ECOLOGY OF SOIL-SURFACE LICHENS

IN

ARID SOUTH-EASTERN AUSTRALIA

by

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Thesis submitted for the Degree

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Sheeptracks carved into a lichen encrusted soil surface in an Arid Woodland, northern Eyre Peninsula, South Australia.

DECLARATION.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University. To the best of my knowledge and belief this thesis contains no material previously published or written by another person, except where due reference is made in the text.

Roderick W. Rogers.

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SUMMARY

Lichens on arid Australian soils have been neglected in the past. This study establishes the extent, composition and ecology of the lichen flora on arid and semi-arid soils in south-eastern Australia.

Lichens were sought at 345 locations scattered over 400,000 square miles. 227 of the sites studied had lichens on the soil surface. From the range of lichens encountered a total of 42 taxa were delimited, and a key to these taxa was prepared. Of the 227 locations with soil surface lichens 118 showed a more or less continuous lichen crust over the surface.

The community structure of the lichen floras was studied, including two computer-facilitated analyses (Principal Components Analysis, and Influence Analysis) which produced similar results, and five species-groups delimited. Two of these groups formed "background" floras. These floras occupied adjacent geographic regions with a small overlap; the remaining three species-groups were superimposed on these background floras to produce five separate geographic zones of lichen distribution.

Studies of climatic and soil variation indicated that species distribution was closely related to mean annual rainfall, and to seasonal rainfall incidence. Soil-extract pH and available soil calcium concentration were also closely related to species distribution. Most species were most frequent on crusted loamy soils.

Studies on the physiology of *Chondropsis semiviridis* (Nyl.) Nyl. demonstrated climatic control of its distribution. *C. semiviridis*, absent from areas with a summer rainfall pattern, was shown to be sensitive to normal summer atmospheric temperatures (40°C) when wet. Adaptation for existence in an environment with repeated short cycles of wetting and drying was also demonstrated.

The effect of sheep stocking on species composition of lichen crusts around watering places was studied at two locations. It was shown that stocking pressure differentially modified the distribution of species, but no lichen species increased in frequency under stocking pressure as do some angiosperm species.

The world biogeographic implications of the new data are discussed. Predictions are made about distribution of crusts in parts of Australia not studied, and a map of probable past and present distributions of lichen crusts compiled. The role of the lichen crust in the ecosystem is considered with special reference to soil nitrogen status. The study has implications about the future of the pastoral industry, and these are examined.

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I thank my supervisor, Dr. R.T. Lange (Botany Department, University of Adelaide) for suggesting the study, and for his guidance and assistance during its course.

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I am indebted to many research personnel in the Botany Department, University of Adelaide, for information, discussion, and technical assistance, especially Mr. P.H. Smith.

I am grateful to Professor P.G. Martin of the Botany Department for allowing his secretarial staff to type this thesis: credit for the final product must go to Miss Carol Wilkins, Miss Bronwyn Cooper prepared the preliminary typescript.

Throughout the study I have appreciated my wife's patience and her continuing assistance.

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CHAPTER I

INTRODUCTION

This thesis has as its context the tradition of ecological studies in the arid zone of South Australia developed in the Botany Department, University of Adelaide. Professor T.G.B. Osborn established that Botany Department in 1912, and introduced scientific plant ecology to South Australia some years later. A tradition of arid zone studies from the Department he founded dates from the early 1920's, but rarely have more than two or three botanists been involved at any one time. At the time of writing Professor Emeritus Osborn still appeared in the Department: the length of this tradition of arid zone studies is shorter than the career of its founder. A situation not very different appears to be the case in the other University centres from which ecological studies of the arid zone of Australia could be mounted.

The Universities have not stood alone in the history of Australian arid zone research. Such institutions as the Soil Conservation Authority of New South Wales, the State Pastoral Boards and Divisions of the Commonwealth Scientific and Industrial Research Organization have made important contributions to arid zone ecology, but, by and large, these contributions have been to applied problems of the pastoral industry, not to academic botany.

Setting this history against the size of Australia's arid zone (over 5 million square km. or 74% of the continent) it is not unexpected that in 1966 whole aspects of the ecology in this region could be found to be the subject of almost no scientific literature.

As part of the Honours requirement for the Bachelor of Science degree, the author investigated the soil surfaces of Yudnapinna Station in northern South Australia. The aim of that investigation was to determine whether or not there were lichens capable of nitrogen fixation on the soil of that station. During the investigation it was discovered that thousands of square miles of arid land at Yudnapinna, and on surrounding stations, were covered by an almost continuous carpet of lichens, including at least one species capable of nitrogen fixation. The significance of this lichen crust on the soil surface was recognized, and adopted as the topic for this doctoral thesis.

From the viewpoint of academic botany the study of these crusts was easily justified. The ecological situation was novel, as the lichens formed a living interface between the soil and the air. Because of this lichen crust, the microclimate of the soil surface layer must be modified by interception of incoming radiation and by alteration of the movement of water in and out of the soil. As a result of its density and continuity, the crust must alter the hydrology of the area it covers by modifying the flow of water over the soil surface. Since it binds and covers the soil surface, the crust must restrict wind, rain drop and sheet erosion, and so affect nutrient status and seed-bed characteristics. It is apparent that the crust must play a role in determining the nature of the angiosperm vegetation that grows in it, especially by affecting the critical stages of seedling establishment. In total this represents a large unexplored system for study.

Apart from the ecological aspects, the organisms dominant in the crust, the lichens, are of considerable interest. Lichens are a little known, poorly understood assemblage of organisms. In Australia, lichen taxonomy has been the subject of very little work as no Australian University or Herbarium has had a professional Lichenologist on its staff until very recently. Lichen collections, particularly from arid areas, are few and scattered, hence a study of their taxonomy and distribution must be profitable. It is also possible that knowledge of such a group could help illuminate biogeographic problems, especially with reference to continental drift. The presence of lichens, themselves, the product of a delicately balanced symbiosis of algae and fungi, on such an exposed surface as an arid soil poses questions of a physiological nature which also warrant investigation.

The lichen crust must also have important economic implications, as the arid shrublands of south-eastern Australia support a multi-million dollar pastoral industry. In South Australia alone the arid lands given over to grazing sheep (almost all falling within the study area) yielded some $21 million in 1967 (Australia, Bureau of Agricultural Economics 1969). This industry is totally dependent on the natural vegetation of the area and hence dependent on the maintenance of a stable ecosystem for its continuity. The role the crust plays in the arid ecosystem has already been noted: If the crust is destroyed, as it may be so easily by trampling stock, there is no assurance that the ecosystem will continue to support the pastoral industry. Without the crust, the vegetation presently existing may not be capable of regeneration.

At the outset, two fields of study were determined; first, a wide ranging survey of the extent and floristic composition of soil-surface lichen floras in arid and semi-arid south-eastern Australia, and second, an examination of the factors influencing the distribution of the taxa involved. Since the outcome of these investigations was not predictable, considerable flexibility in approach had to be preserved; every possible avenue for study that presented itself had to be scrutinized as it arose.

The author pursued these studies during the years 1966 to 1970 inclusive, during which time he held the teaching position of Demonstrator in the Botany Department, University of Adelaide.

During this period the project developed along the two major lines stated above, and along one additional line. Figure 1.1* outlines the conceptual development of the investigation. Chronologically, stages shown as successive often proceeded simultaneously as sufficient information from one stage became available to start work at another.

Preliminary studies showed that the lichen crust was in fact a complex of many organisms; in addition to lichenized forms, free living algae and fungi were found; mosses and liverworts were discovered scattered among lichen thalli and a microfauna of considerable diversity was seen to live in the crust. Because of their possible role in nitrogen-fixation, studies in the blue-green algal flora of the crust were initiated but were discontinued at an early stage because of taxonomic and other problems. Such actions were inevitable in a study which attempted to probe all avenues as they arose, if any avenue was to be studied in depth.

Selection of an area for the study was a difficult problem and the limits of the area changed as the study proceeded. The underlying assumption in delimitation of study area was that the influences determining distribution of the angiosperms (climate, soil and historic land usage) would also determine lichen distribution patterns.

