled during the nearest neighbour analysis
pt = number of times species was hit by a grid point in the nearest neighbour analysis
nn = number of times species was sampled as the neighbour of a lichen hit at a grid point

Table 6.4: Adjacent grid points association analysis (column, 20cm).
Associations between column points 20cm apart

sample size		ur	ut	uh	ul	ms	mg	mo	ch	ps	pp	pm	sr	ln	lp	om	rg	re	rd	rg	rs	rb	ac	bc	st	ga
1317	unc rok	≡																								
584	umb tor		-																							
207	umb hyp																									
117	umb lam		-		+																					
323	mel sty																									
211	mel gra					++																				
367	mel sor																									
129	ost hep																									
55	pha sci																									
490	pse pub			++			+++			-																
201	pse min					=		++																		
634	spi rev						=			+	-															
113	lep neg											-														
160	led pau							=					=													
119	om nor				+																					
256	rhi gra	=																								
125	rhi eup			-								-														
249	rhi dis																		=							
210	rhi geo	=																								
146	rhi sup				+	-					++		=			+										
943	rhi bol			=	≡	≡	≡	=		++	=		++			=		=			=					
528	asp cin					≡										=										
111	bel cin		=			-	-	-			=	-	=		+				-					+		
211	sch ten																				+	=				
59	gri aff									+													-			

Legend: +,- G-test indicates p<0.05, but one of the expected values is less than 5, thus test is unreliable.
++,= G-test gives a value indicating 0.05>p>0.001
+++,≡ G-test gives a value indicating p<0.001
Full species names can be found in Table 6.1.

Table 6.5: Adjacent grid points association analysis (row, 20cm)
Associations between row points 20cm apart

sample size		ur	ut	uh	ul	ms	mg	mo	ch	ps	pp	pm	sr	ln	lp	om	rg	re	rd	rg	rs	rb	ac	bc	st	ga
1330	unc rck	=-																								
592	umb tor		=-																							
211	umb hyp																									
115	umb lsm				+																					
318	mal sty					+++																				
220	mal gra						+																			
377	mal sor							+++																		
134	ost hap																									
55	pha sci																									
501	pse pub					++		=																		
176	pse min											+														
646	spi rev				=-					+			++													
110	lep neg										=															
161	led pau												=													
110	orn mor						+				++															
246	rhi gra	=							-						-											
126	rhi eup					+							=													
252	rhi dis												=													
213	rhi geo	=													+					+						
143	rhi sup		=			-					+++		=-								+					
966	rhi bol			=	=	=-	=				=-	=	+++		=	=-	++			=	=	+++				
536	asp cin						=						=-		=	=			=							
105	bel cin	++				-		-			=-				+									+		
200	sch ten	=									++											=-			+	
57	gri aff												+													

Legend: +,- G-test indicates p<0.05, but one of the expected values is less than 5, thus test is unreliable.
++,= G-test indicates 0.05>p>0.001
+++,=- G-test indicates p<0.001
Full species names can be found in Table 6.1.

Table 6.6: Adjacent grid points analysis (column, 10cm).
Associations between column points 10cm apart.

sample size		ur	ut	uh	ul	ms	mg	mo	ch	ps	pp	pa	sr	ln	lp	om	rg	re	rd	rg	rs	rb	ac	bc	st	ga
1402	unc rok	=-																								
678	umb tor		=																							
209	umb hyp																									
144	umb lam				+																					
312	mel sty		++		-	++																				
250	mel gra						++																			
400	mel sor					=		+++																		
150	ost hep			-	-	+	-		+																	
52	pha sci									+																
557	pse pub		++		+++					+	+++															
227	pse min		=			=		++				+														
709	spi rev				=-	=	=			+			+++													
132	lep nag	=																								
165	led pau			-							-	-	=	-	+											
115	oon mor			+	+								=			+										
286	rhi gra				-	++					=															
139	rhi eup					+							=					+								
263	rhi dis																									
219	rhi geo														+					+						
156	rhi sup						+				++		=	-			-				+					
1046	rhi bol	=			=-	=-	=	=-	=	+	=-		++			=		=-			=-	+++				
609	asp cin	++			=		=			-				=									++			
114	bal cin	=		-		-		-			=									+				+		
196	sch ten			+			+				+++							-			+	=		-	+	
60	gri aff	=					+			+				+												

Legend: +,- G-test indicates $p<0.05$ but one of the expected values is less than 5, thus the test is unreliable
++,= G-test gives a value indicating a probability $p<0.05$, $p>0.001$
+++,=- G-test gives a value indicating a probability $p<0.001$
Full species names can be found in Table 6.1.

Table 6.7: Adjacent Grid Points Analysis Summary

analysis	row 20 cm	column 20 cm	column 10 cm
no. point pairs	5234	5176	5721
no. species pairs where E_a (J(i,j) < 5	153	156	159
no. significant associations expected if species arranged randomly. (5% of above)	8	8	8
total significant associations $p < 0.05$	41	31	47
total sig. +ve	11	7	16
total sig. -ve	30	24	31
intra-specific sig. +ve	4	0	7
intra-specific sig. -ve	2	1	2
inter-specific sig. +ve	7	7	9
inter-specific sig. -ve	28	22	29

Table 6.8: Whole rock association analysis
Associations at the scale of the whole rockface

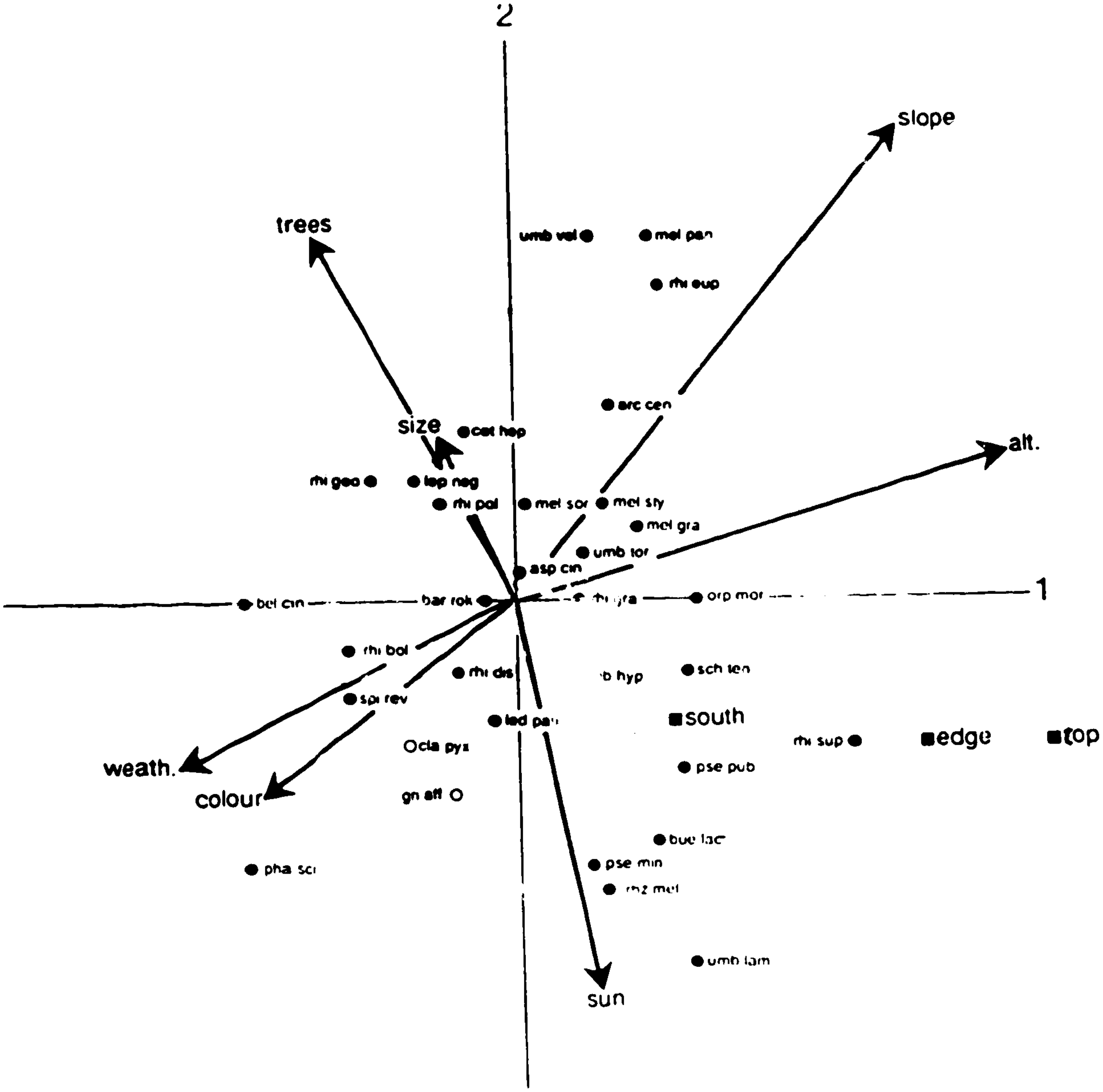
number rocks		ut	uh	ul	ms	mp	mg	mo	ac	ch	ps	pp	pm	sr	ln	rm	lp	om	bl	rg	re	rd	rp	rg	rs	rb	ac	st	ga
113	umb tor																												
79	umb hyp	++																											
32	umb lam																												
73	mel sty	++																											
21	mel pan				+*																								
67	mel gra	++	++	++	+*	++																							
86	mel sor	++			++																								
22	arc cen	+			+*	+	++																						
52	cet hep	+*			+*	+*	++	++	+*																				
20	pha sci									=																			
94	pse pub	++	+*	+*	++		++	++																					
55	pse min			++		=-			=-			++																	
113	spi rev							++			+		++																
49	lep neg	+*			+*	++	++	++	++	+*		++		++															
26	rhi mel		++			-			-		+		++																
63	led pau	=				++					=		-*																
43	orn mor			++	++						=																		
24	bue lac	+		+*								++			++	+													
95	rhi gra	+*	+*		++				++	++		++		+															
48	rhi eup	++			++	+*	++		+*	+*	=		=		+*	=	++												
86	rhi dis										++					++				++									
29	rhi pol	+							+	++					++				++	++									
88	rhi geo																												
64	rhi sup			+*	++							+*	++		=			++	++										
105	rhi bol										++			+			=			++	=								
108	asp cin							+*					++	+		+		=								+			
69	sch ten			++	++		++	++				+*	++		++					++					++				
23	gri aff				++		++			++	+				++					++			++			+			

Legend: +,- G-test indicates p<0.05, but one of the expected values is less than 5, thus test is unreliable
++,= G-test indicates 0.05>p>0.001
+*,=- G-test indicates p<0.001
Full species names can be found in Table 6.1.

Table 6.9: Thallus size summary.

species	sample size	mean diameter (mm)	standard deviation	largest thallus(mm)
Aspicilia cinerea	93	53.6	47.3	313
Bellemerea cinereorufescens	20	87.5	213.3	975
Cetraria hepatizon	36	38.7	89.6	535
Lecidea paupercula	45	65.0	57.3	265
Lepraria neglecta	26	9.6	13.7	68
Melanelia granulosa	34	25.1	23.0	125
M. servdiosa	47	14.1	10.9	52
M. stygia	72	20.0	15.3	80
M. unidentified	22	8.9	20.6	100
Orphniospora moriopsis	21	46.9	52.0	200
Pseudephebe minuscula	30	16.0	15.1	73
P. pubescens	98	18.4	16.9	101
Rhizocarpon bolanderi	194	36.0	75.0	794
R. disporum	56	32.4	26.4	131
R. eupetraeum	30	34.0	37.0	182
R. geographicum	67	28.9	23.0	153
R. grande	70	34.0	32.7	177
R. superficiale	22	55.3	30.3	144
R. unidentified (grey)	131	15.3	18.6	147
R. unidentified (yellow)	25	15.2	19.2	94
Schaeraria tenebrosa	54	30.2	29.4	154
Umbilicaria hyperborea	50	12.5	7.7	56
U. lambii	27	97.3	88.2	434
U. torrefacta	112	14.4	7.8	50
Uncolonised rock	302	39.6	67.0	980

Figure 6.1: CANOCO (Ter Braak 1987) species-environment biplot for the first two canonical axes of a canonical correlation analysis. It was performed using 672 plots obtained by splitting 85 sampled rocksurfaces into eight subsections (see Figure 4.1), so that the effect of rockface position was included in the ordination. The biplot shows arrows indicating the direction of maximum variation of the environmental variables with these axes. The environmental variables used in the analysis were; SLOPE = inclination from horizontal of the rockface, ALT. = elevation above the Sunwapta river of the rockface, WEATH. = an estimation of the degree of weathering of the rockface, SIZE = size of the rockface, based on the number of sample points, SUN = an estimate of the amount of direct solar radiation received by the rockface, TREES = number of trees within a 30m radius of the rockface, COLOUR = estimate of colour of the rockface, low values represent pale colour, SOUTH, EDGE and TOP are nominal positional variables illustrated in Figure 4.1.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slope
trees
umb vel
mel pan
rhi eup
arc cen
size
cet hep
alt.
rhi geo
lep neg
rhi pol
mel sor
mel sty
mel gra
umb tor
asp cin
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bel cin
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spi rev
led pa
south
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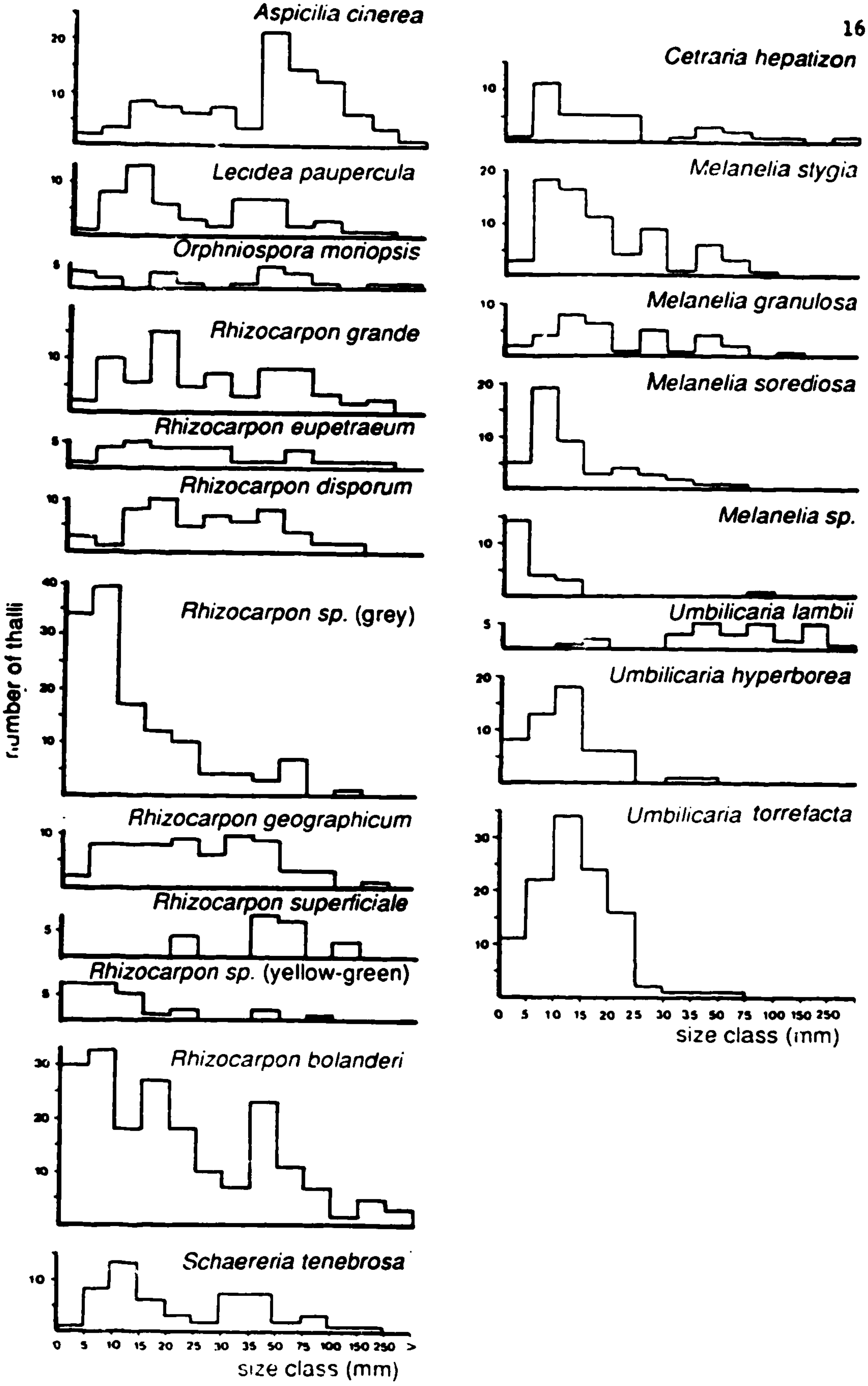

Figure 6.2: Histograms illustrating thallus diameter size class distributions.

VII. NICHE RELATIONS AMONGST RHIZOCARPON SPECIES AT JONAS ROCKSLIDE [6]

Introduction

The lichen genus Rhizocarpon is one of the most important crustose genera growing on exposed acid or neutral rocks, especially in Arctic and alpine environments (Thomson 1967, Runemark 1956). It often supplies early colonisers of recently exposed rock. Jonas Rockslide, Jasper National Park, Alberta supports a mature saxicolous lichen community believed to be over 500 years old, containing over 100 species of lichen. Twenty-seven percent of the surface area of exposed rocks is colonised by one of twelve species of Rhizocarpon present at this site (Table 7.1); thus it is a suitable site for a comparative study of niche relations in this genus. The data used here were collected as part of a broader study of pattern and its causes amongst the species of this saxicolous lichen community.

The genus Rhizocarpon is characterised by a crustose, areolate thallus, a black hypothallus and apothecia, halonate 1-septate to muriform ascospores and anastomosing paraphyses. It is divided into two sub-genera, based on thallus colour (Thomson 1967). Subgenus Rhizocarpon contains green or yellow lichens, while Phaeothallus contains those with a grey, brown or white thallus. The bright yellow-green of some species has been

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7. A version of this chapter has been submitted to THE LICHENOLOGIST for publication as John, E. A. & M. R. T. Dale, Niche relations amongst Rhizocarpon species at Jonas Rockslide.

suggested to have a role in the protection of the lichen from ultra-violet rays in very exposed environments (Gaussla 1984).

Most quantitative ecological work on Rhizocarpon has been done in connection with lichenometry, often with specific aims related to that technique in mind, and very little has been done involving the subgenus Phaeothallus. Lichenometry, used for dating surfaces such as glacial moraines, often uses members of the subgenus Rhizocarpon, and there is a broad body of information on growth rates in this sub-genus, but little of it is species specific (Innes 1985).

There is one notable study on the ecophysiology of Rhizocarpon superficiale (Coxson & Kershaw 1983a & b) in which the photosynthetic rates and ecophysiological tolerances of this species under a variety of conditions were investigated. It was found to be intolerant of temperatures of 45°C or above, even when dry, as indicated by a reduction in photosynthectic ability after exposure to this temperature.

Field work on Rhizocarpon is complicated by difficult taxonomy; many species within a subgenus or section are morphologically similar and must be separated by microscopic and chemical examination. They differ in minute thallus details, ascospore size and septation and lichen product chemistry. It is of interest to know how such morphologically similar species differ in their ecology.

It is reasonable to suppose that these apparently ecologically and morphologically similar congenerics would tend to have similar resource requirements, and would therefore compete. Competition may be part of a dynamic process leading to changes in community composition. Alternatively, competition may be reduced by niche separation between the species, or it may be of little importance in a community in which environmental stress and disturbance have dominant roles in community organisation. Other studies of coexisting congenerics have usually found important differences in resource utilisation between the species concerned (Larson 1980, Werner 1979, Watson 1980). Larson ([illegible]) studied members of the lichen genus Umbilicaria at a single site, and discovered differences in resource use, but the species that shared positions on environmental gradients were sufficiently morphologically different to explain their coexistence (Larson 1984).

Examination of the degree to which Rhizocarpon species occupy the same positions on environmental gradients can contribute to an understanding of the role of competition in this community, and the mechanisms by which apparently similar species can coexist.

Study site and methods

Study site

The field work was conducted at a large rockslide (52° 26'N, 117° 24'W) in Jasper National Park Alberta, Canada. The rockslide is situated on Highway 93, 75km south of Jasper Townsite (Figure 1.1). The rockslide is composed of honey coloured quartzite sandstone (Bruce 1978), forming blocks of a range of sizes, but commonly up to 3m x 3m x 1m. There are many flat rockfaces. Jonas Rockslide is considered one of the major rockslides of the Canadian Rockies (Cruden 1976). It ranges from 1500m to 2200m in elevation, which places it in the subalpine, and is 3.5km long and 1km wide. The average annual temperature at that elevation is 0°C & average annual precipitation over the period 1971 to 1980 was 793mm as recorded at Sunwapta Wardens' station, 3km from the rockslide (Holland & Coen 1983). It is on a southwest facing slope in the Eastern Main Ranges. The rockslide is believed to have fallen at least 500 years ago, based on lichenometric evidence.

The dominant plants at the site are saxicolous lichens, which cover 87% of exposed rock surfaces. 106 species of saxicolous lichens have been recorded at Jonas Rockslide, of which 19 have a cover value greater than 1%. Tree cover is sparse and trees are absent from 80% of the rockslide area. _Picea engelmannii_ is present on the lower slopes and _Pinus albicaulis_ higher up.

Methods

Rockfaces were sampled along six parallel altitudinal transects on the rockslide. The range of altitude was from the Sunwapta River (1500m) to the maximum height of safe travel on the rockslide (2200m). 128 rockfaces were sampled at 90m intervals along the transects.

At each sampling station altitude was measured using an altimeter and the three nearest suitable rockfaces were selected for sampling, using only the criteria that they should be of low microtopographic relief, larger than 1m x 1m in area, between 0° and 90° in slope angle and not closely sheltered by trees. Each rockface was sampled with a grid of points, after the plotless sampling method of Yarranton (1966). The columns of the grid were 20cm appart, and the rows 10cm apart. For details see Chapter 4. At each grid point the species of lichen present was identified with the aid of a portable dissecting microscope. When necessary for identification of species apothecia were collected from fertile thalli and chemical tests were made on the thallus in the field. The chemicals used were $Ca(ClO)_2$ (C), as found in household bleach, Metzler's reagent (I), and 10% KOH solution (K). They were applied with a micropipette (diameter 10u) to the thallus medulla after it had been exposed with a razor blade.

At 25 of the rockfaces data was collected for a detailed 'nearest neighbour' analysis. At each point, in addition to the point species sampled by the grid, the species of lichen touching this lichen nearest to the sampling point was also recorded. Both were identified by the methods described above. Due to the difficulties of distinguishing individual thalli of some species, the next thallus of a different species was recorded. Uncolonised rock was treated as if it were a species. During this analysis, thallus sizes were also measured. The longest and shortest diameter of each sampled thallus were recorded, and these were later averaged to give a 'mean diameter' for each thallus.

At each rockface a number of environmental parameters were measured. Aspect was measured with a compass, as the direction in which the rockface was facing. An inclinometer was placed on a rigid meter ruler and the steepest slope angle of the rockface was measured, ranging from 0° (horizontal) to 90°. As the rockfaces chosen all had low microtopographic relief the above variables do not vary appreciably over the rockface. Slope and aspect were used in the calculation of a 'radiation index' for each rockface using the equations of Gates (1956) and Campbell (1977). This index is a measure of the amount of direct beam insolation received by the rockface. The degree of weathering of the rockface surface was estimated, by assessing how easily the rockface surface could be chipped: unweathered rock does not chip when hit with a hammer, while weathered rock has a crumbly, flaky surface. The number of trees within a 30m radius was recorded. The rock colour was compared with a soil colour chart, and later graded from pale to dark.

For details of all the above measurements see Chapters IV & V.

Analysis

To study the within rockface spatial distributions of lichens, the frequency with which each species was found on certain parts of the rockface was calculated. The grid points for each rockface are classified as being a) edge or non-edge, b) upper or lower, c) northerly or southerly. Figure 4.1 shows the sampling design and the way in which the rock is divided. The frequency with which each species was found in each position is compared with an expected value, calculated as the species overall frequency times the proportion of all grid points in that classification. For instance, the frequency with which a species occurs on the upper parts of rocks is compared to the expected frequency. A goodness of fit test (G-test, Sokal & Rohlf 1981) is used to compare the observed and expected frequencies, based on the null hypothesis of random distribution of each species over the whole rockface.

In order to study the correlations of lichen distributions with the environmental variables of slope, radiation index, degree of weathering, size, altitude, colour and number of trees around the rockface as well as the 'within rockface' spatial categories shown in Figure 4.1, the FORTRAN program CANOCO (canonical correspondence analysis) (Ter Braak 1987) was used. Each rockface was considered as 8 subsections which were treated as sample plots. Eighty-four of the rocks were used in this analysis, resulting in 672 sample plots.

The lichen thallus size data were used to prepare size class distributions and to calculate a mean thallus diameter for each species.

Association analyses were performed at several scales. For the nearest neighbour analysis, only data from the specially sampled rocks were used. For the other analyses, data from all rocks was pooled. In the nearest neighbour analysis, the expected value of joint occurrences of species i with species j was calculated as:

$$E_n(J(i,j)) =(p(i_{pt}) \times p(j_{nn})) \times N_n + (p(j_{pt}) \times p(i_{nn})) \times N_n$$

where: $E_n(J(i,j))$ is the expected number of joint occurrences of species i and species j in the nearest neighbour analysis; $p(i_{pt})$ is the probability that species i is selected as a sampling point; $p(j_{nn})$ is the probability that species j is selected as the nearest neighbour of another lichen; N_n is the total number of point pairs included in the nearest neighbour analysis.

Associations between lichens at adjacent grid points were also calculated, for both columns and rows. As columns were 20cm appart and rows 10cm appart (see Figure 4.1), column associations (i.e. associations between lichens at adjacent points in the same column) were calculated at two scales, 10cm and 20cm. Thus there were three analyses in this section, one between adjacent row points, 20cm apart, one between adjacent column points at a spacing of 10cm and one between alternate column points, at a spacing of 20cm. In each of these analyses, points were only used once, to permit an assumption of statistical independence. 'Expected' values for each association were calculated as:

$$E_a(J(i,j)) = n_a(i) \times n_a(j)/ 2N_a$$

where $E_a(J(i,j))$ is the expected number of joint occurrences of species i and species j in each of the adjacent grid points analyses; $n_a(i)$ & $n_a(j)$ are the number of occurrences of species i & species j in the analysis, and N_a is the number of point comparisons in each analysis.

In the whole rockface association analysis, whole rockfaces were used as the sampling unit, and all the data from one grid pooled. In the above analyses uncolonised rock was treated as if it were a species, whereas it was not included in the whole rockface analysis. The number of occurrences of two species on one rockface was compared to the expected value of joint occurrences, which is approximated as:

$$E_r(J(i,j)) = n_r(i) \times n_r(j) / N_r$$

where $E_r(J(i,j))$ is the expected number of rocks on which species i and species j both occur; $n_r(i)$ & $n_r(j)$ are the number of rocks on which species i & j occur respectively and N_r is the total number of rocks.

In all analyses the significance of the results was assessed using the log-likelihood ratio test ('G-test', Sokal & Rohlf (1981)). A 2 x 2 contingency table was prepared for each pair of species and each of the cells was included in the calculation. A test value greater than 3.8

indicates a value significant at the 5% level, based on the chi-squared distribution with one degree of freedom. It should be remembered that species with small sample sizes are unlikely to have statistically significant associations.

In all the analyses associations between species are designated as positive, when two species tend to occur together more often than expected at the 5% probability level (using a two-tailed test), as negative, when two species occur together significantly less often than expected, or as non-significant.

Results

The twelve species of Rhizocarpon present at Jonas Rockslide are listed in Table 7.1, with % cover in sampled grids. All other species included in this analysis are listed in Table 7.2.

Spatial Distribution Analysis

Figure 7.1 illustrates the proportion of each species occurrences that were on each part of the rockface. The seven species show a range of responses. The two members of the subgenus Rhizocarpon are more likely to be found on the upper parts of rocks and R. superficiale is also more often on the edges and southerly parts of rocks. Those in the subgenus Phaeothallus either appear randomly distributed with respect to these microhabitat variables or are more likely to be on the lower parts of rocks. R. bolanderi and R. polycarpum are the most frequently found in lower and non-edge positions on the rockface.

CANOCO analysis

The CANOCO ordination diagram is shown in Figure 7.2 for ordination axes 1 & 2 and in Figure 7.3 for axes 1 & 3. This analysis was performed on the 71 species with cover values greater than .05% at the site, however only Rhizocarpon species and species thought to be their major associates are shown. This is a canonical analysis in which the ordination axes are constrained to be linear combinations of the environmental variables. The arrows on the plot represent the direction of maximum variation in a particular environmental variable and the length of the arrow is a measure of the amount of variation in that plane. The nominal variables of top, edge and south are represented by squares, which indicate the approximate position of the centroids, or medians, for these variables. The position of a species on the ordination can be used to estimate the correlation of its distribution with a particular environmental variable by drawing a perpendicular to the line of the environmental arrow from the species point. Thus, for instance, R. eupetraeum is positively correlated with increasing slope, whereas R. bolanderi is negatively correlated.

It can be seen that the members of this genus are well dispersed over the diagram, each species respondingly differently to the environmental variables. Species such as R. grande at the centre of the ordination are probably generalists with respect to these variables, rather than being found more often at the means of these variables.

Examination of axis 3 (see Figure 7.3) allows separation of the effects of number of trees from the effects of the size of the rock, which had both been positively correlated with axis 2. This separation shows that R. polycarpum is positively correlated with the size of the rock, whereas R. alpicola is correlated with 'trees'.

Effects of environmental variables

From the ordination diagrams it can be seen that slope, 'sun', altitude and 'trees' are the most important correlates of lichen distributions at this site. Slope affects water available at the rocksurface, also snow retention and insolation. Steeper rocks are likely to receive and retain less precipitation per unit area. They are also likely to receive less summer sunshine, on average, than more horizontal rocks, although this effect is compounded by aspect. Rocks approaching horizontal are likely to weather more rapidly, as they retain water for longer periods.

Altitude is another complex environmental gradient, combining the effects of being further from the river at the base of the rockslide with the effects of cooler temperatures and a more exposed position.

'Sun' is an estimate of direct beam radiation received by the rock and probably affects temperatures at the rocksurface, as well as the amount of light available for photosynthesis.

Trees around a rock not only provide shelter, shade and a more humid environment in themselves but may also indicate those areas of the rockslide where there is soil close to the rockslide surface.

Species with shared responses to the environmental variables appear close together in the ordination diagram. Rhizocarpon bolanderi and its associated species are found on flat, well weathered rocks at low altitude. These species are not often found around the edges or upper parts of a rockface, thus avoiding the most exposed places, but eaching higher summer temperatures, due to shelter from cooling winds. R. superficiale and its associates are found in exposed, sunny places, such as the edges and upper parts of rockfaces, and at higher altitudes. The microenvironment is cooler and drier than that of the previous group due to the increased air currents received at the edges of a solid object (Creveld 1981). *R. eupetraeum* is found on steep rocksurfaces with low insolation, quite xeric situations, as less precipitation is received and run-off is faster than at shallower inclinations. *R. geographicum* and its associated species are found in shaded but less steep positions, moister than the environment of *R. eupetraeum*.