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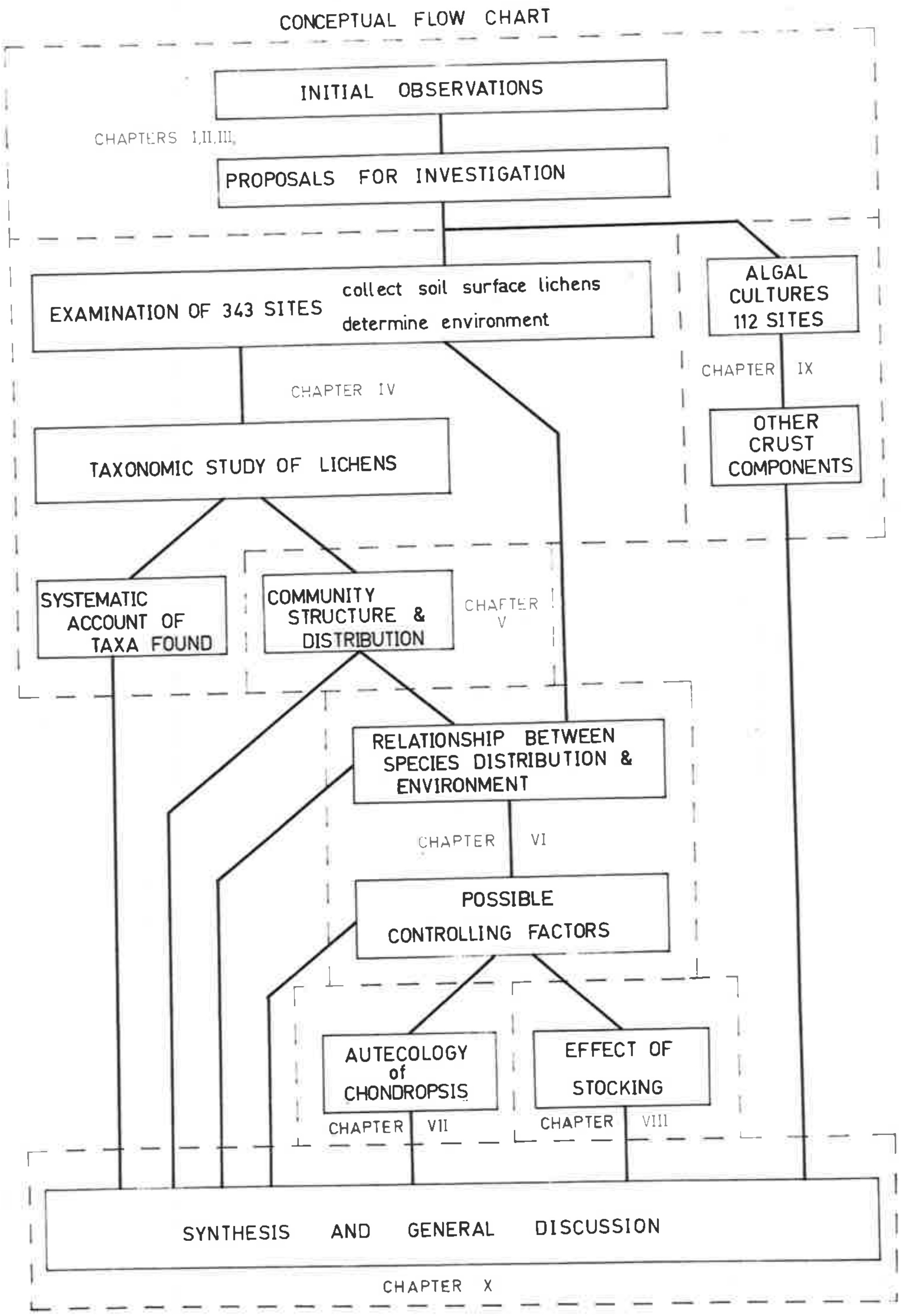
* Figures and Tables in this thesis are numbered as follows: Chapter number, period (.), sequence number of appearance in the chapter.

FIGURE 1.1

The conceptual development of the study in relation to the physical structure of the thesis. Broken lines indicate the segments in each chapter.

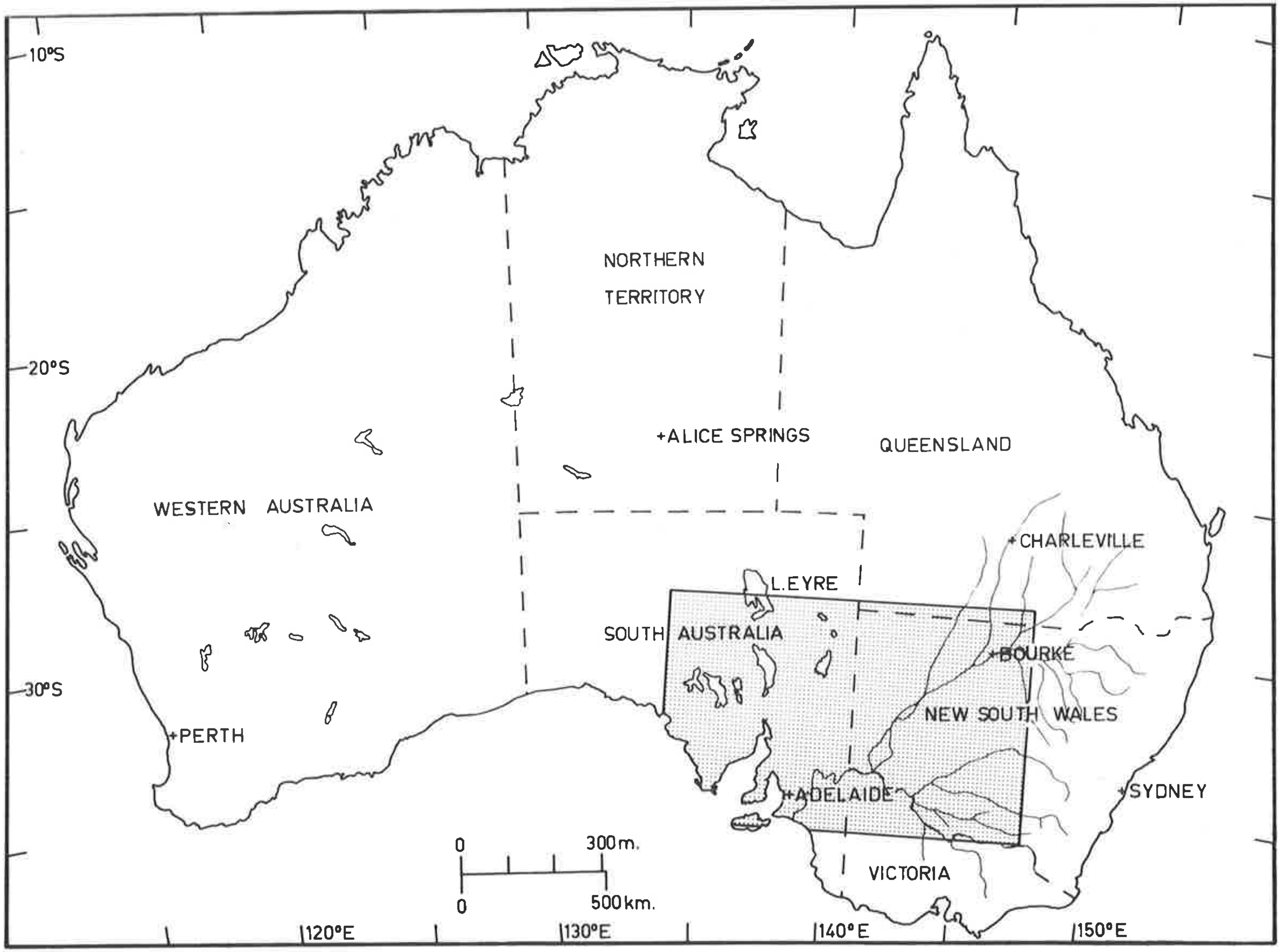

CONCEPTUAL FLOW CHART
INITIAL OBSERVATIONS
CHAPTERS I,II,III,
PROPOSALS FOR INVESTIGATION
EXAMINATION OF 343 SITES
collect soil surface lichens
determine environment
ALGAL CULTURES 112 SITES
CHAPTER IX
OTHER CRUST COMPONENTS
CHAPTER IV
TAXONOMIC STUDY OF LICHENS
SYSTEMATIC ACCOUNT OF TAXA FOUND
COMMUNITY STRUCTURE & DISTRIBUTION
CHAPTER V
RELATIONSHIP BETWEEN SPECIES DISTRIBUTION & ENVIRONMENT
CHAPTER VI
POSSIBLE CONTROLLING FACTORS
AUTECOLOGY of CHONDROPSIS
CHAPTER VII
EFFECT OF STOCKING
CHAPTER VIII
SYNTHESIS AND GENERAL DISCUSSION
CHAPTER X

The area for the study had therefore, to be a compromise: large enough to embrace wide climatic, soil and historic variations, yet small enough to be conveniently studied from a base in Adelaide. Adelaide which has a relatively high rainfall with a marked seasonal variation, most rain falling in the winter, was selected as one climatic pole for the study. A second pole was located near Bourke in northern New South Wales, where rainfall is also seasonal, but shows a marked summer rainfall maximum. Between these two is a large area with rainfall erratically distributed throughout the year. Included is an area around Lake Eyre (due north of Adelaide) which has the lowest average annual rainfall recorded on the Australian continent. Inspection of soil maps indicated great diversity of soils in the area, which lies across three States (South Australia, New South Wales and Victoria) with three diverse histories of land usage. Thus for this study a rectangle including Adelaide, part of Lake Eyre, and Bourke, (Fig. 1.2) was accepted as optimal in balance between scope of variation and technical resources available.

The flow chart in Fig. 1.1 outlines the development of the study: the body of this thesis contains the details of the study, which are discussed and summarized.

FIGURE 1.2

The location of the study area in south-eastern Australia, in relation to some major centres of population, and to political boundaries. The stippled portion is that area reproduced in detailed maps of the study zone.



10°S
20°S
30°S
120°E
130°E
140°E
150°E
NORTHERN
TERRITORY
+ALICE SPRINGS
QUEENSLAND
WESTERN AUSTRALIA
+CHARLEVILLE
L.EYRE
SOUTH AUSTRALIA
+BOURKE
NEW SOUTH WALES
+PERTH
+ADELAIDE
+SYDNEY
VICTORIA
0
300m.
0
500km.

CHAPTER II

REVIEW OF LITERATURE

1. SOIL LICHEN CRUSTS

(1) An introduction to the world literature

Elenkin (1901b) appears to be the first to have reviewed the literature relevant to lichens on arid soil surfaces. In that paper he dealt principally with the unattached "Manna" lichens. Pallas (1771-1776), quoted in Elenkin (1901b) noted a crust of lichens on the soil in Russia and probably made the earliest report of lichens widespread in a crust over arid soils. Elenkin (1901a) listed lichens from the steppes of Russia, and he also (1901c) discoursed further on the "wanderflechten" (migratory or vagant lichens) of steppe and desert.

More recent literature has been divided into papers discussing lichen crusts as such, and papers discussing the floristics of lichens on arid soils.

(a) Reports of lichen crusts

Reichert (1937) briefly reviewed the literature on arid soil surface lichens and asserted as a general principal, based largely on his knowledge of the Turko-Iranian and North African deserts, that ".....the bare soil of the desert, when firm and not drifting, is mostly covered by lichens". This general assertion has been supported by a number of workers. Galun & Reichert (1960) studied the soil crusts of the Negev in Israel, as did Galun (1962) who reported ".....vast areas covered by lichens, consisting mostly of a big variety of species". Workers in North America have also reported soil-surface lichen crusts. Looman (1964a) discussed crusts on the Canadian Great Plains; Shields, Mitchell and Drouet (1957) and Cameron and Blank (1966) reported lichen crusts from California; and Shields and Drouet (1962) reported them from Nevada.

(b) Floristic studies

In addition to the reports of Elenkin (1901a,b,c) of lichens from the Russian steppes, Keller (1930) published lists of species of lichens from those steppes, along with a fine series of photographic plates illustrating his paper. Klement (1955) recently described soil-surface lichen associations from Europe. In North America, Fink (1909), Herre (1911), and Weber (1963) studied the lichen floras of essentially arid areas. The flora of the area studied by Fink was depauperate when compared with that at Reno studied by Herre, whereas the Chiricahuan mountains studied by Weber had a very rich flora. Looman (1964a,b) studied the lichen flora of both the

Canadian Great Plains and the Prairies of northern United States. The lichens from Syria and Lebanon, including arid areas, have been studied at length by Werner (1954-1966).

The literature relevant to North African lichen floras was reviewed and extended by Faurel, Ozenda and Schotter (1953) with special emphasis on arid and semi-arid floras. Since that review, Werner (1966) has studied the lichen flora of Egypt.

Two papers concerning the lichen flora of central Asia (Magnusson 1940, 1944, cited in Weber 1962) have not been seen by the author.

The above review does not pretend to be complete; reference to those papers described as review papers will lead to further literature. There have, however, been few papers of substance directly relevant to this topic: the checklist if enlarged would consist basically of lists of new species collected from various desert areas, not of floristic studies of those deserts.

(2) Australian Studies

Other than a preliminary report preceding the present study (Rogers, Lange and Nicholas 1966) no reports have been made of continuous lichen crusts on arid Australian soils. There are, however, a small number of publications that deal with collections made from arid Australian soils.

During the Elder Expedition across central Australia in the years 1890-1891, Richard Helms collected lichens which were sent to J. Müller (of Argau) for determination. These determinations were published in reports from the Elder Expedition (Müller 1893). Helm's collections included 17 species off the soil.

During studies at the Koonamore Vegetation Reserve, lichens were collected and sent to Kew for determination (Osborn, Wood and Paltridge 1935). Regrettably, the name of the worker who determined the material was not mentioned. The comments made by Osborn, Wood and Paltridge about the six species recorded on the soil at Koonamore suggest that the sets of specimens retained in Adelaide to form a basis for discussion did not match those sent to Kew. Their account of species growth habits is completely at variance with information collected in the present study.

The Grimwade Expedition of 1947, organized by the National Museum of Victoria, collected lichens across the southern margin of the Nullarbor plain. Studying the collections, P. Bibby recorded species that had not been collected since the type material was found on the Elder Expedition over 50 years earlier (Willis 1951).

(3) Lichen Biogeography of Arid Areas

Weber (1962) noted similarities in the lichen floras of arid areas in south-western United States, Asia, North Africa, South America, and, to a lesser extent, Australia.

Discussing the biogeographic implications of his study of the lichens of the Chiricahua mountains Weber (1963) commented that the most significant biogeographic observation was the virtual absence of narrow endemic species within the area. He did, however, group some species together as "desert-steppe disjuncts", occurring in arid areas around the world. Almborn (1966) made a similar observation about the lichen flora of South Africa.

In his study of lichens on Prairie soils Looman (1964b) noted a close similarity between an association he described, and a pair of associations reported by Klement (1955) from Europe. Some of the species and genera common in the three associations also occur in other areas. Thus evidence has accumulated for similarity rather than difference in the composition of lichen floras of soils in arid areas. Table 2.1 presents the records of some of the more common species and genera reported from a number of arid areas. Among higher plants correspondence of this sort at the species level would be extremely unusual. Nomenclature in Table 2.1 follows the suggestions of Weber (1962, 1967a, 1968).

In discussing the disjunction between very similar floras in Europe and North America, Looman (1964b) followed Thomson (1963) in considering three possible explanations. The three were:

TABLE 2.1

Distribution of some species and genera common on arid and semi-arid soils.

	Algeria (Faurel et al.)	Israel (Galun; Galun & Reichert)	Russia (Keller)	Europe * (Klement)	Europe * (Klement)	North America (Looman)	Arizona (Weber)
Acarospora schleicheri			+		+	+	+
Aspicilia calcarea		?	+		+	+	+
Buellia epigaea		+		+		+	
Collema sp.	+	+	+	+	+	+	+
Dermatocarpon lachneum	+	+	+	+	+	+	+
Diploschistes scruposus		+	+				+
Endocarpon pusillum				+		+	+
Fulgensia sp.	+	+	+	+		+	
Heppia lutosa	+			+		+	+
Lecidea decipiens	+	+	+	+	+	+	+
Parmelia vagans			+		+	+	
Toninia caeruleonigricans		+	+	+	+	+	

* Klement listed two communities, the *Fulgensietum fulgentis* and the *Parmelietum vagantis*, which Looman believed had merged to form the *Parmelietum chlorochroae* in North America.

(a) that under similar ecological conditions, convergent evolution had produced similar organisms

(b) that lichens had unusual powers of dispersal

(c) that the lichen floras of Europe and North America were relics of a once much more widely distributed flora.

Looman rejected the first explanation, and stated that it might explain a few of the similarities, but not all. He also rejected the second, claiming that it required that sexual reproduction be invoked, which was rare in arid lichens. He favoured the third possibility, and suggested that continental drift accounted for the present disjunctions.

A number of attempts have been made to demarcate the boundary between "steppe" and "desert" using lichens as phytogeographic indicators. Keller (1930) suggested that the presence of vagant lichens characterized steppes, as deserts were climatically too severe for them. Reichert (1936, 1937, 1940) has suggested use of the genus *Diploschistes* to characterize steppe and to differentiate it from desert. Faurel, Ozenda and Schotter (1953) reviewing the literature on lichen distribution in North Africa, claimed that disappearance of soil lichens provided a more sensitive indicator of the steppe-desert boundary than did higher plants. All the above authors agreed that the disappearance of all, or selected lichens, could be used as a climatic indicator.

(4) Associated Algal Floras

A number of reports of soil lichen crusts from arid areas also noted the presence of an associated algal flora, living free in the soil, in addition to lichenized algal forms (Keller 1930, Shields 1957, Shields and Drouet 1962, Cameron and Blank 1966). The literature relating to soil algae has been reviewed by Shields and Durrell (1964), and the literature especially relevant to arid zone soil algae was reviewed by Cameron and Blank (1966). Algae have been found in dry soils on every continent. Considering only selected examples, algae are recorded from dry soils in Antarctica (Drouet 1962, cited in Cameron & Blank 1966), South America (Schwabe 1960), Central Asia (Shtina & Bolyshev 1963), India (Singh 1961), Central Africa (Duvigneaud and Symoens 1950), North Africa (Killian and Feher 1939), North America (Cameron 1960, 1964a,b,c), and Europe (Shtina 1961). In all cases the blue-green algae (Cyanophyta) dominated the soil algal flora.

In Australia very little work has been done on soil algae. Phillipson (1935) described and determined soil algae from near Melbourne, and Moewus (1953) determined algae from the desert near Broken Hill. Apart from these two attempts there have been no systematic accounts of Australian soil algae, although a number of other studies on soil algae have been pursued. Jensen (1940) and Tchan and Beadle (1955) studied soil algae in western New South Wales from the point of view of nitrogen balance but found no significant role for them. Tchan and Whitehouse (1953) studied the movement of algae in sand, and Bond and Harris (1964), studied the effect of algae, detected by Specht and Rayson (1957), on the stability of sand hills in southern South Australia.