Association Analyses

The nearest neighbour analysis (Table 7.3) shows that most *Rhizocarpon* species have a positive relationship with bare rock, i.e. they contact uncolonised rock more often than expected by chance. *Spilonema revertens* has a series of negative and positive relationships with the *Rhizocarpons*, but generally at this scale of analysis there are very few relationships that are significantly different from expected values.

The most striking aspect of the results of the adjacent points analyses (Table 7.4) is that at all three scales, *R. bolanderi* and *R. superficiale* have a large number of associations and that these are always opposites: for instance, *R. superficiale* and *Pseudephebe pubescens* have a positive relationship, whereas the relationship of *R bolanderi* and *P. pubescens* is a negative one. *R. bolanderi* has a negative relationship with all the foliose lichens except *Phaeophyscia sciastra*. Overall there are more negative than positive associations in these analyses and relationships usually reflect species responses to environmental variables, in that negative relationships are usually between species appearing in different parts of the ordination diagram.

The whole rock association analysis (Table 7.5) also reflects species groupings found in the ordination diagrams. Positive relationships are usually between species in the same quadrant of the ordination diagram.

Thallus Sizes

Table 7.6 shows mean thallus diameters and Figure 7.4 shows size class distributions. In interpreting these results it should be remembered that the probability of sampling a large thallus is far greater than that of sampling a small thallus, small thalli are probably grossly under-represented in this analysis, as no attempt was made to census all thalli present. If this is borne in mind it can be seen that rapid recruitment is occuring into some of these lichen populations, especially when one considers that smaller thalli are likely to be sterile and will be classified as sterile *Rhizocarpon*. Recruitment into the subgenus *Rhizocarpon* does not appear as great as into *Phaeothallus*.

Average thallus size is greater in *Rhizocarpon* than in *Phaeothallus*, and there is remarkable similarity between the average thallus sizes of *R. grande*, *R. eupetraeum* and *R. disporum*.

Discussion

Although it is likely that the largest thalli on a substrate are the oldest, the converse may not necessarily be true for small thalli, as a number of factors, such as sub-optimal environmental conditions could lead to a lichen growing at less than its optimal growth rate. However it is likely that at least some of the smaller thalli represent new recruits to the population. Thus it is clear that recruitment is occurring into a number of the Rhizocarpon populations. This appears to be more rapid in subgenus Phaeothallus than in subgenus Rhizocarpon. As there are fewer small thalli in subgenus Rhizocarpon this may indicate that these species are not colonising as rapidly as they have in the past and that they may be better adapted to early successional situations, or to previous environmental conditions.

Although a population exhibits rapid recruitment, it may not be expanding, as mortality rates may match those of recruitment. This can only be measured in a long term study.

The positive relationships of Rhizocarpon thalli with uncolonised rock in the nearest neighbour analysis may indicate that they are not strong competitors, or alternatively that they avoid competition by producing allelopathic chemicals, creating a 'zone of inhibition' around each thallus. The need to obtain and maintain rock surface area must be very important in crustose lichen biology.

In the next part of the discussion the position of each Rhizocarpon species in the community will be discussed.

Rhizocarpon bolanderi

This is the most common saxicolous lichen at Jonas Rockslide, covering over 8% of the sampled rockfaces. Although in the subgenus Phaeothallus, it is in a different section from the other members of this subgenus present at Jonas Rockslide. It has a brown, peltate thallus, as distinct from the grey, areolate thalli of the other species. It is not often found in highly exposed microhabitats, avoiding upper and edge portions of rocks. It is associated with rocks of low slope, low altitude, a high radiation index and a high degree of weathering. Its large number of negative associations with other lichens can be explained in one of two ways: either it is highly competitive and excludes other lichens or it grows in microclimatic situations which are ecophysiologically unsuitable for other species. The surfaces on which it grows are likely to reach high temperatures and this factor may exclude heat- intolerant lichens. It is often associated with the filamentous lichen _Spilonema revertens_, which can grow on its thallus. The thalli of _R. bolanderi_ are rarely discrete, often spreading over the whole rocksurface with areoles intermingling with those of other species. Its association with uncolonised rock is in part due to growing on a weathered flaky substrate, and partly due to the fact that its thalli are rarely discrete entities and may surround small areas of bare rock. It is undoubtedly of great importance in this community. Its relationship to other species in the community is always opposite to that of _R. superficiale_, probably because they occupy two extremes of microhabitat.

It grows on the only surfaces on which plants indicative of a later successional stage, such as _Grimmia affinis_ and _Cladonia pyxidata_ also grow. The apparently high rate of recruitment in this species may in part be due to fragmentation of larger thalli.

R. disporum

There is some question as to the taxonomic delimitation of this species. Thomson (1979, 1967) includes specimens with both one and two spores per ascus as _R. disporum_, whereas other lichenologists separate out those with two ascospores as _R. geminatum_ (Clauzade & Roux 1985). Here, both one and two spored specimens are treated as _R. disporum_. This species is not found in exposed positions on the rockslide and is associated with larger rockfaces. Its position in the ordination diagrams is close to that of R. bolanderi, although not as extreme. As it has a cover value of 2.4% it is an important lichen in this community. The large number of small thalli is evidence that this is a rapidly recruiting species.

R. grande

This species appears in the centre of both ordination diagrams, and would seem to have a generalist role at Jonas Rockslide as it has no apparent preferences as to position on a rockface, or on any other gradients. It is not associated with uncolonised rock in the nearest neighbour analysis, as the other Rhizccarpons are, and this may indicate that it is a more aggressively competitive species, not avoiding contact with other lichens. It is not colonised by Spilonema revertens as are some other Rhizocarpon species, which may indicate an ability to resist colonisation by this lichen. It has a cover value of 2.4%, and also has a high recruitment rate.

R. eupetraeum

This species occurs with a frequency of 1.2% on sampled rockfaces. It is characteristic of a group of lichens tending to grow on steep north facing or shady rocks. Such environments are also dry, because little precipitation is received and run-off is rapid. Its thalli are usually very distinct and often surrounded by uncolonised rock in a very striking manner. This may indicate that it has allelopathic properties.

R. polycarpum

This is a rarer member of this community, having a cover value of only 0.4%. It is found on moister, shaded rocks. Its thalli are the smallest on average in Phaeothallus, possibly due to a slower growth rate.

R. alpicola

This species is not common at Jonas Rockslide, with a cover value of only 0.1% on sampled rocks. It is only known from one sampling station. The strong association of this species with trees may thus reflect an artefact of sampling, or may be due to an ecological requirement. This is a rare species in the North American flora.

R. eupetraeoides

This species is relatively rare, covering only .17% of sampled rocksurfaces. However, this partly reflects the choice of rocks for study, as the smaller shadier rocks on which it tends to grow were not often used in grid sampling. Its thalli may reach tremendous sizes; 800mm was recorded for one, apparently single, thallus.

R. superficiale

This is a characteristic species of exposed positions where it forms large round thalli. It is known that it suffers heat stress when exposed to the temperatures that a sheltered rock can reach in summer (Coxson & Kershaw 1983a & b) and this may explain its restriction to exposed parts of rocks, which may be cooled by air currents. In the adjacent grid points association analyses it showed a large number of negative and positive associations. This could be because it has a relatively specialised microenvironment, shared with a correspondingly specialised flora. It exhibits low rates of recruitment, as indicated by a lack of smaller thalli.

R. geographicum

Over 2% of the surface area of the rockslide is covered by this lichen. Its position in the community is unclear. It prefers upper parts of rockfaces, yet appears in the ordination diagram as a species that avoids high altitude positions.

Overall Discussion

There is evidence to support the idea that the yellow green pigment of the subgenus *Rhizocarpon* is an adaptation to exposed, high radiation environments, as the two species most frequently found on the upper parts of rockfaces belong to this subgenus, and none of the species in *Phaeothallus* are more often found on the upper parts of rocks.

Despite their similar morphology these *Rhizocarpon* species exhibit niche separation and the resources avalable at the site are not shared equally between them. Each of the *Rhizocarpon* species has a separate place in the community and competition between certain of these congenerics is probably minimal, as each has a separate response to the complex of environmental gradients measured at the site. It is possible that the separate responses to the measured environmental factors are at least partly the result of ecophysiological specialisation of each species. The work of Coxson & Kershaw (1983b) indicates that this is the case for *Rhizocarpon superficiale*.

Competition between pairs of *Rhizocarpon* species will vary greatly, depending on their tendency to share the same microhabitat. *R. superficiale* and *R. bolanderi* will compete very little, as they are rarely found in the same microenvironments, whereas competition between *R. bolanderi* and *R. disporum* is likely to be greater, as they appear very close on the ordination diagram, implying that they often occur in similar micohabitats. However all the environmental factors important to the lichens in this community have not been measured, and species that appear close in this analysis may be separated by some other ecological requirements. For instance, some species may have specific requirements for ascospore establishment. In addition, there is the problem of measuring environmental variables at a scale that is relevant to the plants concerned. Plants may not respond to the environmental variables at the same scale that they are percieved by the investigator.

It is possible that the realised niches seen in this study are the product of past competition at this site or of more long term evolutionary processes. The observed niches may only reflect a part of the fundamental niche of each species, and the observed niche separation may be as a result of past competition reducing the resources available to each species, or as a result of adaptations to reduce competition amongst the species. Similar studies at other sites where these species coexist might help to answer this question.

Summary

Twelve species of Rhizocarpon coexist with 94 other species of saxicolous lichens at Jonas Rockslide, Jasper National Park, Alberta, Canada. The position of each Rhizocarpon species in the community is assessed with respect to environmental factors and biotic processes. Each species has a different response to the measured environmental factors and a different set of interactions with other species. R. bolanderi and R. superficiale stand out as opposites with regard to their biotic associations and environmental correlations. Competition between pairs of Rhizocarpon species varies in intensity, but is unlikely to have a large

impact in any one case, because each species occupies a distinct microhabitat. Using thallus diameter as a measure, there is evidence of high recruitment into populations of the subgenus *Phaeothallus* and lower recruitment rates in subgenus *Rhizocarpon*.

Bibliography

Bruce, I. (1978) The Field estimation of shear strength on rock discontinuities. Ph.D. thesis, Department of Civil Engineering, University of Alberta.

Campbell, G. S. (1977) An introduction to environmental biophysics. Heidelberg Science Library. Springer-Verlag New York, Heidelberg, Berlin.

Clauzade, G. & Roux C. (1985) Likenoj de Okcidenta Europo. Ilustrita determinlibro. Bulletin de la Societe Botanique du Centre-ouest Nouvelle serie, Numero Speciale: 7.

Coxson, D. S. & Kershaw, K. A. (1983a) The ecology of *Rhizocarpon superficiale*. I. The rock surface boundary-layer microclimate. Canadian Journal of Botany, 61: 3009-3018.

Coxson, D. S. & Kershaw, K. A. (1983b) The ecology of *Rhizocarpon superficiale*. II. The seasonal response of net photosynthesis & respiration to temperature, moisture and light. Canadian Journal of Botany, 61: 3019-3030.

Creveld, M. (1981) Epilithic lichen communities in the alpine zone of southern Norway. Bibliotheca Lichenologica. J. Cramer. Fl. 9490 Vaduz.

Cruden, D. M. (1976) Major rock slides in the Rockies. Canadian Geotechnical Journal, 13: 8-20.

Egan, R. S. (1987) A fifth checklist of the lichen-forming, lichenicolous & allied fungi of the continental United States and Canada. The Bryologist, 90: 77-173.

Gates, D. M. (1965) Radiant energy, its reciept and disposal. In Waggoner, P. E. (ed.) Agricultural Meteorology. Meterorological Monographs, 6: NO.28 American Meteorological Society Boston 1-26.

Gauslaa, Y. (1984) Heat resistance and energy budget in different Scandinavian plants. Holarctic Ecology, 7: 1-78.

Holland, W. D. & Coen, G. M. (1983) Ecological (Biophysical) land classification of Banff & Jasper National Parks. Volume II. Soil and vegetation resources. Alberta Institute of Pedology & Environment Canada.

Innes, J. L. (1985) Lichenometry. Progress in Physical Geography, 9: 187-254.

Larson, D. W. (1984) Habitat overlap/niche segregation in two *Umbilicaria* lichens: a possible mechanism. Oecologia, 62: 118-125.

Larson, D. W. (1980) Patterns of species distribution in an Umbilicaria dominated community. Canadian Journal of Botany, 58: 1269-1279.

Runemark, H. (1956) Studies in Rhizocarpon. I. Taxonomy of the yellow species in Europe. Opera Botanica, 2: 1-152.

Sokal, R. R. & Rohlf, F. J. (1981) Biometry. The Principles and Practice of Statistics in Biological Research. 2nd Edition. W. H. Freeman & Company, New York.

Ter Braak, C. J. F. (1987) CANOCO - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO Institute of Applied Computer Science, Wageningen, The Netherlands.

Thomson, J. W. (1979) Lichens of the Alaskan Arctic Slope. University of Toronto Press, Toronto.

Thomson, J. W. (1967) Notes on Rhizocarpon in the Arctic. Nova Hedwigia, 14: 421-481.

Watson, M. A. (1980) Patterns of habitat occupation in mosses - relevance to considerations of the niche. Bulletin of the Torrey Botanical Club, 107: 346-372.

Werner, P. A. (1979) Competition and coexistence of similar species. Chapter 12 in Topics in plant population biology. pp 287-312 Edited by Solbrig, O. T., Jain, S., Johnson, G. R., & Raven, P. H. Columbia University Press, New York.

Yarranton, G. A. (1966) A plotless method of sampling vegetation. Journal of Ecology, 54: 229-237.