Shields and Durrell (1964) attempted to show the similarities in various soil algal floras from arid areas around the world. They present data ostensibly from Duvigneaud and Symoens (1950) and Moewus (1952), which differ from those actually published by those authors. The value of such biogeographic correlation is at best extremely doubtful, because of the confusion current in the taxonomy of the Cyanophyta, and is more so when the confusion is compounded by error of the kind mentioned. As an illustration of the scale of confusion in the taxonomy of the Cyanophyta, Drouet (1968) reduced the number of specific and subspecific taxa in the family Oscillatoriaceae from 2,400 historical types to some 23 autonomous species, some of which he believed may prove synonymous. His radical redefinition of genera and species makes biogeographic correlation impossible without examination of the original material.

(5) Role of the Lichen Crust

A large number of roles for the lichen crust on arid soils are postulated in the literature, or may be inferred from it. The role that originally gave impetus to this study was the established role of crust organisms as nitrogen fixers (Shields, Mitchell and Drouet 1957, Cameron and Fuller 1960, Rogers, Lange and Nicholas 1966, Mayland, McIntosh and Fuller 1966). In addition to nitrogen fixation, it has been shown that, because of their ability to survive drought intact, soil lichen crusts act as a reservoir of soil nitrogen when other sources are destroyed (Shields 1957, Shields, Mitchell and Drouet 1957). These crusts are also reputed to be important sources of organic matter in desert soils (Shields and Durrell 1964, Cameron and Blank 1966).

The ability of lichen crusts to stabilize soils over long periods has been commented on by Booth (1941), Fletcher and Martin (1949), Shields (1957), Shields, Mitchell and Drouet (1957), Durrell and Shields (1961), Weber (1962) and by Cameron and Blank (1966). The effect of these stabilizing crusts on rainfall infiltration is not clear; Booth (1941) found crusts might slow the rate of infiltration a little, whereas Fletcher and Martin (1949) believed crusts increased the rate of infiltration.

It has been demonstrated by Rondon (1966) and Pyatt (1967) that extracts from some lichens inhibit germination of seeds; it is thus possible that elution of inhibitors from the lichen crust inhibits germination of seeds. The antibacterial effect of lichen acids discussed by Stoll, Brack and Renz (1947) and the antifungal effect discovered by Harder and Uebelmesser (1958) could have a role in inhibiting nitrogen fixation by free living bacteria, and also slowing down re-cycling of organic nitrogen by preventing decay organisms from acting on organic matter.

While the literature suggests many roles for the crust few have been tested, and those that have been tested, not studied at depth. The approach to the soil lichen crust has generally been superficial: a much wider range of questions could be asked about the crust with profit.

2. FACTORS AFFECTING THE DISTRIBUTION OF LICHENS

Factors affecting the distribution of lichens have been reviewed by Lange (1953), Smith (1962) and Haynes (1964). Most of the information available deals with water relations, drought resistance or the effects of heat.

(1) Water relations

It is generally acknowledged that lichens have no particular organs for water absorption, but act like a hydrophilic gel, absorbing water either as a liquid or directly as vapour from the air (Smyth 1934, Haynes 1964). The uptake of water must be passive, since Smith (1961) showed that metabolic inhibitors do not affect the rate of uptake. In studies of water uptake, Barkman

(1958) estimated a saturation deficit for epiphytic lichens in the range of 300-1000 atmospheres.

Scofield and Yarman (1943) noted that while lichens absorbed water vapour from the air they did not reach saturation water content. Reid (1960a) demonstrated that absorption from the air rarely exceeded 30-50% whereas Smyth (1934) found that absorption reached 70% of saturation water content. Scofield and Yarman, and Reid, found that if relative humidity fell to 70%, water content of the lichen very rapidly fell from the saturation level to some value in the vicinity of 20% of saturation content. None of these workers, however, studied an arid zone lichen.

Smyth (1934) and Lange and Bertsch (1965) found that at low water content the respiration rate exceeded the photosynthesis rate. Smyth, studying *Peltigera polydactyla*, found that below 30% of saturation water content respiration exceeded photosynthesis; Lange and Bertsch, working with the desert lichen *Ramalina maciformis*, found that at about 20% of saturated water content photosynthesis fell to zero, but that respiration was still detectable until water content fell to about 15% of saturated content. There is thus a range of water content within which respiration proceeds but photosynthesis does not. Within this range, between about 15% and 20% of saturated water content, lichens must slowly exhaust their food reserves. This depletion of food reserves would be less marked at lower humidities, as respiration fell away to undetectable levels. Thus, prolonged periods of humidity a little less than 70% could be damaging to lichens, and so, distribution of species could be related to extended periods of relatively high humidities, as well as to rainfall.

(2) Drought Resistance

In his review paper Lange (1953) presented a considerable block of data about drought resistance for a number of lichen species. He estimated drought resistance by measuring carbon-dioxide production and by studying viability of the algal symbiont after varying lengths and intensities of drought. His basic finding was that length rather than intensity of drought was the critical factor, most lichens being able to survive longer droughts than they would ever meet in nature. Despite this, he found a correlation between drought resistance and distribution. This work has been criticized because of its failure to take into account long term effects of drought, and for failure to measure changes in photosynthesis as well as changes in respiration (Smith 1962). It does seem to over-estimate ability to survive drought.

Reid (1960b) showed that after-effects of drought may not manifest themselves for a considerable time after the drought period. In the same study he suggested that the stress associated with drought may be most acute when the thallus absorbs water, for respiration was shown to surge to unusually high levels very rapidly, whereas photosynthesis climbed only slowly towards its normal level. It was suggested that perhaps not duration of drought, but frequency of alternation of rain with dry periods, limited the distribution of lichens (Smith 1962, 1968). A study published by Lange, Schulze and Koch (1970) showed that for the lichen *Ramalina maciformis* in the Negev, early morning dew was sufficient to allow a 3 hour burst of photosynthesis, with a nett gain in fixed carbon-dioxide in that time. This showed that arid lichens may behave differently to temperate ones, and that the stress period associated with re-wetting after drought need not be a serious problem.

(3) High temperatures

Lange (1953) reviewed the effect of high temperature on lichens, and also tested the heat resistance of a large number of different species. Lange exposed lichen thalli to varying temperatures for 30 minute periods, then assessed heat resistance by measurements of respiration of wetted thalli: the temperature which reduced respiration to 50% of the normal level was taken as an index of heat resistance. Temperatures in the range 70°C - 100°C were found to reduce the respiration to half in lichens exposed to heat, while dry, whereas temperatures in the range 30°C - 45°C reduced the respiration to half in wet material. However, these tests were short term only, a more recent paper (Lange 1966) has shown that such experiments would in some cases overestimate and in others underestimate heat resistance. Lange (1953) found a close correlation between heat resistance and distribution, and believed this to be a prime factor controlling lichen distribution.

(4) Light intensity

The role of light as a factor in lichen physiology has been reviewed by Quispel (1959). He drew particular attention to the data of Stalfelt (1939) which showed that the photosynthetic compensation point of lichen thalli was roughly equivalent to that of sun leaves. Stalfelt also demonstrated seasonal variation in response to light, and showed that the light intensity at compensation point for various species varied by a factor of up to four. Yarranton and Beasleigh (1969) found a relationship between light intensity and species distribution of lichens on limestone in Canada. While light is unlikely to be a limiting factor in typically sparse arid vegetation, it is possible that species from arid areas may not survive in the more shaded conditions of temperate areas.

(5) Nutrient supply

It has been shown that lichens have very efficient absorptive mechanisms for nutrients, and that these nutrients are actively absorbed and bound to the cells (Harley and Smith 1956, Smith 1960a,b, 1961). While this ability has undoubted advantages in areas of minimal nutrient supply, (lichens having no organs for absorption) this very active absorption can have unfortunate side effects, causing the death of lichens near industrial areas from absorption of pollutants (Brodo 1966) making lichens sensitive indicators of atmospheric pollution. While not necessarily fatal to the lichen this ability is of considerable danger to reindeer-eating Eskimos, as lichens have actively accumulated radio-isotopes from the atmosphere (Gorham 1959, Hanson 1966, Hanson, Watson and Perkins 1966), and reindeer eat lichens.

It is unlikely, therefore, that in a dusty environment like the arid zone nutrient supplies will limit distribution of most species.

It has been suggested that some lichens are "calciphiles" or "nitrophiles" (Smith 1921, Trumpener 1926) but these terms, because of the imprecision attached to them, mean little. However, Masse (1966a,b) has demonstrated a relationship between nitrogen in the substrate and distribution of some lichen species. Masse (1966a) grouped several species as "ornithocoprophiles" or "ornithocoprophobes" related to the nitrogen concentration of their substrates.

(6) Substrate pH

Alvin (1960) found a close correlation between distribution of lichens on sand-dune heath soils and soil pH. Mattick (1932) had also studied the pH of the soils upon which a large number of different lichen species occurred. In his report he presented figures showing the number of occasions on which he found each species to occur on soils of each pH interval used. Using these figures he stated the pH range and pH optimum for each species. While the range is valid, the optimal figures are not. The so-called optimum probably reflected little more than the soil pH most common in the area. Mattick perpetrated the fallacious argument by which Ashby (1936) showed that telegraph poles could be demonstrated to have an optimum soil pH. Statements of optimum soil pH require a percentage presence (frequency) calculation based not only on sites upon which a species is found, but on the pH of all sites searched for the species whether the species was found or not.