Table 7.1: List of *Rhizocarpon* species known from Jonas Rockslide. (t indicates that % cover is less than 0.1)

Sub-genus *Rhizocarpon*	% cover on exposed rocks
sterile specimens	1.2
Section *Superficiale*	
R. superficiale	1.5
Section *Alpicola*	
R. eupetraeoides	0.2
R. alpicola	0.1
Section *Rhizocarpon*	
R. geographicum	2.1
R. macrosporum	t
R. riparium	t
Sub-genus *Phaeothallus*	
sterile specimens	5.5
Section *Rittokense*	
R. bolanderi	8.9
Section *Fuscothallus*	
R. eupetraeum	1.2
R. grande	2.4
R. polycarpum	.5
R. disporum	2.4**
R. geminatum	

** This value includes specimens of *R. geminatum*

Table 7.2: Species included in the analyses of Chapter 7 . Nomenclature follows Egan (1987).

code	Species	Percent cover
asp cin	*Aspicilia cinerea* (L.) Körber	5.1
bel cin	*Bellemerea cinereorufescens* (Ach.) Clauz. & Roux	1.0
cet hep	*Cetraria hepatizon* (Ach.) Vainio	1.3
cla pyx	*Cladonia pyxidata* (L.) Hoffm.	.2
led pau	*Lecidea paupercula* Th. Fr.	1.7
lep neg	*Lepraria neglecta* (Nyl.) Lettau	1.1
mel gra	*Melanelia granulosa* (Lynge) Essl.	2.1
mel pan	*M. panniformis* (Nyl.) Essl.	.3
mel sor	*M. sorediata* (Ach.) Goward & Ahti	3.5
mel sty	*M. stygia* (L.) Essl.	3.0
orp mor	*Orphniospora moriopsis* (Massal.) D.Hawks.	1.1
pha sci	*Phaeophyscia sciastra* (Ach.) Moberg	.5
pse min	*Pseudephebe minuscula* (Arnold) Brodo & D. Hawks.	1.9
pse pub	*P. pubescens* (L.) M. Choisy	5.0

Table 7.2: (continued)

code	Species	percent cover
rhi alp	Rhizocarpon alpicola (Anzi) Rabenh.	.1
rhi bol	R. bolanderi (Tuck.) Herre	8.9
rhi dis	R. disporum (Hepp) Mull. Arg.	2.3
rhi eud	R. eupetraeoides (Nyl.) Blomb. & Forss.	.2
rhi eup	R. eupetraeum (Nyl.) Arnold	1.2
rhi geo	R. geographicum (L.) DC.	2.1
rhi gra	R. grande (Flotow) Arnold	2.4
rhi pol	R. polycarpum (Hepp) Th. Fr.	.4
rhi sup	R. superficiale (Schaerer) Vainio	1.5
rhi ugr	R. sp. (grey thallus)	5.5
rhi uyg	R. sp. (yellow-green thallus)	1.2
sch ten	Schaereria tenebrosa (Flotow) Hertel & Poelt	2.0
spi rev	Spilonema revertens Nyl.	5.9
umb hyp	Umbilicaria hyperborea (Ach.) Hoffm.	5.6
umb lam	U. lambii Imsh.	1.3
umb tor	U. torrefacta (Lightf.) Schrader	1.9

Table 7.3: Associations in the nearest neighbour analysis

	gr	eu	di	ge	su	bo	ug	uy
unc roc		+++	++	++	++	+++	+++	+++
umb tor								
umb hyp								
umb lam					+	-		
mel sty		+	-					
mel gra								
mel sor								
cet hep								
pha sci								
pse pub	++							
pse min			+					
spi rev	=	=				+++	++	=
lep neg				-			-	
lec pau						=	=	
orn mor								
asp cin							=	-
bel cin				+		++		
sch ten								
rhi gra						-	=	
rhi eup						-	-	
rhi dis								
rhi geo								
rhi sup						-	-	
rhi bol								
rhi ung								
rhi uny								

Legend: +,- G-test indicates $p<0.05$, but one of the expected values is < 5 thus test unreliable
++,= G-test significant $0.05>p>0.001$
+++,=- G-test significant $p< 0.001$
At the top of the table the first two letters of the specific name of each *Rhizocarpon* species is given. Full species names can be found in Table 7.2.

Table 7.4: Associations of Rhizocarpon species in the adjacent grid points analyses.

	row associations (20cm)								column associations (20cm)								column associations (10cm)								
	gr	eu	di	ge	su	bo	ug	uy	gr	eu	di	ge	su	bo	ug	uy	gr	eu	di	ge	su	bo	ug	uy	
unc roc	=			=			++		=			=													unc roc
umb tor					=											-						=			umb tor
umb hyp						=				-				=									=		umb hyp
umb lam						=							+	=-	=		-					=-			umb lam
mel sty		+			-	=-		-					-	=-			++	++				=-			mel sty
mel gra						=								=-							+	=-			mel gra
mel sor														=								=-			mel sor
ost hep	-																					=			ost hep
pha sci														++								++			pha sci
pse pub					+++	=-		=					++	=			=				++	=-			pse pub
pse min						=				-															pse min
spi rev		=	=		=-	+++							=	++				=			=	+			spi rev
lep neg																					-				lep neg
lec pau	-			+		=									=					+					lec pau
orn mor						=-							+	=								=	=		orn mor
asp cin			=						+						=								=		asp cin
bel cin								+		-	-					+				+				+	bel cin
sch ten						=-	=						+	=	=			-			+	=		+	sch ten
rhi gra						++															-				rhi gra
rhi eup														=				+				=-			rhi eup
rhi dis											=														rhi dis
rhi geo				+		=										+				++					rhi geo
rhi sup					+	=								=	=						+	=-			rhi sup
rhi bol						+++										=						+++			rhi bol
rhi ung																							++		rhi ung
rhi uny																									rhi uny

Legend: +,- G-test indicates $p<0.05$, but an expected value is less than 5, making the test unreliable

++,= G-test gives significance level of $0.05>p>0.001$

+++,=- G-test gives significance level of $p<0.001$

At the top of the table the first two letters of the specific name of each Rhizocarpon species is given.

Full species names can be found in Table 7.2

Table 7.5: Associations at the whole rock scale

	rr	re	rd	rg	rs	rb	ru	ru	rp
umb tor	+++	++							+
umb hyp	+++								
umb lam					+++				
mel sty	++	++			++				
mel gra		++							
mel sor									
cet hep	++	+++							++
pha sci		=	++			++			
pse pub	++				+++				
pse min		=			++				
spi rev	+					+			
lep neg		+++			=				++
lec pau		++				=			
orn mor					++				
asp cin						+			
bel cin									
sch ten	++				++				
rhi gra			++			++			++
rhi eup						=			
rhi dis									
rhi geo									
rhi sup									
rhi bol									
rhi ung									
rhi uny									
rhi pol									

Legend:

+	G-test indicates $p<0.05$, but one one of the expected values is < 5 thus test is unreliable
++,=	G-test gives a value with a probability level of $p<0.05$, $p>0.001$
+++	G-test gives a value with a probability level of $p<0.001$

At the top of the table the first two letters of the specific name of each *Rhizocarpon* species is given. Full species names can be found in Table 7.2.

Table 7.6: Thallus sizes summary.

species	sample size	mean diameter (mm)	standard deviation	largest diameter
Rhizocarpon bolanderi	194	36.0	75.0	794
R. disporum	56	32.4	26.4	131
R. eupetraeum	30	34.0	37.0	182
R. geographicum	67	28.9	23.0	153
R. grande	70	34.0	32.7	177
R. superficiale	22	55.3	30.3	144
R. sp. (grey)	131	15.3	18.6	147
R. sp. (yellow)	25	15.2	19.2	94

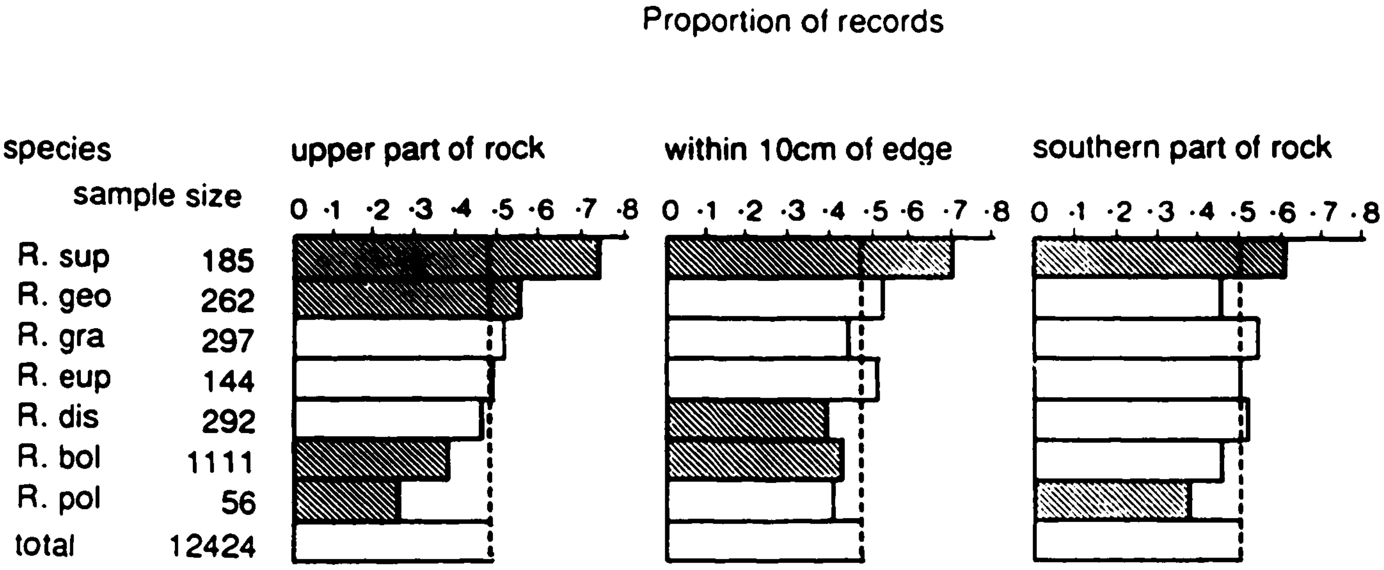
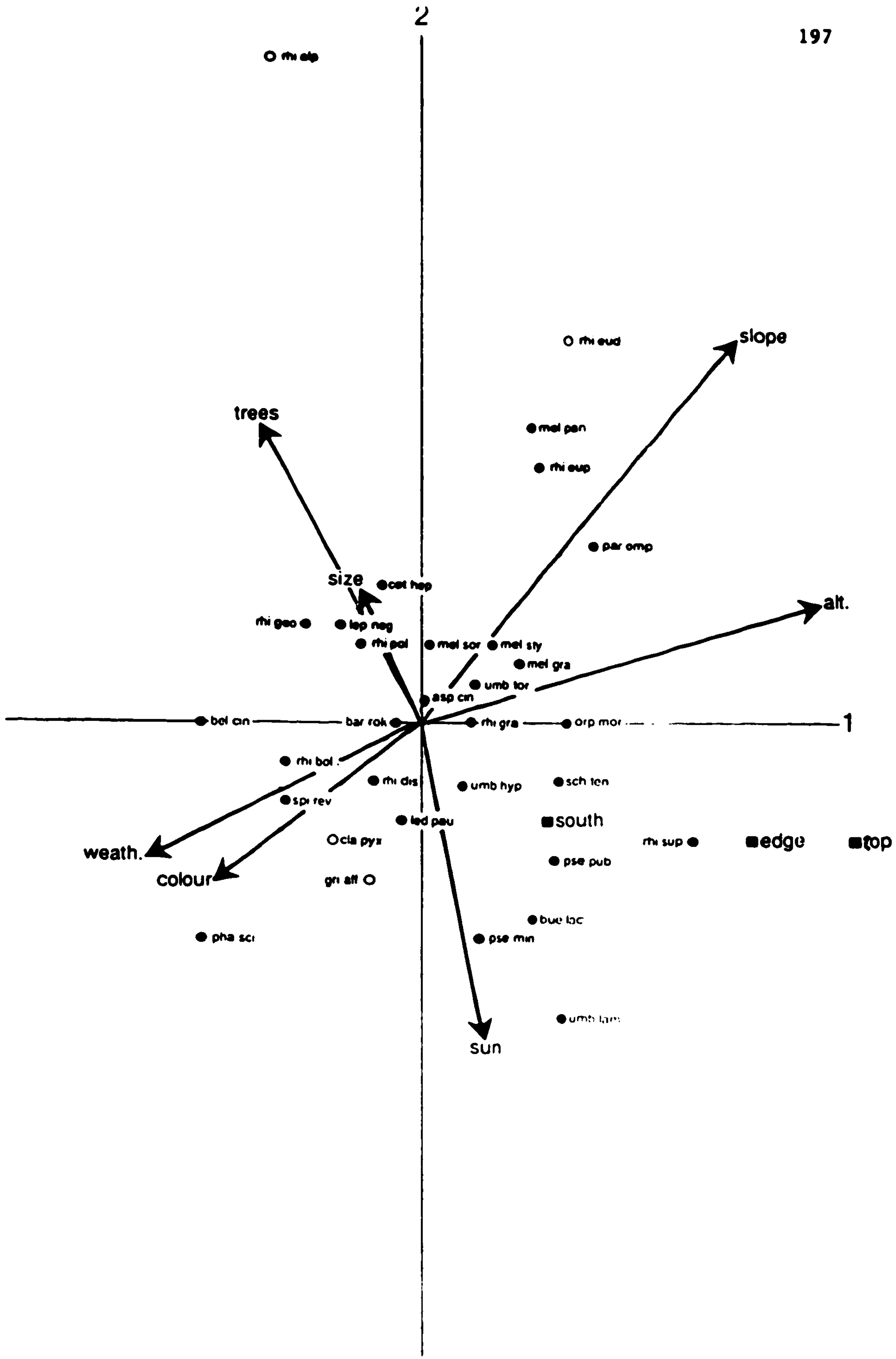


Figure 7.1: Within rockface microhabitat distributions of *Rhizocarpon* species. The bars show the proportion of a species' occurrences that were found in that category. Shaded bars differ significantly from the expected value (proportion of all points in that category) as indicated by the G-test.

Figure 7.2: CANOCO ordination diagram showing positions of species and environmental variables in relation to the first and second ordination axes. Obtained using a canonical correlation analysis available in the CANOCO (Ter Braak 1987) program. The arrows show the direction of maximum variation of each of the measured environmental variables. Slope = inclination from horizontal of the rockface; alt. = altitude of the rockface above the Sunwapta River; sun = estimated amount of direct solar radiation received by the rockface; colour = colour of the rockface on a scale from 1 (pale) to 5 (dark); weath. = an estimate of the degree of weathering of the rockface on a scale of 1 (no weathering) to 5 (very weathered); trees = the number of trees within a 30m radius of the rockface; size = the area of the rockface. The squares show the centroids of the nominal environmental variables of 'top', 'edge', and 'south'.


2
rhi alp
rhi eud
slope
trees
mel pen
rhi eup
par omp
size
cat hep
alt.
rhi geo
lep neg
rhi pol
mel sor
mel sty
mel gra
umb tor
asp cin
bel cin
bar rok
rhi gra
orp mor
1
rhi bol
rhi dis
umb hyp
sch ten
spi rev
led pau
south
rhi sup
edge
top
weath.
cla pyx
pse pub
colour
gri aff
bue lac
pha sci
pse min
umb lam
sun

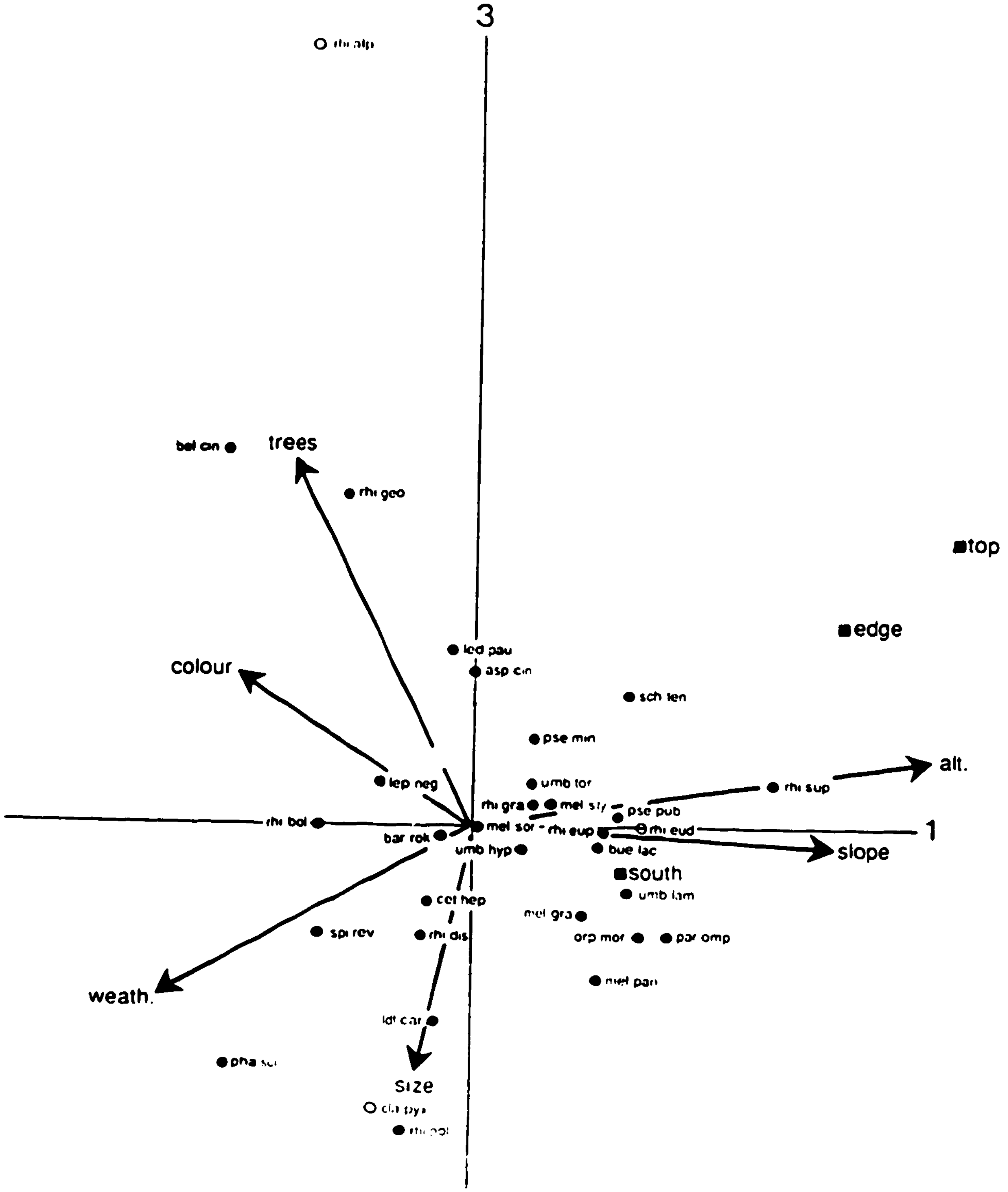


Figure 7.3: CANOCO Ordination diagram showing positions of species and environmental variables in relation to the first and third ordination axes. See Figure 7.2 for explanation.