Yarranton and Beasleigh (1969) found in a study of lichens in deep limestone "grikes" (fissures) that while species distribution was related to topography, topography was not related to surface pH. They therefore considered pH not to be important in determining lichen distribution within their study area, nevertheless Yarranton (1970) included pH in the variables used to construct a predictive mathematical model of lichen distribution.

(7) Stocking pressure

Llano (1944) cited Lynge (1921) at length concerning the effect of grazing on Arctic lichen pastures, and remarked that trampling alone can do much to destroy such vegetation. Although no mammals have been reported to eat arid soil crust lichens, it is certain that trampling sheep have badly damaged the soil surface over vast areas of the Australian interior (Beadle 1948, Jessup 1951) and so presumably destroyed the lichen crusts.

The claim by Scott (1960) that the lichen symbiosis is maintained by the conjoint action of limiting nutrient, moisture and light adds further dimensions to consideration of controlling factors. This interaction also raises problems relating to long term physiological experiments on lichens, especially the possibility of disintegration of the symbiosis when materials are used under laboratory conditions.

CHAPTER III

DESCRIPTION OF THE STUDY AREA

An appreciation of the field work performed in this study requires an understanding of the physical context within which that work was executed. No single work adequately describes that context as much of the information is scattered in detailed studies of single aspects of the environment. There are, however, two very valuable general resources the *Atlas of Australian Resources* (Australia, Department of National Development 1951-65) and *The Australian Environment* (Australia, C.S.I.R.O. 1960).

The following account strikes a balance between brevity and complete description of the study area.

1. LANDSCAPE

The physical geography of the area is the subject of diverse publications, many of which are detailed by Lustig (1968). While there are many papers dealing with the detail of single facets of the physiography of the study area, very few integrated studies or maps have been prepared. A valuable discussion by Mabbutt (1969) dealt with the geomorphology of a large part of the area. The most detailed physiographic map of the whole study area was that prepared by Lobeck (1951), which served as the source for the physiographic regions on Fig. 3.1, and as the basis for regional nomenclature.

The predominant landscape form is the vast desert plain, interrupted only occasionally by relatively low hills. The generally slight relief of the whole region is apparent from the small area over 300m in altitude (Fig. 3.1), and is further illustrated by the fact that St. Mary's Peak in the Flinders Range, which is the highest point in the whole area, reaches a height of only 1,200m. Apart from the Mount Lofty and Flinders Ranges of the South Australian Shatter Belt, the only significant hills are the Gawler and Middleback Ranges on Eyre Peninsula, and the Olary Ridge and Barrier Range to the east of the Shatter Belt.

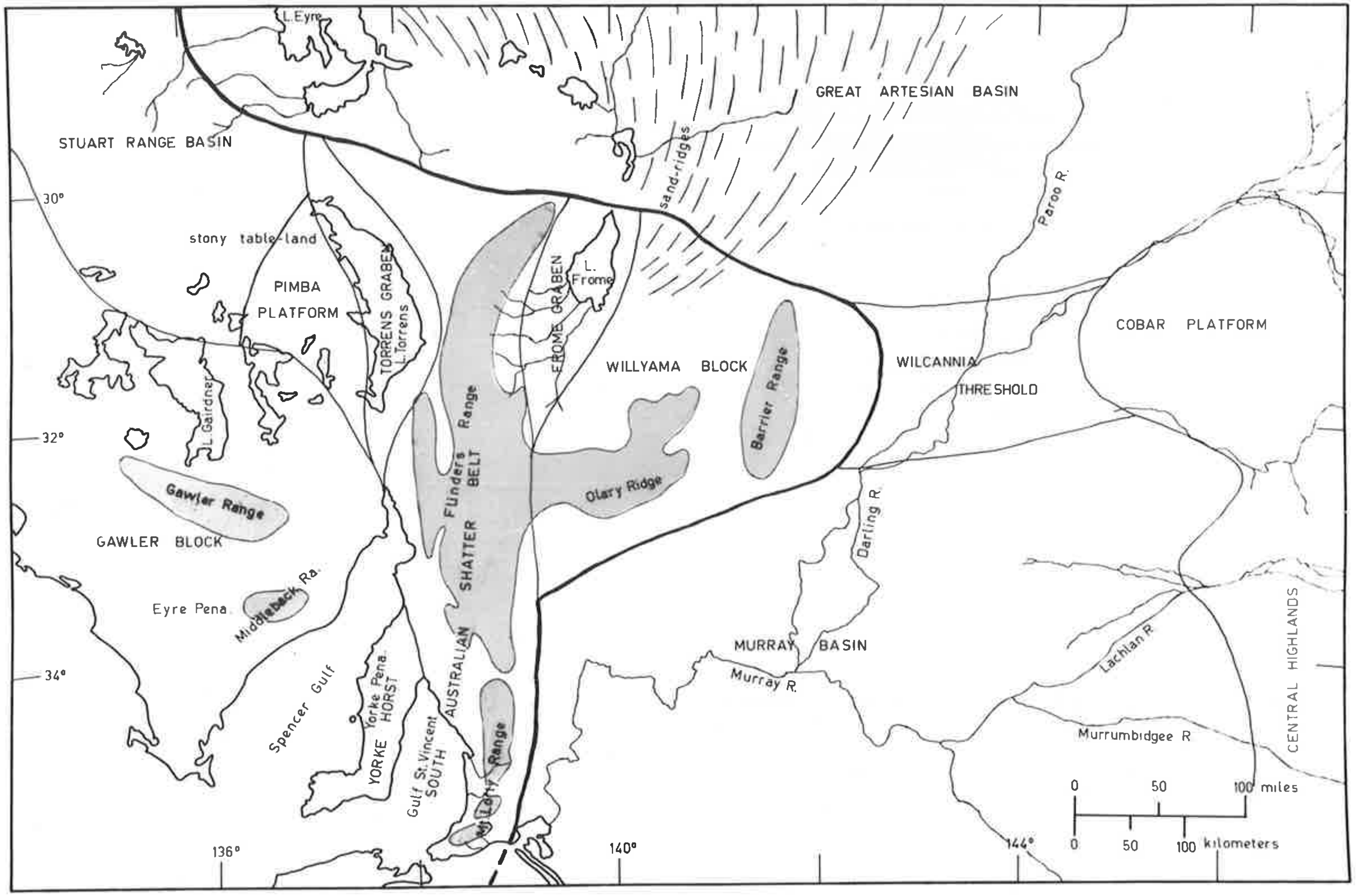
Arching around the east and north of the Shatter Belt is the sweep of the Eastern Australian Basins; the Murray Basin in the south, the Great Artesian Basin in the north. Both are virtually without relief.

The Murray Basin is a flat, low-lying area across which rivers from the eastern ranges flow towards the sea. Because of the very low gradient of the basin, the rivers meander and anastomose, not all of them ever reaching the main Murray-Darling river system. These rivers do not drain the Murray Basin itself but simply flow across it.

The Great Artesian Basin is also crossed by rivers originating on the eastern highlands, draining either towards the Darling River or Lake Eyre. Only rarely do many of these rivers actually

FIGURE 3.1

The physiography of the study area, adapted from Lobeck (1951). The heavy line represents the eastern limit of the Western Australian Shield.


L. Eyre
GREAT ARTESIAN BASIN
STUART RANGE BASIN
sand-ridges
Paroo R.
30°
stony table-land
PIMBA
PLATFORM
TORRENS GRABEN
L. Torrens
L. Frome
EROME GRABEN
COBAR PLATFORM
WILLYAMA BLOCK
WILCANNIA
THRESHOLD
Barrier Range
L. Gairdner
Flinders Range
SHATTER BELT
32°
Olary Ridge
Darling R.
Gawler Range
GAWLER BLOCK
Eyre Pena.
Middleback Ra.
AUSTRALIAN
MURRAY BASIN
Lachlan R.
CENTRAL HIGHLANDS
34°
Murray R.
Spencer Gulf
Yorke Pena.
HORST
YORKE
Gulf St. Vincent
SOUTH
Mt Lofty Range
Murrumbidgee R
0
50
100 miles
136°
140°
144°
0
50
100 kilometers

discharge into either the Darling or Lake Eyre as they usually dissipate their waters on broad floodplains. The north-west portion of the basin is crossed by a series of parallel desert sand dunes.

At the junction of these two basins lies the Cobar platform, an ancient dissected peneplain, and the Wilcannia Threshold; both areas of low stony hills.

West of the Shatter Belt lies a series of salt-pans associated with internal drainage. In the north-west the Stuart Range Basin and Pimba Platform are both areas of stony pavement either on broad flat tableland areas, or on outlying mesas, overlying the Pre-Cambrian Australian Shield.

2. CLIMATE

(1) Climatic zones

The study area has been zoned climatically in different ways by a number of workers; probably the most widely known classification being that proposed by Meigs (1953). On Meigs' zonation as shown in Figure 3.2, virtually all the study area is classed as arid or semi-arid, with a small temperate area included in the hills near Adelaide. The UNESCO - FAO (1963) bioclimatic map shows that the study area has within it two basic climatic types. These are the desert type (with various modifications also present) and the mediterranean type (which also is represented by a series of modified forms).

Perry (1967) mapped the limits of "rangeland" on the basis of climatic variables in the light of land usage. For the purpose of this study, the area described by Perry as rangeland has been treated as arid. For convenience, the 38cm* rainfall isohyet has been taken as the upper rainfall limit of the sub-arid zone, all areas wetter than that being considered humid.

The choice of the 38cm isohyet to demarcate temperate and sub-arid lands was entirely arbitrary, but it more or less divided the study area outside of the arid zone into equal portions. The limits of the arid zone, sub-arid zone and humid zone as defined above are shown in Fig. 3.3. This classification has been used throughout this study.

(2) Rainfall

Rainfall in the area varies from less than 12cm in the Lake Eyre Basin to more than 100cm in restricted areas of the Mount Lofty Ranges, near Adelaide. Rainfall isohyets form a nested series paralleling the coast, except for the disturbance caused by the Mount Lofty-Flinders Ranges, which have the effect

---

* Rainfall in Australia is measured and mapped in inches; these figures have been converted to the nearest centimetre for this study.

of increasing precipitation on the western faces of the range and creating a rain-shadow on the eastern face. The distribution of rainfall isohyets as shown in Fig. 3.4 was based largely on information in climatological surveys published by the Australian Bureau of Meteorology (1955-1963).

In the north-east of the study area, rainfall is concentrated in relatively intense summer showers whereas in the south-west rainfall is mostly in the winter, falling in frequent light showers (Leeper 1960). Fig. 3.5 shows mean number of rain days per annum, and was drawn from official statistics (Australia, Bureau of Meteorology, 1966). The area with a seasonal maximum precipitation in the winter is delimited in Fig. 3.4. (Australia, Department of the Interior, Meteorological Branch, 1954).

(3) Temperature

An indication of variation in temperature is given in Fig. 3.6 and Fig. 3.7 which show respectively the normal maximum temperature for January (southern summer) and the normal minimum temperature for July (southern winter) (Australia, Department of the Interior Meteorological Branch, 1953). Some areas with a normal July minimum of less than 5°C have a normal January maximum of more than 35°C, diurnal variations in excess of 15°C not being uncommon (Jackson 1958).

FIGURE 3.2

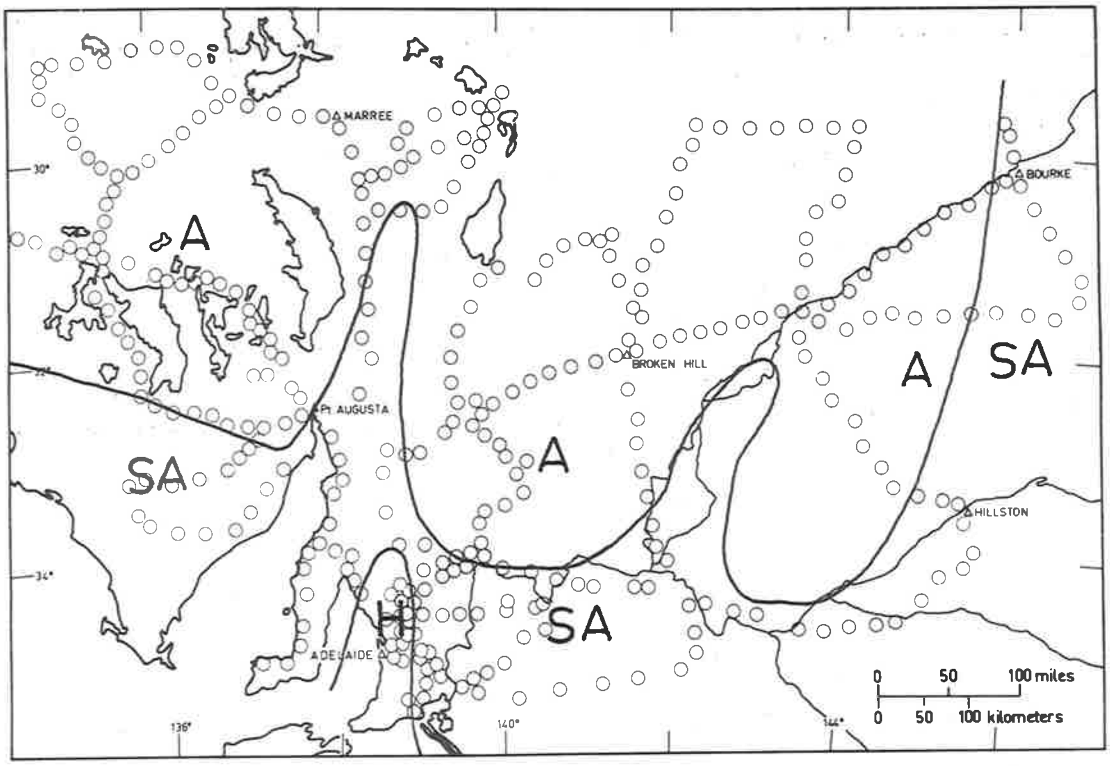
Climatic zonation after Meigs (1953).

A	---	arid
SA	---	sub-arid
H	---	humid

FIGURE 3.3

The climatic zonation used in this study. The arid / sub-arid boundary is adapted from Perry 1967.

A	---	arid
SA	---	sub-arid
H	---	humid


MARREE
BOURKE
BROKEN HILL
Pt AUGUSTA
HILLSTON
ADELAIDE
A
SA
H
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

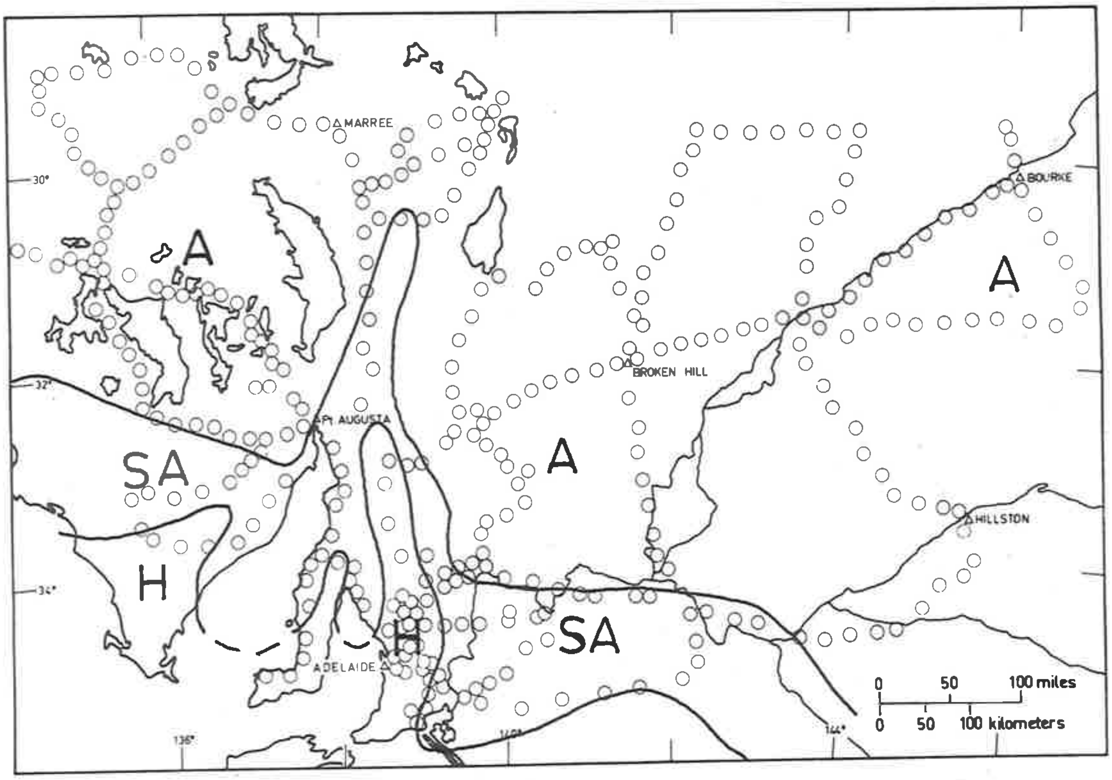
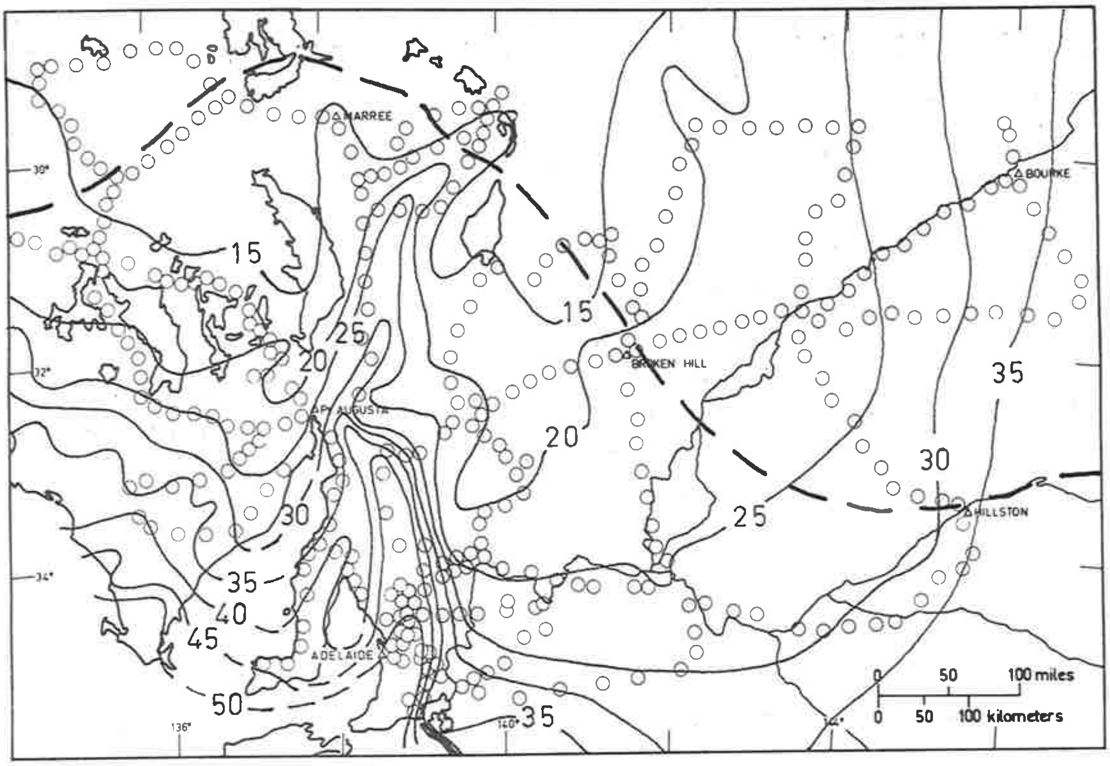