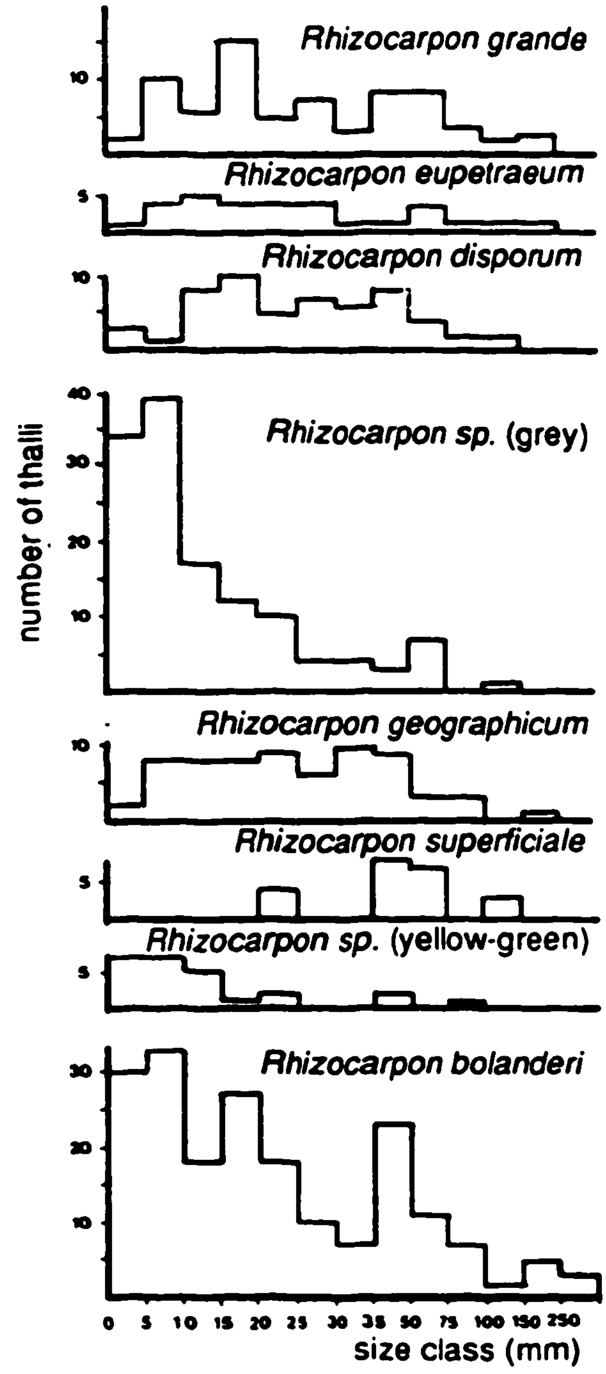


Figure 7.4: Histograms showing number of Rhizocarpon thalli in each diameter size-class.

CONCLUSIONS

A review of the preceding chapters will be followed by a synthesis in which the answers to the questions posed in the introduction will be discussed.

The flora of Jonas Rockslide is discussed and over 100 species of saxicolous lichens are reported. Some of these are rare or unusual species only recently reported in the Canadian flora. Most species in the community have a very low cover value; only 21 species have a cover value greater than 1%, and 5 species have a cover value greater than 5%. Most species are restricted to specific microhabitats at the site, others are generalists over the range of habitats studied.

The rockslide is shown to be at least 500 years old, using the sizes of lichen thalli from the genus Rhizocarpon for which growth rates are available. It is possible that the rockslide is much older than this. A knowledge of the age of the rockslide is important in the interpretation of the processes acting within this community as it implies that community processes have had at least 500 years to act on the species present. The sizes of three species of Rhizocarpon, subgenus Rhizocarpon are found to differ significantly. This result has important implications for the technique of lichenometry, indicating that the species of Rhizocarpon used in making measurements is very important.

Spatial distributions of lichens are found to be correlated with position on the rockface. Lichens belong to one of three categories; those which are more often on the upper and edge portions of rockfaces, those more often on the lower and non-edge portions of rockfaces, and those apparently randomly distributed on the rockface. Simple microclimatic measurements provide a basis for understanding these microhabitat distributions in terms of microenvironmental differences. Temperature, snow cover and drying rates vary across a rockface. An understanding of boundary layer conditions is essential in interpreting these results.

A plausible hypothesis is that the observed microhabitat distributions are due to ecophysiological adaptations to specific microenvironments, rather than processes such as competition restricting realised niches. Previous ecophysiological work on the temperature tolerances of species found at Jonas Rockslide, although on only two species, supports this conclusion (Coxson & Kershaw 1983, MacFarlane & Kershaw 1982). However, in a crowded plant community, it is impossible to conclude that species are growing at their ecophysiological optima, as the role of competition in determining species distributions cannot be gauged, and could have a considerable effect in restricting the least competitive species to suboptimal habitats.

Concurrent with the effects of within rockface variables are factors common to the whole rockface, such as inclination of the rockface, its elevation and amount of solar radiation received. A canonical correlation analysis, CANOCO (Ter Braak 1987), is used to calculate the correlation between these factors and the distributions of species. At this scale, important correlates of species distributions were found to be elevation, inclination of the rockface and direct beam solar radiation received. None of these variables acts in a simple way on the microenvironment at the rocksurface, but they control temperature, humidity and light regime at the rock surface. Although clear species groupings are not found, the ordination allows an assessment of which species are likely to occur in the same microhabitats. It is recognised that all the environmental factors that are determinants of lichen distributions have not been measured. There is also a problem of scale in measuring environmental factors and relating them to plant distributions, as the scale at which a variable is easily measured may not be the same as that 'perceived' by the plants.

Thus abiotic factors are shown to be correlated with species distributions. The biotic environment and dynamic processes of this lichen community are also assessed. Associations between species are compared at a variety of size scales. In the nearest neighbour analysis the species of lichen touching a sampled lichen is recorded, so that a 'plants eye view' (Turkington & Harper 1979) of its neighbours is obtained. It is found that crustose lichens are more likely to contact bare rock as a neighbour than would be expected by chance, whereas foliose lichens are more likely to contact another lichen. This reflects a fundamental biological difference, the crustose lichens being less able to compete in the presence of another lichen due to their growth form. It may also indicate the presence of a 'contact avoidance' mechanism, possibly mediated by allelopathic substances.

Associations at the 10cm and 20cm scales reflect shared microhabitats, as do those at the whole rockface scale.

Thallus size distribution data shows that there are many small thalli, indicating an ongoing colonisation process, if the assumption that small thalli are younger than large thalli is accepted. This implies that the community is dynamic and that opportunities for colonisation must occur. It is possible that the reason for the lack of dominance by foliose lichens, despite the competitive advantages of the foliose growth form, is because of cyclic successional and senescence processes (Watt 1947).

The ecology of the genus Rhizocarpon is discussed in a separate chapter because of its importance in the ecology of the community, and interesting problems posed by the coexistence of its members. There are twelve Rhizocarpon species at Jonas Rockslide, and their remarkable morphological similarity raises questions regarding their ecological differences, and why competitive interactions have not eliminated some of these species. They are found to occupy the range of microhabitats available at the site, each species having a specific response to the measured environmental variables, as assessed by the CANOCO analysis. Competition between most species pairs is unlikely to be severe, as they tend to occupy different microhabitats, and this could explain their coexistence. Whether the observed niches represent the limits of ecological tolerance of each species, or whether they are restricted by competitive interactions could only be resolved by further research.

Some of the questions posed in the introduction will now be restated, and an attempt made to answer each of them.

1) How are the species in this community organised spatially?

2) What dynamic processes are occurring among the species of this community and what prevents domination by the apparently competitively superior foliose species?

3) How can so many species coexist without competitive exclusion occurring?

4) How could the role of competition in this community be assessed?

It is clear that spatial organisation of many of the species in this community can be related to microenvironmental variables, and most species show a high degree of microhabitat specificity. However certain species appear to be randomly distributed with respect to any of the measured environmental variables, at least over the range measured. It is possible that they show microhabitat specificity for some other factors not measured here, for instance microtopographic features of the rock surface.

Whether the microhabitat specificity shown by most species is as a result of ecophysiological limitation in a stressful environment or due to competitive interactions is unknown, but it seems likely that both would operate. The avoidance of competition seems important in crustose lichen biology at Jonas Rockslide, as indicated by the nearest neighbour analysis. However, there is evidence that ecophysiological adaptation to specific habitats is of great importance in lichen biology. This is an area amenable to further research. The direct assessment of the importance of competition is difficult in a slow-growing community such as this, but the sensitivity of lichens to environmentally imposed stresses can readily be assessed in the laboratory after the fashion of Coxson & Kershaw (1983). Armstrong (1977) has pioneered field experiments monitoring the performance of lichens after transplant to rocksurfaces of different aspect and similar experiments could be performed at Jonas Rockslide, although they would probably require many years of monitoring.

Dynamic processes are probably very important in the biology of this community, although the only evidence available is indirect. The large number of smaller lichens present indicates that there are opportunities for recruitment into populations, and some factor prevents the complete dominance by foliose lichens. I hypothesise that dynamic patterns at the site follow a cyclic successional sequence like that described by Watt for a *Calluna* dominated heath community (Watt 1947). In that community senescence patterns in individual *Calluna* plants allow other species to coexist with it. At Jonas Rockslide this pattern is probably imitated by the effects of wind and weather on the thalli of foliose lichens, which are very brittle and friable when dry, and by senescence of the central portions of older crustose thalli. The overgrowth of crustose thalli by foliose lichens, causing death of the crust and the subsequent erosion of the foliose thallus would also release space for recolonisation of the rock surface by other lichens. This hypothesis can only be tested by a long term monitoring program. It would be necessary to set up permanent quadrats and keep a detailed photographic record of changes occurring within the quadrats. Little is known about the growth rates of most of the species present in this community, so the necessary length of a monitoring project is in determinable. However, it is probable that many of the species grow faster than the 11mm per century estimated for Rhizocarpon geographicum at a nearby site (Mount Edith Cavell, Luckman (1977)). The dynamic processes observed will depend on the species present in that particular microhabitat. For instance, on Rhizocarpon bolanderi dominated rocks there are few foliose species and R. bolanderi is likely to dominate cyclic successional processes. In other microhabitats within the community biotic processes may not be important, and species may be limited by ecophysiological adaptations to particularly stressful microhabitats.

The high number of species present in this community is likely to be the result of three processes. The first is the microhabitat specificity of many species, probably due to the extreme nature of the boundary layer environment. The second is the cyclic successional sequence proposed above, which would tend to prevent dominance of a particularly competitive species, and also means that recolonisation sites are frequently being made available. Most of the species in this community are rare, and occupy less than 1% of the rock surface area. It is possible that they fulfil the role of 'fugitive species' (Watson 1980), either in space or time. That is, they are restricted to particularly rare microhabitats (such as cracks in the rock surface) or they are able to move rapidly into sites that become available for colonisation before competitive processes can act. The third is the influx of lichen propagules from outside the community. Lichen propagules are presumed to travel large distances, and it is possible that there is a continual influx of propagules from surrounding areas.

It is impossible to gauge objectively the role of competition in a plant community from a purely descriptive study. However this study suggests a number of ways in which its importance could be assessed. Long term stud involving species removals would be impractical, but not impossib An example of a possible experiment would be the removal of foliose species from a rockface and the observation of the effects of such a removal on other species. This would probably have to be a 'press' experiment rather than a 'pulse' experiment (Bender _et_. _al_. 1984), that is, removals would be continued rather than allowing the system to return to normal. Another long term possibility would be to change the microenvironment of a rockface (_e_._g_. by tilting it) and observe changes in its species composition over time.

This study is probably the most detailed study of a saxicolous lichen community to date. It is clearly a complex community, both in terms of species diversity and the responses of the species to their environment, despite its structural simplicity. The microhabitat specificity of these organisms has been confirmed, while finding that the community is a highly dynamic one. The information provided in this study has suggested a number of testable hypotheses concerning the processes organising this community.

BIBLIOGRAPHY

Armstrong, R. A. (1977) The response of lichen growth to transplantation to rock surfaces of different aspect. New Phytologist, 78: 473-478

Bender, E. A., Case, T. J. & Gilpin, M. E. (1984) Perturbation experiments in community ecology: theory and practice. Ecology, 65: 1-13.

Bertness, M. D. & Ellison, A. M. (1987) Determinants of pattern in a New England salt marsh plant community. Ecological Monographs, 57: 129-147.

Coxson, D. S. & Kershaw, K. A. (1983a) The ecology of *Rhizocarpon superficiale*. I. The rock surface boundary-layer microclimate. Canadian Journal of Botany, 61: 3009-3018.

Coxson, D. S. & Kershaw, K. A. (1983b) The ecology of *Rhizocarpon superficiale*. II. The seasonal response of net photosynthesis & respiration to temperature, moisture and light. Canadian Journal of Botany, 61: 3019-3030.

Luckman, B. H. (1977). Lichenometric dating of holocene moraines at Mount Edith Cavell, Jasper, Alberta. Canadian Journal of Earth Sciences, 14, 1809-1822.

Turkington, R. & Harper, J. L. (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I Ordination, pattern and contact. Journal of Ecology, 67: 201-218.

Watson, M. A. (1980) Patterns of habitat occupation in mosses - relevance to considerations of the niche. Bulletin of the Torrey Botanical Club, 107: 346-372.

Watt, A. S. (1947) Pattern and process in the plant community. Journal of Ecology, 35: 1-22.

APPENDIX 1 - RESULTS OF GRID SAMPLING

In this appendix the results of the grid sampling of individual rockfaces is presented. Each rockface is represented by a grid of points, which can be interpreted as follows:

The first line of each rock's data gives its number, e. g. R11. Rocks 1 to 43 were sampled in 1985, rocks 45 to 133 were sampled in 1986.

The second line consists of a series of numbers which give the dimensions of the rock followed by the values of the environmental variables measured for that rock. A 999 anywhere on this line indicates that the value was unavailable. The sequence of numbers is as follows:

1. The number of rows in the sampling grid.
2. The number of columns in the sampling grid.
3. Aspect of the rockface (uncorrected for magnetic declination).
4. Altitude of the rock in metres above the Sunwapta River.
5. Inclination from horizontal (slope) of the rockface (in degrees).
6. Number of transect
7. Palest colour recorded on rockface (1 pale, 5 dark)
8. Darkest colour recorded on rockface.
9. Estimated degree of weathering of rockface (1 unweathered, 5 weathered)
10. Number of trees within a 30m radius of the rockface.
11. Estimated degree of exposure of the rockface (1 exposed, 5 sheltered)

The third and subsequent lines represent the grid data. Each point on the rockface is given as a non-zero number. Zeros are not part of the rockface. Each species is given a number, and these are listed below.

001	Uncolonised (bare) rock.
002	Unlichenised fungal hypothallus.
003	Unidentified crustose lichen
004	Uncolonised purple rock
005	Uncollected or lost data.
010	Umbilicaria torrefacta.
011	U. deusta.
013	U. hyperborea
015	U. polyphylla
016	Unidentified Umbilicaria
017	U. proboscidea
018	U. vellea
020	Parmelia saxatilis
021	P. omphalodes
022	Melanelia stygia
023	M. panniformis
024	M. granulosa
025	M. sorediata
026	Unidentified Melanelia
030	Arctoparmelia centrifuga
031	Unidentified Arctoparmelia
032	A. incurva
033	A. subcentrifuga
040	Cetraria hepatizon
041	Brodoa oroarctica
042	Umbilicaria lambii
043	Hypogymnia austerodes
046	Lecanora epibryon
051	Physcia sp.
052	P. dubia
053	P. caesia
055	Phaeophyscia sciastra
056	P. endococcinia
059	Porpidia cristulata
060	Pseudephebe pubescens
061	P. minuscula
062	Spilonema revertens
063	Leprocaulon subalbicans
064	Spilonema revertens
065	Lepraria neglecta
068	Bryoria sp.
070	Rhizoplaca melanopthalma
071	R. chrysoleuca
072	Lecanora frustulosa
073	L. intricata
074	Lecanora sp.
075	L. polytropa
078	L. cenisea
079	L. badia

080	Lecidea atrobrunnea.
081	L. paupercula
082	L. plana
083	L. confluens
084	L. sp.
086	Porpidia macrocarpa
087	Lecidea auriculata
088	L. tesselata
089	L. lapicida
090	Lecidella stigmatea
092	L. carpathica
094	Schaereria cinereorufa
095	Dimelaena oreina
096	Rinodina turfacea
099	Porpidia sp.
101	Buellia sp.
104	Orphniospora moriopsis
105	Buellia papillosa
108	B. lacteoidea
110	Rhizocarpon grande
111	R. eupetraeum
112	R. disporum
113	R. polycarpum
114	R. sp. (section pheaothallus)
119	R. grande/eupetreaum
120	R. geographicum
121	R. superficiale
122	R. sp. (section Rhizocarpon)
123	R. eupetraeoides
124	R. alpicola
125	R. riparium
126	R. crystellaginum
130	R. bolanderi
140	Aspicilia cinerea
141	Bellemerea cinereorufescens
142	Aspicilia caesiocinerea
143	Bellemerea alpina
144	Aspicilia sp.
145	Schaereria tenebrosa
146	Aspicilia 'supertegens'
150	Grimmia affinis
151	Ptilidium sp.
152	Hedwigia ciliata
153	Grimmia rivularis
155	Cladonia pyxidata
156	C. phyllophora
159	Caloplaca sp.
160	Acarospora fuscata
161	Caloplaca jungermanniae
162	Diploschistes scuposus
163	Candellariella vitellina

164 Staurothele clopima
165 Sporastatia testudinea
166 Caloplaca epithallina
167 Phylliscum demangionii
168 Caloplaca sp.