MARREE
BOURKE
BROKEN HILL
Pt AUGUSTA
HILLSTON
ADELAIDE
A
SA
H
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

FIGURE 3.4

Mean annual rainfall, isohyets are at 5cm intervals. The broken line represents the northern limit of the area with a pronounced seasonal maximum precipitation in winter.

FIGURE 3.5

Mean annual number of rain days. Isolines are at 20 day intervals.


MARREE
BOURKE
BROKEN HILL
Pt AUGUSTA
HILLSTON
ADELAIDE
15
20
25
30
35
40
45
50
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

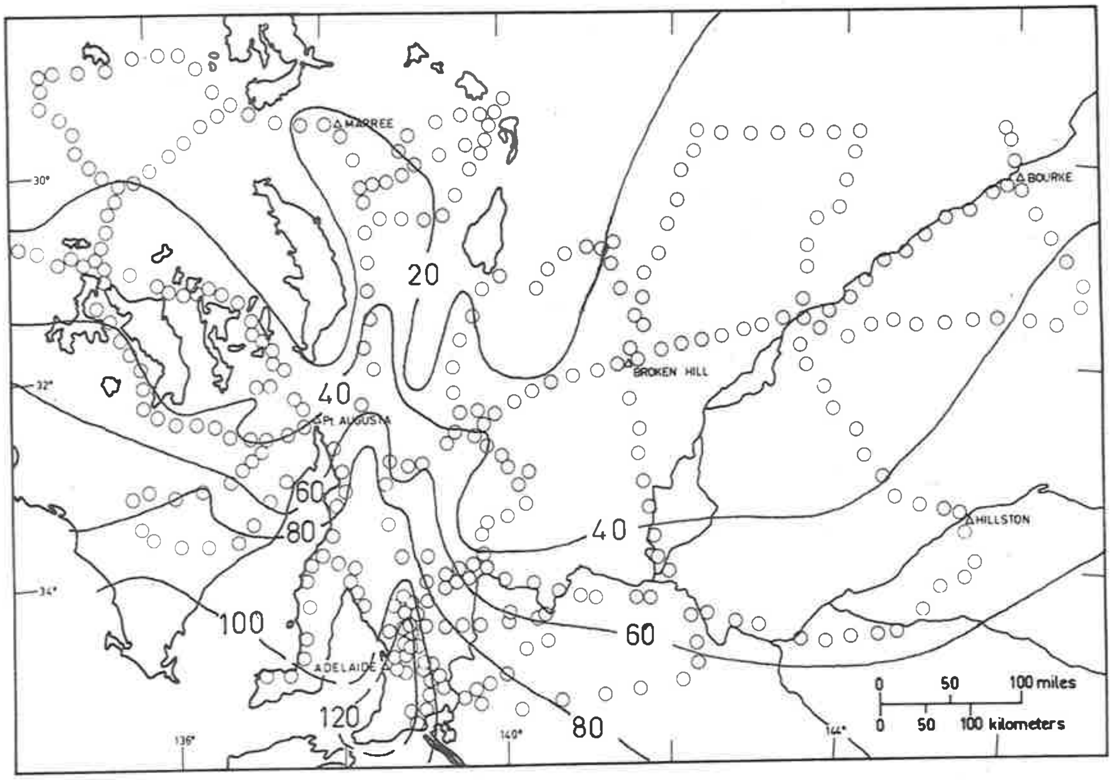
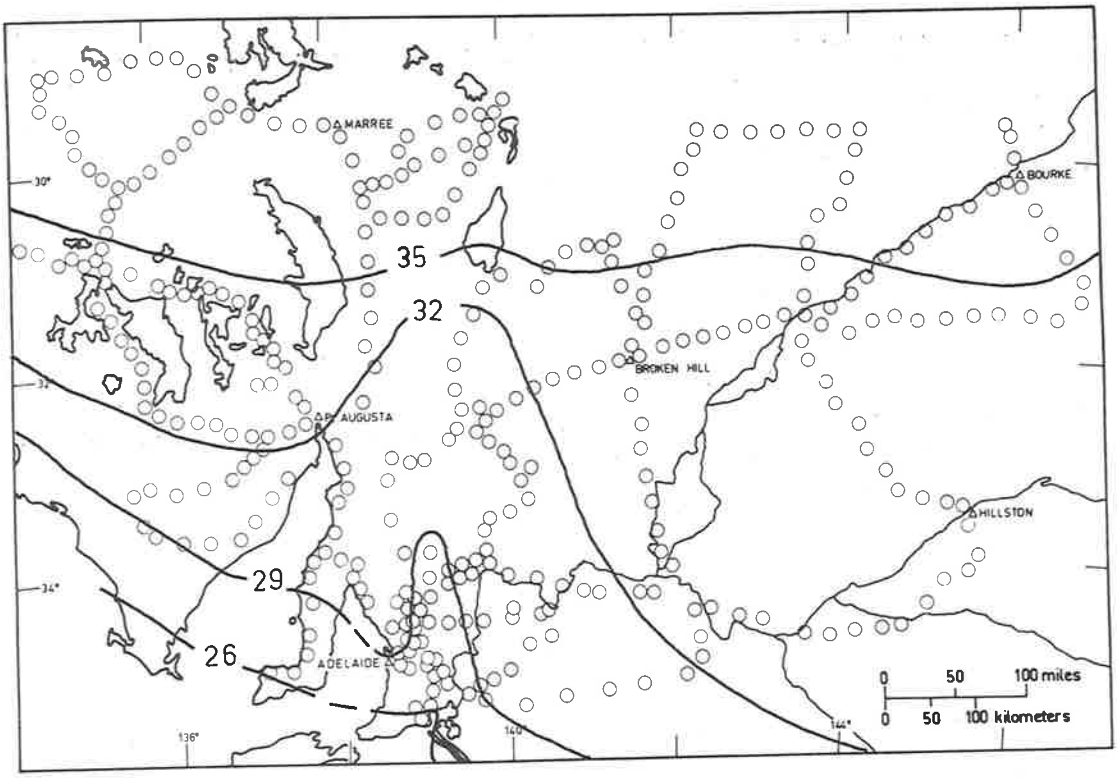

MARREE
BOURKE
BROKEN HILL
Pt AUGUSTA
HILLSTON
ADELAIDE
20
40
60
80
100
120
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