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119 031 121 119 000 000
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001 119 119 119 111 026
111 111 104 119 001 080
031 111 111 111 001 114
111 031 111 140 026 111
111 111 140 140 001 026
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111 010 000 000 000 000
005 003 000 000 000 000
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000 145 003 122 130 112 001 062 150 130 000
000 140 024 001 001 110 055 001 010 130 144
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000 000 002 113 002 140 001 092 130 144 010
000 000 130 140 055 060 060 060 150 060 120
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000 010 041 010 041 061 001 025
000 110 062 001 010 001 144 025
041 070 130 144 140 010 113 061
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119 144 140 062 114 062 112 061
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040 120 001 144 001 001 061 061
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026 119 002 108 062
062 010 130 001 114
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001 140 112 112 001 000
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001 001 003 130 001 001
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r36
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R37
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060 024 130 003 130 010 024 120
018 018 025 130 140 114 002 140
018 018 096 112 130 130 001 001
018 040 073 060 001 073 010 010
121 040 024 001 073 020 024 025
018 150 150 062 024 020 060 070
110 000 024 114 001 000 140 000
000 000 000 000 062 000 026 000
R51
09,13,149,82,40,4,2,6,2,1,999
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021 145 112 001 130 010 024 002 000
024 062 024 130 002 001 060 060 000
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000 145 060 002 110 010 000 000 000
000 000 001 130 002 000 000 000 000
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R52
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023 123 122 026 114 087 001 010 001 001 110 124 074 030
104 110 010 026 111 104 122 122 046 046 024 002 030 110
001 001 104 122 080 023 002 122 001 001 122 000 122 001
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000 000 111 120 026 114 001 122 000 000 000 000 000 000
000 000 111 010 001 120 114 002 000 000 000 000 000 000
000 000 000 002 001 111 046 114 000 000 000 000 000 000
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R53
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000 000 002 092 114 062 010 111 [illegible]
000 110 112 130 001 002 024 104 [illegible]
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010 110 022 060 040 092 062 072 121
003 001 130 022 040 002 145 112 026
130 110 114 010 022 022 024 022 013
145 001 114 001 114 001 119 022 142
040 026 062 022 001 013 022 065 022
130 130 030 001 130 001 024 013 010
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000 000 000 000 000 033 001 030 024
000 000 000 000 000 000 000 130 075
R54
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000 112 130 065 001 130 010 110 000 000 000
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000 000 000 000 000 150 060 130 055 030 000
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000 060 060 145 112 114 000
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000 060 002 130 060 120 060
060 112 114 114 060 060 121
060 001 130 130 130 013 000
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000 104 000 026 145 000 000
000 000 000 000 145 000 000
000 000 000 000 060 000 000
R56
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000 000 000 000 000 001 111 018 114 001 001 000
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000 001 040 002 018 022 002 000 065 010 001 065
000 022 114 000 002 001 062 000 000 023 023 096
040 111 000 000 000 010 000 000 000 000 000 130
062 120 000 000 000 002 000 000 000 000 000 120
000 072 000 000 000 000 000 000 000 000 000 000
000 010 000 000 000 000 000 000 000 000 000 000
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000 000 000 000 000 000 000 000 000 000 000 000
R57
06,24,260,92,23,4,1,3,2,7,999
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114 022 130 022 022 060
114 040 020 026 002 001
144 060 020 130 024 010
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010 094 003 001 001 000
002 112 130 130 001 000
119 062 130 122 145 000
142 062 060 061 000 000
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110 060 144 060 000 000
022 140 114 026 000 000
001 112 060 001 000 000
024 072 145 060 000 000
R58
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010 155 112 001 113 063 062 002 112
031 030 062 011 062 065 120 112 110
003 130 114 130 062 062 062 002 040
040 001 062 062 065 062 062 113 001
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000 062 001 062 114 130 145 130 000
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000 000 011 022 112 110 000 000 000
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R59
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000 001 062 112 119 114 001 022 130 114
010 013 001 114 130 112 155 001 130 130
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010 145 000 000 000 000 000 000 000 000
000 013 000 000 000 000 000 000 000 000
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000 021 114 082 002 140 104
000 001 023 022 024 001 026
026 024 114 111 010 018 080
073 140 026 021 062 080 000
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000 062 040 120 031 065 000
000 140 040 001 040 130 000
000 140 001 002 130 010 000
000 000 000 073 001 000 000
R61
11,25,208,96,37,4,2,2,1,11,999
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000 000 000 000 000 025 144 010 144 022 000
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000 000 000 000 000 024 023 062 000 000 000
000 000 000 000 000 000 140 000 000 000 000
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R62
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000 000 110 025 001 024 130 018 001 001 119 000 000
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000 073 002 024 024 130 056 130 026 003 001 000 000
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092 062 002 080 122 140 057 167 024 024 130 010 000
123 023 002 080 110 130 062 130 110 130 001 001 023
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122 120 002 003 001 002 110 110 051 024 024 001 130
122 002 003 010 003 073 144 130 140 122 110 013 010
114 000 026 002 001 002 002 130 001 122 010 026 001
010 000 000 000 000 000 001 051 001 001 024 010 010
000 000 000 000 000 000 000 003 110 001 002 122 002
000 000 000 000 000 000 000 000 001 144 130 001 140
000 000 000 000 000 000 000 000 000 010 140 001 001
000 000 000 000 000 000 000 000 000 000 010 114 000
000 000 000 000 000 000 000 000 000 000 010 024 000
000 000 000 000 000 000 000 000 000 000 001 000 000
R63
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000 112 112 002 001 065 130 062 000
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130 024 114 114 022 140 022 022 000
140 130 155 114 110 000 010 001 000
002 065 000 001 130 000 111 022 000
000 000 000 114 110 000 110 000 000
R64
08,19,311,110,41,4,1,1,2,11,999
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024 114 022 018 010 022 022 000
013 114 119 010 001 119 010 000
000 022 002 111 021 010 022 000
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000 000 112 062 112 119 010 022
000 000 140 120 022 114 065 140
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000 000 000 000 002 023 118 010
000 000 000 000 000 001 023 024
000 000 000 000 000 111 013 000
R65
12,19,72,110,41,4,2,2,2,10,999
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000 000 114 140 140 010 001 130 002 096 140 000
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000 112 001 130 114 140 114 002 022 001 000 000
023 022 114 130 062 062 062 026 001 000 000 000
144 002 040 040 140 010 096 025 000 000 000 000
001 114 022 111 026 026 065 000 000 000 000 000
000 003 112 114 025 010 010 000 000 000 000 000
000 022 060 001 114 001 000 000 000 000 000 000
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000 000 000 026 026 000 000 000 000 000 000 000
R66
08,20,239,124,11,4,1,2,2,0,999
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000 000 000 002 033 130 060 145
000 000 060 060 002 112 114 121
000 108 150 010 140 001 060 060
000 010 040 031 062 114 112 140
000 022 001 065 130 167 024 130
000 022 140 010 024 114 065 010
000 110 140 003 113 130 018 025
024 113 144 150 114 114 026 010
024 022 033 060 001 062 010 078
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063 112 065 024 002 061 114 000
010 140 130 096 110 130 060 000
022 114 060 022 024 062 112 000
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060 112 144 140 002 145 001 000
000 000 140 024 114 024 145 000
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R67
11,17,230,124,31,4,1,3,2,12,999
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000 000 000 000 000 000 080 003 121 000 000
000 000 000 130 080 010 080 114 024 000 000
000 000 080 140 010 022 025 024 140 130 022
000 000 001 002 002 010 023 080 010 140 040
000 000 022 002 001 062 021 062 025 033 110
000 089 001 001 082 112 010 022 024 024 010
000 130 001 002 001 001 010 114 094 033 060
000 022 002 062 062 078 025 001 023 025 114
001 140 096 040 001 140 003 140 010 140 110
010 062 001 024 001 010 114 024 112 082 000
002 062 010 112 112 130 110 001 025 082 000
002 001 062 120 025 112 024 040 026 082 000
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000 000 000 000 000 000 062 002 026 000 000
000 000 000 000 000 000 000 062 140 000 000
000 000 000 000 000 000 000 040 082 000 000
R68
07,10,261,124,59,4,1,1,1,4,999
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022 022 001 001 111 010 114
001 010 114 010 010 080 018
022 022 010 080 022 022 001
111 080 111 026 119 140 010
023 013 065 024 112 010 001
003 111 030 080 010 030 060
000 001 111 001 026 002 040
000 000 119 031 001 060 023
000 000 000 000 000 111 114
R69
07,14,232,143,40,4,1,4,1,4,999
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000 000 000 000 000 010 140
000 000 000 000 092 062 010
000 000 002 022 022 060 040
000 010 001 022 010 023 145
000 121 112 060 002 010 024
000 022 062 022 080 001 112
000 022 024 060 003 024 025
042 022 023 010 130 112 021
042 024 112 010 010 112 021
010 020 010 001 114 022 060
001 010 010 080 001 060 013
030 060 010 080 003 024 062
000 024 060 000 010 010 025
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R70
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000 060 150 060 000 000 000
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000 010 060 165 060 104 000
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001 013 024 001 024 010 060
024 025 114 003 022 046 032
060 022 001 001 111 026 046
111 018 010 060 119 114 000
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114 024 026 111 000 000 000
R71
06,34,302,143,19,4,3,1,3,0,999
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111 104 042 000 000 000
042 021 060 000 000 000
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060 114 112 042 080 000
010 112 001 002 042 000
025 112 130 042 042 000
024 162 114 112 021 000
024 111 114 060 022 000
001 140 162 001 002 000
114 130 130 001 111 000
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120 062 001 022 065 114
002 026 065 112 130 140
114 010 112 155 013 010
119 002 001 060 001 022
003 065 062 130 025 022
002 065 130 062 042 144
010 030 013 112 119 110
000 030 113 002 013 140
000 010 013 013 062 140
000 026 120 114 120 120
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000 104 026 024 062 013
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000 000 030 112 042 000
000 000 110 001 104 000
000 000 119 024 104 000
000 000 060 024 112 000
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R72
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000 080 145 104 001 121 080 000
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122 026 026 110 022 026 144 026
000 001 025 026 003 023 001 023
000 001 026 002 001 078 001 119
000 000 026 026 002 000 078 119
000 000 000 000 114 000 000 000
R73
11,17,148,159,48,4,1,5,1,0,1
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000 000 000 000 000 001 060 121 120 003 000
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121 114 121 120 145 022 060 060 104 114 002
121 104 062 122 010 022 140 001 130 144 000
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000 122 104 062 062 026 000 000 000 000 000
000 000 145 010 060 001 000 000 000 000 000
000 000 114 024 003 000 000 000 000 000 000
R74
09,15,157,159,37,4,1,3,2,2,1
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001 013 060 060 145 060 000 000 000
001 110 024 001 145 026 000 000 000
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000 000 120 002 000 000 000 000 000
000 000 002 000 000 000 000 000 000
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R75
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000 150 150 140 110 155 112 022
000 130 112 113 112 022 022 013
000 000 150 113 000 022 130 000
000 000 101 000 000 000 000 000
R76
09,11,76,154,4,4,4,1,5,4,6,3
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000 000 130 062 062 033 061 130 062
000 130 001 001 110 005 114 062 145
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000 062 096 033 033 114 110 130 001
000 010 001 062 110 120 062 001 130
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114 060 001 114 022 113 040 000 000
013 144 062 061 063 062 000 000 000
000 000 145 114 000 000 000 000 000
R77
10,15,354,154,52,4,1,1,2,3,2.5
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000 000 111 114 114 114 114 021 040 000
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111 022 001 112 002 021 104 001 013 000
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000 110 030 025 040 113 040 024 000 000
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000 000 000 040 113 113 073 000 000 000
000 000 000 040 002 021 000 000 000 000
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R78
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000 000 000 104 104 001 104 042 060
000 000 042 104 001 121 133 026 104
000 042 024 104 104 042 133 104 000
042 001 023 042 144 060 104 060 000
001 024 001 030 024 111 112 001 000
001 024 114 060 080 060 002 060 000
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121 130 112 088 110 110 001 123 010 010 114
000 010 024 145 082 024 110 010 001 000 000
000 145 140 130 130 130 122 144 002 000 000
000 000 010 130 061 001 025 000 000 000 000
000 000 000 130 001 130 010 000 000 000 000
000 000 000 000 001 141 000 000 000 000 000
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000 000 000 000 000 140 000 000 000 000 000
R116
08,15,52,134,28,6,1,1,2,4,2.5
000 000 000 082 110 000 000 000
000 000 114 140 140 010 000 000
000 000 140 110 140 140 000 000
000 140 083 110 130 024 013 000
000 083 010 140 140 110 145 000
010 145 020 114 010 130 024 000
144 144 010 065 140 140 140 145
010 130 010 065 140 065 010 060
000 130 140 002 110 060 062 144
000 130 140 002 025 062 096 114
000 130 062 025 130 025 025 145
000 000 140 025 062 114 113 001
000 000 110 010 026 130 001 062
000 000 062 130 025 025 110 130
000 000 000 001 025 000 000 114
R117
07,16,148,134,31,6,1,5,1,5,2
000 000 000 080 082 144 000
000 000 000 001 082 130 000
000 000 140 140 140 140 000
000 145 144 010 062 130 000
000 145 059 010 130 130 000
000 010 130 025 140 130 000
000 122 114 140 130 130 000
000 010 140 140 130 130 130
000 001 010 140 130 130 000
120 013 110 140 130 130 000
024 110 130 062 130 130 000
121 001 062 025 140 000 000
000 110 070 110 140 000 000
000 001 140 110 000 000 000
000 140 144 002 000 000 000
000 000 130 000 000 000 000
R118
08,22,95,181,9,6,1,4,2,2,1.5
000 000 000 065 000 000 000 000
000 000 000 060 121 000 000 000
000 000 145 110 061 145 000 000
000 000 114 145 110 060 000 000
000 000 120 001 145 001 060 000
000 144 110 140 114 104 060 060
000 121 061 104 001 013 001 108
000 121 025 060 060 144 001 062
000 060 070 013 140 013 026 145
000 144 110 013 001 144 070 120
000 112 062 024 110 062 144 062
000 144 024 110 001 130 060 121
000 121 062 002 121 025 010 000
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000 145 140 121 010 001 108 000
000 114 003 003 145 001 000 000
000 062 062 140 140 001 000 000
000 140 062 140 003 080 000 000
001 062 001 104 041 000 000 000
024 060 111 110 000 000 000 000
042 042 001 114 000 000 000 000
042 042 104 112 000 000 000 000
042 001 042 000 000 000 000 000
R119
13,16,341,181,26,6,1,6,3,2,1.5
000 000 000 042 042 000 000 000 000 000 000 000 000
000 000 080 145 042 010 000 000 000 000 000 000 000
000 000 144 121 001 060 024 000 000 000 000 000 000
000 000 060 111 043 030 063 000 000 000 000 000 000
000 060 001 024 060 022 024 001 000 000 000 000 000
000 080 080 064 060 024 001 122 000 000 000 000 000
000 121 120 080 062 110 025 001 001 042 000 000 000
003 022 040 060 040 111 140 123 022 144 000 000 000
026 040 140 060 010 025 024 010 140 144 024 000 000
000 000 001 025 140 025 002 140 060 062 141 121 042
000 000 000 000 060 022 144 002 143 001 010 010 114
000 000 000 000 025 025 112 022 040 003 144 042 042
000 000 000 000 000 000 140 001 143 092 122 042 112
000 000 000 000 000 000 122 060 144 144 060 060 025
000 000 000 000 000 000 000 000 060 144 065 144 000
000 000 000 000 000 000 000 000 000 000 001 144 000
R120
07,13,214,181,14,6,1,5,2,2,2.5
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000 000 140 001 000 000 000
000 000 080 119 022 000 000
000 060 062 002 060 000 000
000 080 065 140 120 000 000
000 080 022 013 144 010 000
000 010 140 025 001 001 000
040 140 140 140 070 026 000
010 140 140 001 110 001 140
010 001 062 062 024 065 001
060 060 065 140 110 065 060
000 000 000 000 119 112 000
000 000 000 000 025 060 000
R121
09,15,222,209,54,6,1,6,2,6,2
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000 060 140 000 000 000 000 000 000
000 104 144 122 000 000 000 000 000
000 110 010 001 000 000 000 000 000
145 013 013 001 001 000 000 000 000
144 145 120 080 144 144 000 000 000
144 090 062 145 140 144 145 000 000
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040 130 144 140 001 114 080 010 000
010 114 025 145 122 144 001 001 000
026 145 001 010 068 060 013 140 000
130 025 001 010 010 114 144 000 000
140 001 010 114 010 144 000 000 000
080 010 001 124 000 000 000 000 000
000 000 001 000 000 000 000 000 000
R122
08,20,179,209,41,6,1,4,2,4,2
060 145 000 000 000 000 000 000
042 121 121 000 000 000 000 000
060 121 121 000 000 000 000 000
061 140 001 104 000 000 000 000
060 145 060 001 114 000 000 000
061 061 001 060 001 001 000 000
061 140 060 010 110 130 144 000
145 001 070 121 140 010 145 060
061 145 114 001 144 060 062 000
060 130 110 002 013 001 013 000
010 114 062 144 108 013 000 000
121 110 001 062 013 130 000 000
000 140 010 140 145 000 000 000
000 113 140 140 112 000 000 000
000 010 062 026 060 000 000 000
000 061 010 130 000 000 000 000
000 145 140 013 000 000 000 000
000 000 140 010 000 000 000 000
000 000 061 080 000 000 000 000
000 000 061 000 000 000 000 000
R123
14,15,236,209,46,6,1,5,2,4,2
000 000 000 000 000 000 000 060 022 082 000 000 000 000
000 000 000 000 000 000 140 122 013 060 060 000 000 000
000 000 000 000 000 121 140 001 145 001 060 110 000 000
000 000 140 108 110 114 122 001 121 110 010 145 140 000
000 022 140 108 140 114 001 140 001 114 145 060 110 000
145 145 144 061 001 013 114 022 112 114 060 060 070 060
060 120 060 110 114 022 022 144 121 025 060 001 070 140
000 000 144 061 022 062 110 145 024 021 145 104 130 060
000 000 060 061 121 060 140 001 025 002 024 121 110 140
000 000 000 145 144 121 060 110 013 104 001 145 000 000
000 000 000 000 104 061 002 060 060 121 108 001 000 000
000 000 000 000 000 110 140 130 060 112 122 000 000 000
000 000 000 000 000 001 130 145 001 108 140 000 000 000
000 000 000 000 000 000 140 060 060 130 000 000 000 000
000 000 000 000 000 000 000 060 013 001 000 000 000 000
R124
05,15,199,226,39,6,1,5,2,17,3
000 145 000 000 000
000 001 122 000 000
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000 060 120 114 144
000 061 061 060 026
060 060 144 110 061
010 150 065 013 122
145 110 145 060 001
060 144 062 062 010
140 060 114 060 130
096 013 001 013 010
130 110 026 062 000
130 140 062 145 000
010 001 062 114 000
114 001 001 013 000
060 024 144 062 000
R125
07,17,202,226,28,6,1,6,2,14,2.5
000 001 110 000 000 000 000
000 060 025 145 000 000 000
000 001 062 026 000 000 000
000 062 110 013 120 000 000
000 144 013 013 010 000 000
121 001 130 010 010 001 144
013 013 062 010 003 130 144
144 062 096 001 120 110 101
013 062 062 140 130 061 060
013 001 096 140 110 062 130
140 110 140 140 130 022 010
110 096 130 140 010 001 001
112 120 010 130 130 140 000
130 130 010 140 140 025 000
001 130 130 130 140 001 000
000 001 140 001 140 000 000
000 000 000 114 000 000 000
R126
10,16,157,226,10,6,1,4,2,12,2
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000 000 000 001 130 130 000 000 000 000
000 000 000 130 010 001 000 000 000 000
144 010 130 060 114 013 010 000 000 000
061 022 130 062 140 130 070 000 000 000
000 110 110 060 002 022 041 060 000 000
145 062 110 013 140 130 022 092 000 000
145 130 062 013 120 001 022 001 000 000
001 062 140 140 140 060 022 104 000 000
060 140 001 062 062 062 060 104 002 000
145 104 145 060 060 114 022 104 114 024
000 060 108 145 060 130 022 001 022 084
000 001 140 002 130 022 104 010 121 000
000 108 140 121 001 022 000 000 000 000
000 042 042 065 104 024 000 000 000 000
000 000 000 000 002 000 000 000 000 000
R127
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11,10,354,81,25,4,1,6,3,2,999
000 000 000 000 000 000 060 080 110 000 000
000 000 114 145 122 144 144 001 073 108 010
000 140 111 060 024 110 010 144 111 001 024
000 001 110 001 010 022 001 022 040 140 060
000 010 001 001 112 010 010 113 144 000 000
060 040 155 003 114 011 021 010 000 000 000
001 040 060 096 140 010 144 040 000 000 000
000 030 001 001 113 001 031 065 000 000 000
000 000 001 010 114 112 031 000 000 000 000
000 000 000 000 000 114 000 000 000 000 000
R128
09,13,153,82,35,4,1,5,1,2,999
000 000 000 000 022 000 000 000 000
144 121 114 010 010 122 144 000 000
001 013 025 110 010 130 144 000 000
121 060 060 082 155 144 026 000 000
144 110 140 062 001 065 022 000 000
001 026 112 055 144 155 060 013 000
110 130 062 150 110 130 022 024 000
060 001 040 150 073 144 130 013 000
060 130 130 150 110 013 062 145 000
060 155 130 030 010 001 110 145 144
150 062 026 062 001 065 022 010 024
155 130 113 113 000 026 150 112 000
022 010 001 000 000 000 000 000 000
R129
11,18,219,80,14,4,2,5,3,4,999
000 000 000 000 000 000 000 013 114 000 000
000 000 000 000 000 000 112 013 114 001 000
000 000 000 000 000 022 114 144 065 114 000
000 000 000 000 001 031 114 022 062 001 121
000 000 000 001 022 025 114 114 110 114 013
000 000 114 010 114 062 010 022 144 010 062
000 022 112 025 065 140 022 140 062 010 060
064 001 114 030 001 150 001 130 022 111 144
130 055 112 030 030 001 031 062 010 010 060
065 112 114 001 001 072 062 022 001 001 000
010 001 055 010 001 072 114 062 110 010 000
000 020 022 155 130 062 062 062 001 053 000
000 150 001 130 092 163 062 114 062 162 000
000 040 001 001 140 001 001 062 062 001 000
000 023 001 155 062 001 062 062 130 062 000
000 062 001 001 062 003 001 000 000 000 000
000 062 062 001 130 065 000 000 000 000 000
000 062 062 010 130 000 000 000 000 000 000
R130
07,11,38,92,49,4,1,5,2,4,999
000 000 000 024 000 000 000
000 000 033 111 111 000 000
000 000 023 001 111 000 000
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022 018 114 001 111 111 000
003 018 010 111 022 040 114
022 022 003 111 023 021 026
000 114 033 114 130 030 000
000 010 113 022 110 111 000
000 114 130 110 030 000 000
000 000 040 000 000 000 000
R131
12,17,156,96,32,4,1,5,1,9,999
000 000 000 145 022 022 065 022 114 144 000 000
000 000 001 030 114 022 025 145 144 160 000 000
000 015 114 140 140 110 022 001 015 010 140 000
000 018 001 130 001 022 001 144 144 010 013 000
000 001 022 110 140 119 110 022 144 001 001 000
000 130 110 022 001 022 022 111 082 022 022 010
000 140 111 140 111 023 023 001 025 022 114 001
000 110 111 026 001 114 022 124 114 001 144 114
025 119 140 114 025 140 023 025 023 120 111 001
010 001 111 125 001 114 010 022 130 022 001 040
018 140 001 016 130 026 160 119 022 022 001 022
000 022 140 126 130 140 130 022 130 001 111 114
000 000 000 000 000 001 001 065 062 001 022 001
000 000 000 000 000 000 001 025 022 130 065 000
000 000 000 000 000 000 001 001 040 001 082 000
000 000 000 000 000 000 082 130 001 111 000 000
000 000 000 000 000 000 000 000 000 111 000 000
R132
11,11,141,110,28,4,1,3,1,6,999
000 114 060 022 062 001 010 010 010 000 000
000 024 001 144 062 062 025 010 140 000 000
003 024 060 010 060 001 025 010 061 001 000
001 003 140 060 060 140 150 130 040 144 000
121 060 104 112 062 130 140 001 001 130 130
060 112 001 060 130 001 062 001 130 001 010
150 001 144 024 144 001 001 144 145 010 000
024 001 062 140 062 150 001 001 025 000 000
060 112 130 130 144 001 062 062 000 000 000
000 060 001 145 062 112 130 000 000 000 000
000 000 000 000 025 120 140 000 000 000 000
R133
08,18,328,124,30,4,1,5,2,0,999
000 000 000 000 000 121 000 000
000 000 000 080 024 042 000 000
000 000 080 080 080 121 000 000
000 000 001 080 060 111 060 000
000 060 080 022 060 001 054 000
022 001 040 119 001 060 042 000
001 022 060 024 024 024 144 000
000 130 065 140 001 111 080 000
000 111 022 080 001 144 080 000
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001 001 140 023 111 080 010 042
001 040 130 021 001 120 030 042
144 040 001 023 022 060 108 060
065 002 040 002 113 024 060 111
130 001 010 065 021 104 130 080
060 062 111 130 040 080 023 000
040 111 130 040 010 000 114 000
130 111 065 000 000 000 000 000
065 144 000 000 000 000 000 999
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APPENDIX 2 - 'NEAREST NEIGHBOUR ROCKS'

This appendix contains the results of the nearest neighbour sampling technique. Under the code name for each rock are the species that were the nearest neighbours of the lichens shown in the grids for the appropriate rock in Appendix 1. Species codes are listed in Appendix 1. For details of the sampling technique see Chapter 6.

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R76
000 000 000 000 000 104 104 114 000
000 000 000 096 013 114 062 120 120
000 000 001 001 092 060 065 062 122
000 001 130 150 001 005 001 130 114
000 130 013 145 062 150 062 120 150
000 001 062 065 001 026 001 025 112
000 022 026 114 065 062 114 062 001
000 130 062 130 062 130 021 114 005
001 062 150 062 025 062 065 000 000
130 001 096 120 150 130 000 000 000
000 000 062 140 000 000 000 000 000
R79

000 140 130 001 025 000 000 000 000
000 130 130 110 010 000 000 000 000
130 114 065 062 062 001 000 000 000
062 130 062 062 073 130 061 060 000
062 001 140 130 130 130 001 001 140
130 001 062 163 114 025 062 130 060
163 130 062 114 003 062 140 110 092
001 062 062 163 140 163 163 110 062
163 163 065 010 144 062 062 062 087
001 001 112 026 025 062 140 062 140
000 130 130 062 062 096 140 130 110
000 114 062 001 062 003 062 062 130
000 130 163 001 062 140 004 130 001
000 026 065 130 026 140 062 096 062
062 130 130 062 062 062 062 062 001
114 110 065 002 062 026 062 130 013
121 061 062 001 096 062 062 000 000
R82
000 000 000 060 010 001 000 000 000
001 001 001 114 026 001 001 000 00
010 122 060 062 122 001 140 145 060
000 025 001 025 001 096 130 122 010
000 001 108 010 001 013 013 121 114
000 120 112 001 112 130 001 062 114
000 120 025 062 130 110 010 062 000
000 060 025 096 013 120 001 062 000
000 000 062 010 120 062 062 114 000
000 000 001 026 096 062 060 010 000
000 000 110 144 062 061 080 104 000
000 000 060 062 130 001 110 000 000
000 000 000 130 140 062 013 000 000
000 000 000 140 003 005 062 000 000
000 000 000 062 001 065 000 000 000
000 000 000 000 062 000 000 000 000
000 000 000 000 062 000 000 000 000
R83
000 061 110 001 062 121 000 000 000 000 000 000
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060 110 110 130 061 114 003 060 000 000 000 000
001 130 010 001 001 114 060 062 001 000 000 000
140 010 130 062 122 130 120 001 122 010 001 000
010 010 130 062 062 062 120 062 062 144 010 142
130 001 163 001 114 114 130 001 120 112 060 001
010 130 114 010 001 112 114 062 025 096 130 120
010 022 025 062 130 001 114 062 062 001 062 000
000 022 062 062 062 120 122 062 120 062 122 000
000 000 000 062 001 062 114 062 001 145 010 000
000 000 000 114 062 001 062 062 062 130 001 000
000 000 000 114 062 001 001 062 062 130 072 000
000 000 000 000 001 130 001 130 114 025 114 000
000 000 000 000 096 061 025 112 061 001 060 000
000 000 000 000 000 000 000 122 096 140 010 000
R85
000 000 000 000 000 104 000 000
000 000 000 000 026 024 166 000
000 000 001 000 060 104 062 000
000 000 000 104 060 001 024 000
000 001 030 114 080 001 145 000
000 001 030 060 111 104 013 000
000 026 111 022 024 110 026 000
000 033 073 104 104 073 010 000
000 104 060 026 001 060 122 000
000 060 060 119 073 001 060 000
000 001 114 061 060 001 022 013
000 010 010 022 145 062 096 010
000 112 010 001 092 001 062 130
065 073 110 120 092 114 062 060
001 022 096 062 062 062 113 010
010 065 040 065 130 040 001 155
025 119 062 120 040 060 040 040
001 022 040 062 155 065 065 062
010 167 001 065 040 065 114 114
060 001 065 114 001 062 001 062
022 065 062 040 000 062 001 001
022 040 065 003 000 061 001 001
000 065 000 001 000 026 120 000
R88
000 000 112 062 000 000 000 000
000 000 144 001 119 114 000 000
000 000 001 130 114 062 060 000
000 000 130 001 114 114 114 000
000 000 065 055 130 130 060 000
000 000 062 001 062 001 119 000
000 144 130 112 114 110 130 110
000 026 001 060 114 062 130 000
000 114 130 130 026 062 110 000
114 062 114 130 001 114 001 000
022 130 112 026 001 062 060 000
130 130 130 112 062 092 062 000
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000 001 112 001 062 000 000 000
000 001 013 130 000 000 000 000
000 150 071 000 000 000 000 000
R91
000 000 000 042 000 000 000
000 000 000 001 000 000 000
000 000 042 060 121 000 000
000 000 060 024 110 080 000
000 000 145 042 114 001 000
000 042 160 145 001 001 060
000 001 060 001 110 001 060
001 114 024 062 042 114 000
000 071 104 062 140 022 000
000 114 114 160 001 000 000
000 071 114 122 000 000 000
000 000 114 145 000 000 000
000 000 000 114 000 000 000
R94
001 060 001 000 000 000
123 060 145 060 145 001
060 060 026 122 145 145
114 110 001 026 001 025
060 060 065 010 108 061
060 010 061 001 001 121
061 061 001 001 112 024
000 060 026 112 145 000
000 072 114 144 144 000
000 062 140 060 140 000
000 130 000 145 120 000
000 000 000 000 010 000
r97
000 000 000 000 000 121 000 000 000
000 000 001 108 000 121 000 000 000
000 000 001 120 024 001 121 000 000
000 060 060 061 060 004 144 000 000
000 114 112 114 013 004 003 112 000
000 001 112 060 024 001 122 010 000
112 120 025 060 120 130 130 130 000
112 142 112 140 060 026 062 001 122
112 140 130 130 001 112 092 130 120
001 114 130 062 062 112 092 062 062
000 130 163 062 062 062 001 062 001
000 112 114 062 001 001 120 001 130
000 000 163 163 130 130 062 114 000
000 000 130 001 001 130 062 114 000
000 000 130 114 130 114 062 001 000
000 000 000 114 062 062 002 000 000
000 000 000 130 010 001 000 000 000
000 000 000 163 130 001 000 000 000
000 000 000 000 062 130 000 000 000
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R100
000 000 000 000 000 000 114 000
000 000 000 000 000 112 001 000
000 000 000 000 000 114 001 000
000 000 000 000 112 130 001 000
000 000 000 004 002 110 001 000
000 001 001 001 001 130 001 110
001 130 110 001 114 003 130 001
001 001 001 130 001 001 130 130
001 001 001 001 062 001 001 001
000 001 001 130 001 114 001 000
000 001 001 001 130 001 000 000
000 001 001 130 001 001 000 000
000 000 062 001 130 000 000 000
000 000 001 001 000 000 000 000
R104
000 000 122 000 000 000
000 [illegible] 122 130 000 000
000 [illegible] 001 112 000 000
001 001 080 110 001 000
062 080 001 080 001 080
120 003 001 001 001 080
001 080 001 080 112 130
112 001 001 122 001 122
080 001 080 080 080 001
001 002 001 003 112 001
062 001 114 001 080 080
000 112 001 114 080 002
000 001 001 080 001 080
000 090 001 002 001 080
000 002 001 003 001 000
000 002 153 003 164 000
000 000 001 001 002 000
R107
000 000 001 122 120 096 080 000
000 000 114 120 120 122 122 130
000 130 130 141 073 120 001 122
000 141 120 141 130 120 001 120
000 120 141 141 073 082 120 000
000 001 073 114 001 130 001 000
141 130 130 141 130 001 001 000
130 001 001 001 130 141 000 000
114 141 001 141 141 062 000 000
003 001 003 062 001 001 000 000
001 001 164 001 164 001 000 000
000 000 001 001 164 062 000 000
R109
000 000 001 120 000 000
000 000 001 141 000 000
000 000 001 080 001 000
000 000 120 001 080 000
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000 130 120 080 001 140
000 110 001 141 080 080
000 001 122 120 130 130
000 130 141 141 122 141
130 001 062 120 141 001
062 001 122 130 120 001
141 001 120 130 120 000
001 140 141 141 130 000
141 120 096 062 000 000
144 144 062 001 000 000
120 001 114 000 000 000
R112
000 114 001 001 022 000 000 000 000 000 000
001 001 111 022 080 022 065 000 000 000 000
024 082 021 022 040 140 026 073 000 000 000
001 021 001 022 145 025 096 144 000 000 000
144 001 140 001 130 022 001 025 062 060 001
010 023 060 122 [illegible] 060 001 040 [illegible] [illegible] [illegible]
022 062 065 065 062 013 122 025 073 [illegible] [illegible]
022 130 062 120 120 114 025 001 [illegible] [illegible] [illegible]
001 062 062 120 120 001 001 025 [illegible] [illegible] [illegible]
130 025 130 025 130 001 062 001 010 [illegible] 000
111 122 062 140 000 000 000 001 001 [illegible] 000
R115
[illegible] [illegible] 000 031 120 000 000 001 000 000 000
[illegible] [illegible] 140 031 140 025 060 114 080 000 000
024 060 060 120 001 140 001 080 110 114 114
121 024 001 026 025 061 001 001 001 010 001
110 042 060 026 140 140 025 062 001 001 062
042 114 001 110 024 025 110 010 001 140 001
000 145 130 114 140 140 130 140 002 000 000
000 001 130 001 104 026 001 001 001 000 000
000 000 145 062 130 130 130 000 000 000 000
000 000 000 024 003 110 001 000 000 000  00
000 000 000 000 120 001 000 000 000 000 000
000 000 000 000 000 062 000 000 000 000 000
R118
000 000 000 [illegible] 000 000 000 000
000 000 000 065 144 000 000 000
000 000 001 001 001 001 000 000
000 000 130 120 001 145 000 000
000 000 001 114 001 110 001 000
000 001 062 026 001 062 121 001
000 060 080 060 110 013 122 001
000 145 140 145 013 001 062 144
000 001 062 121 062 [illegible] 122 062
000 062 062 060 130 [illegible] 060 060
000 110 140 060 060 130 145 010
000 060 001 140 130 062 140 080
000 041 013 001 001 060 130 000
000 001 024 001 114 145 062 000
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000 001 114 160 001 024 000 000
000 130 111 013 062 120 000 000
000 062 067 062 062 024 000 000
060 145 080 013 010 000 000 000
001 001 001 001 000 000 000 000
060 024 042 001 000 000 000 000
062 022 060 042 000 000 000 000
060 080 060 000 000 000 000 000
R121
000 000 121 000 000 000 000 000 000
000 110 060 000 000 000 000 000 000
000 001 061 001 000 000 000 000 000
000 001 060 060 000 000 000 000 000
001 120 114 145 122 000 000 000 000
120 114 114 001 120 001 000 000 000
[illegible] 062 145 001 124 080 001 000 000
060 060 001 140 121 002 001 060 114
060 025 001 025 010 060 001 001 000
110 001 062 140 001 060 110 002 000
010 [illegible] 140 001 001 001 060 010 000
026 062 110 130 060 060 130 000 000
001 062 120 001 114 010 000 000 000
120 001 062 010 000 000 000 000 000
000 000 025 000 000 000 000 000 000
R124
000 001 000 000 000
000 108 060 000 000
000 024 001 001 025
000 144 001 114 001
114 114 062 025 110
060 065 062 060 025
130 060 130 025 144
001 060 130 140 061
060 130 061 026 061
062 130 130 025 060
024 110 062 013 000
013 061 140 001 000
062 110 096 061 000
062 062 145 062 000
062 145 001 001 000
R127
000 000 000 000 000 000 080 024 001 000 000
000 000 001 001 001 060 114 114 001 001 060
000 001 001 114 110 024 003 001 010 022 060
000 060 001 114 001 024 040 001 080 144 114
000 024 150 024 024 110 001 001 022 000 000
024 060 150 022 140 001 022 030 000 000 000
060 024 040 062 011 025 001 060 000 000 000
000 110 010 114 030 114 010 040 000 000 000
000 000 030 024 001 001 026 000 000 000 000
000 000 000 000 000 030 000 000 000 000 000
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R128
000 000 000 000 001 000 000 000 000
001 001 010 001 114 010 001 000 000
112 024 062 001 024 001 001 000 000
061 001 001 114 150 130 062 000 000
001 001 062 073 150 150 060 000 000
145 062 026 150 062 150 114 060 000
060 001 112 065 060 073 096 060 000
001 010 130 065 130 022 073 060 000
001 025 [illegible] 065 025 022 144 001 000
145 150 062 130 003 022 150 013 060
065 096 130 130 026 150 010 060 001
001 062 062 150 000 001 066 060 000
130 [illegible] 040 000 000 000 000 000 000
R129
000 000 000 000 000 000 000 060 001 000 000
000 000 000 000 000 000 001 110 022 062 000
000 000 000 000 000 060 030 010 010 060 000
000 000 000 000 062 065 022 144 140 150 010
000 000 000 030 062 062 010 001 064 001 060
000 000 001 062 022 065 130 062 062 112 010
000 150 010 001 062 130 031 130 073 073 111
001 104 140 114 062 096 026 001 130 030 062
122 150 001 001 001 062 [illegible] 022 022 001 001
062 023 114 062 062 [illegible] 114 062 114 030 000
110 130 110 114 [illegible] [illegible] 071 040 122 022 000
000 001 062 150 001 001 096 001 062 150 000
000 155 062 010 062 062 113 062 001 150 000
000 092 062 062 062 052 062 072 114 150 000
000 130 062 150 001 062 130 130 052 130 000
000 001 130 003 001 064 062 000 000 000 000
000 001 001 062 062 150 000 000 000 000 000
000 001 001 072 065 000 000 000 000 000 000
R130
000 000 000 112 000 000 000
000 000 010 022 001 000 000
000 000 123 114 001 000 000
000 114 018 001 114 001 000
001 114 021 111 001 001 000
073 003 111 022 114 001 073
030 023 022 021 001 040 122
000 022 022 130 026 130 000
000 001 040 113 021 030 000
000 040 040 023 060 000 000
000 000 130 000 000 000 000
R131
000 000 000 001 010 010 062 010 001 022 000 000
000 000 110 001 001 026 062 010 001 140 000 000
000 001 001 022 119 022 144 010 001 026 022 000
000 140 114 010 140 010 022 001 160 015 010 000
000 130 001 144 001 130 023 140 025 144 114 000
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000 111 003 140 130 140 130 001 001 010 144 022
000 022 144 023 001 022 114 026 065 144 001 022
000 001 025 140 114 022 065 065 026 022 001 010
001 023 001 001 140 026 065 065 022 001 001 111
001 013 022 001 140 001 001 065 062 010 113 140
022 022 002 001 001 130 001 065 065 114 003 010
000 111 073 082 073 130 026 065 022 112 001 001
000 000 000 000 000 026 114 062 114 111 065 022
000 000 000 000 000 000 130 022 130 001 022 000
000 000 000 000 000 000 010 062 003 130 062 000
000 000 000 000 000 000 073 025 111 001 000 000
000 000 000 000 000 000 000 000 000 026 000 000
R132
000 025 114 062 060 013 001 060 001 000 000
000 062 130 062 096 022 130 023 062 000 000
001 144 062 144 040 062 062 002 119 013 000
114 001 130 112 024 022 001 001 114 062 000
001 024 062 061 013 112 010 130 062 001 060
145 061 111 025 025 112 001 130 010 130 072
003 060 096 001 062 130 130 062 001 062 000
060 114 001 062 114 065 062 144 144 000 000
024 001 114 001 062 130 130 130 000 000 000
000 024 114 112 145 060 062 000 000 000 000
000 000 000 000 111 140 062 000 000 000 000
R133
000 000 000 000 000 001 000 000
000 000 000 010 001 121 000 000
000 000 001 001 001 001 000 000
000 000 080 001 024 001 042 000
000 001 001 080 111 021 060 000
001 010 065 130 144 024 080 000
002 021 022 140 114 114 080 000
000 001 001 062 144 001 001 000
000 001 060 065 026 112 001 000
130 002 001 022 021 104 108 060
130 001 001 065 021 001 144 060
001 001 111 040 023 024 140 042
040 001 023 119 001 144 065 042
060 130 065 022 003 001 022 040
144 065 001 040 001 060 140 000
065 001 001 111 122 000 001 000
040 001 025 000 000 000 000 000
026 001 000 000 000 000 000 999
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APPENDIX 3 - DISTRIBUTIONS OF ENVIRONMENTAL VARIABLES

Distributions of each of the environmental variables for all rockfaces sampled during this project. See methods (Chapter 5) for details. Where the number of rocks does not add up to 128, data for that variable were not collected for all rockfaces.

A. Altitude.

Class range (m)	0-10	11-30	31-50	51-100	101-150	151-200	200-250
number of rocks	18	13	12	31	23	13	18

B. Slope.

Class range (o)	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-90
number of rocks	11	31	28	23	20	5	2	6

C. Aspect.

Class range (o)	0-44	45-89	90-134	135-179	180-224	225-269	270-314	315-359
number of rocks	8	15	10	24	21	24	9	13

D. Direct beam radiation.

Class range (arbitrary units)	0-40	41-80	81-120	121-160	161-200	201-240	240-280
number of rocks	5	6	7	21	36	42	8

E. Trees within 30m of rockface.

Class range (number of trees)	0	1-5	6-10	11-15	16+
number of rocks	17	41	11	9	8

Appendix 3: (continued)

F. Rock colour.

Class (1=pale, 6=dark)	1	2	3	4	5	6
number of rocks	14	10	13	22	35	27

G. Weathering of rock.

Class (1=little weathered)	1	2	3	4	5
number of rocks	28	48	10	9	0

H. Size.

Class (number of points on rock)	40-60	61-80	81-100	101-120	121-140	141-180
number of rocks	13	38	27	20	15	14