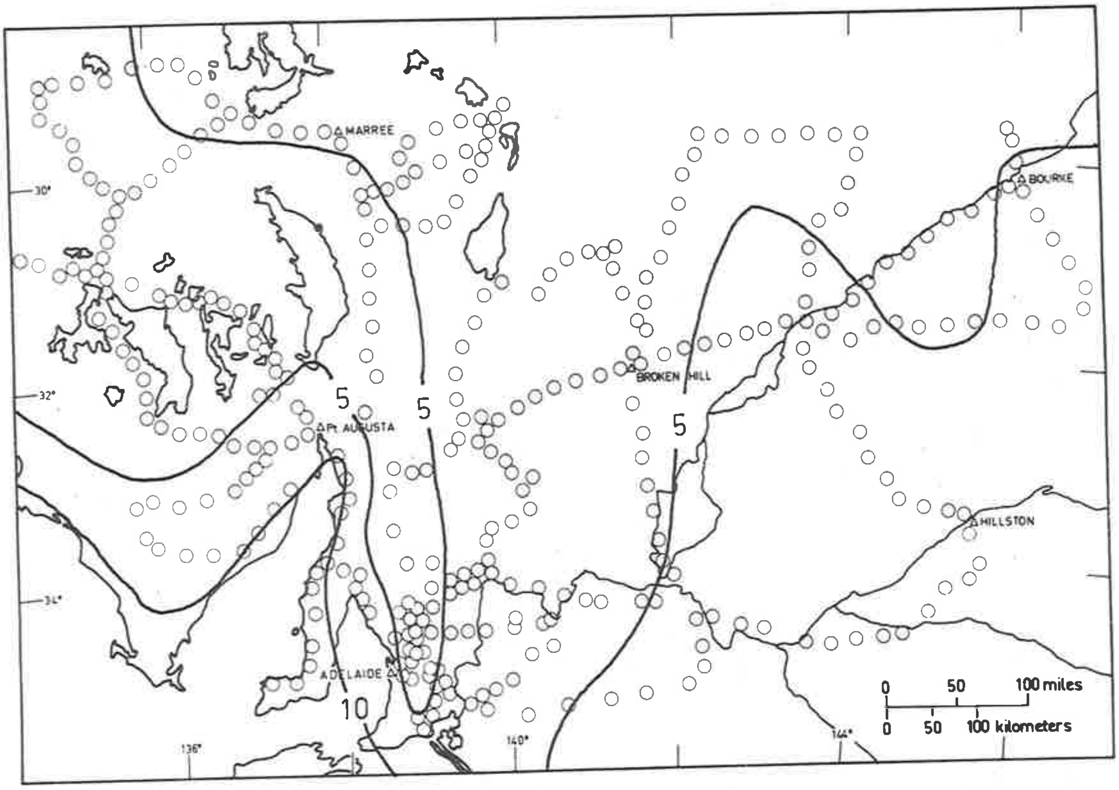
FIGURE 3.6

Mean daily maximum temperature for January. Isotherms are at 3°C intervals.

FIGURE 3.7

Mean daily minimum temperature for July. Isotherms are at 5°C intervals.


MARREE
BOURKE
30°
35
32
BROKEN HILL
32°
Pt. AUGUSTA
HILLSTON
34°
29
26
ADELAIDE
0 50 100 miles
0 50 100 kilometers
136°
140°
144°


MARREE
BOURKE
30°
BROKEN HILL
32°
5
5
5
Pt. AUGUSTA
HILLSTON
34°
ADELAIDE
10
0 50 100 miles
0 50 100 kilometers
136°
140°
144°

3. SOILS

Soils of the area have been mapped in soil associations by Northcote (1960, 1966) and Northcote *et al* (1968). With the exception of skeletal types on hilly areas, the soils are climatically zoned. In the humid zone are small areas of podzolic, solodized solonetz and solodic soils, but the soils in most of the areas with rainfall between 38cm and 50cm per annum are red-brown earths. In the sub-arid zone highly calcareous solonized brown soils (Mallisols) predominate. In the arid zone of South Australia there are large areas of highly calcareous brown soils, with calcareous desert soils and stony desert loams in the drier parts. In southern New South Wales is a vast area of grey or brown soils of heavy texture, mostly cracking clays. In northern New South Wales there are expanses of arid red earths, notable because they are particularly susceptible to erosion (Beadle 1948) and are neutral to acid in reaction, whereas virtually all of the other arid or sub-arid soils are neutral to strongly alkaline in reaction.

4. VEGETATION

The vegetation of most of the area has been described by Wood (1937), Beadle (1948) and Jessup (1951), each of whom published maps and floristic lists; Wood for eastern South Australia, Beadle for western New South Wales, and Jessup for a large area in arid central South Australia. The vegetation of the whole area has been mapped by Williams (1955) on the basis of physiography.

The vegetation of the study area can be conveniently considered in three broad units, the desert complex, the mallee and the dry sclerophyll.

The dry sclerophyll fascies is virtually restricted to the humid zone, and varies from *Eucalyptus* forests near Adelaide to open *Eucalyptus* savannah, but is always marked by the presence of *Eucalyptus* trees. An under-storey of grasses, herbs and forbs is common (but not universal) in these vegetation types.

The mallee vegetation form is a distinctive sub-arid form, characterised by low, many-trunked *Eucalyptus* species, ranging in density from that comparable with open woodland to that resulting in a closed canopy. In wetter areas the mallee may have a sclerophyllous shrub layer below. However, in most of the sub-arid bare soil is common between the trees and bushes with a cover of forbs and grasses appearing seasonally.

The desert complex is very varied indeed. Within the study zone there are areas of layered arid woodland, of arid shrubland (sometimes called "shrub-steppe") and also of virtually bare desert sandhills and plains.

Common to the arid shrubland, arid woodland and also some Mallee areas, is a layer of low shrubs of the family Chenopodiaceae, especially *Atriplex* and *Kochia* species. The soil in the desert complex is bare except for a growth of forbs and grasses in exceptionally wet seasons.

The shrub vegetation which forms the basis of the arid zone pastoral industry, has been extensively damaged by grazing sheep (Beadle 1948, Jessup 1951), leaving many areas formerly clad with Chenopodiaceae devoid of any perennial shrub vegetation.

5. LAND USAGE

The temperate area is utilized for horticultural, agricultural and pastoral activities. Within the temperate zone are most of the dairy cattle, market gardens and orchards (other than those in irrigated areas in the Murray Valley) to be found in South Australia. The sub-arid zone is virtually a wheat-belt, with sheep as a secondary interest. The arid zone is almost entirely used for grazing of sheep or cattle on native shrub pastures. These patterns of land usage have now been in existence for over 70 years.

Development of land usage proceeded from the coastal fringes of the continent slowly inland. This development was a steady progression with flocks of sheep in the vanguard, wheat farmers following after, and more intensive agriculture developing around urban centres. A notable reversal of this pattern occurred in South Australia in the years 1880-1890, when wheat farmers who had tried to grow crops in areas with a rainfall as low as 20cm per annum, retreated precipitously under stress of drought (Meinig 1963). This over-expansion and subsequent retreat of the wheat farmers left wide areas on the fringes of the arid-zone in South Australia devoid of its natural shrub covering, all of it destroyed by the plough.

CHAPTER IV

TAXONOMY AND DISTRIBUTION OF THE SOIL-SURFACE LICHEN FLORA

The first stage of the study of soil surface lichens involved widespread travel across the study area, collecting materials to determine the lichen taxa involved, and to circumscribe the distribution of those taxa within the area. In this chapter, therefore, sampling method and lichen floristics of the area are detailed. In addition a key to the lichens found on the soil surface has been included.

1. SAMPLING METHOD

Faced with the problem of sampling an extremely large area (about one million square km), a sampling system had to be devised that compromised between the strict statistical requirement of random sampling and the biological requirement that the variation across the entire area be sampled. It was decided to sample at regular intervals along transects formed by the roads and tracks across the area. The exact interval between samples, although never in excess of 32km was determined by an assessment of the variation shown in the landscape of the area. If it was found that sharp changes occurred in the vegetation, samples were taken from the various vegetation types found.

The routes were selected to form a grid across the study area, with the transects normal to rainfall isohyets, one of the factors predicted to control distribution. As collection and sorting of samples proceeded, the information so gained was used to modify the planned number of transects, their locations and the total extent of the sampled area.

At each sampling site specimens of the soil surface lichen crust were collected from areas about 50m in diameter, usually a few hundred metres from the road or track to avoid the damaged area associated with roads. Anticipating an effect of soil type on distribution patterns, a sample of about 400gm from the top 2cm was taken of the typical soil at each site. All samples were placed in serially numbered paper bags and stored in boxes for return to the laboratory. Notes on soil and vegetation were made at each site. This collecting involved travelling in excess of 17,000km, largely on unformed tracks in remote, very sparsely occupied areas. A number of the tracks used were passable only in a four-wheel drive vehicle.

In the laboratory the samples of soil surface lichens were sorted under a dissecting microscope, and placed into form-groups for determination. An herbarium record was kept of every apparently different form from each site. These groups were periodically reviewed to allow ranges in variation to be assessed, and species limits to be determined. Form-groups were ultimately determined by reference to the literature, in the first instance to the *Lichen Flora of the United States* (Fink, 1935).

To aid determination of species from arid soil, lichens from various substrates in arid, semi-arid and temperate areas were also collected and determined. This ensured knowledge of variation likely to be encountered and also provided a background which allowed decisions involving relative terms such as "large" and "small" to be made as well as providing familiarization with such unique lichen structures as soredia and isidia. Determinations of material from soil in the study area are discussed at length below (Section 3.1). Determinations of other South Australian materials in the author's herbarium are listed in Appendix 1.

Herbarium specimens were compared with holdings in the Herbarium of the Botany Department, University of Adelaide (ADU), the State Herbarium of South Australia (AD) and the National Herbarium, Melbourne (MEL). Materials were also sent to W.A. Weber at the University of Colorado Museum (COLO), Colorado, U.S.A.

2. THE DISTRIBUTION OF SAMPLES

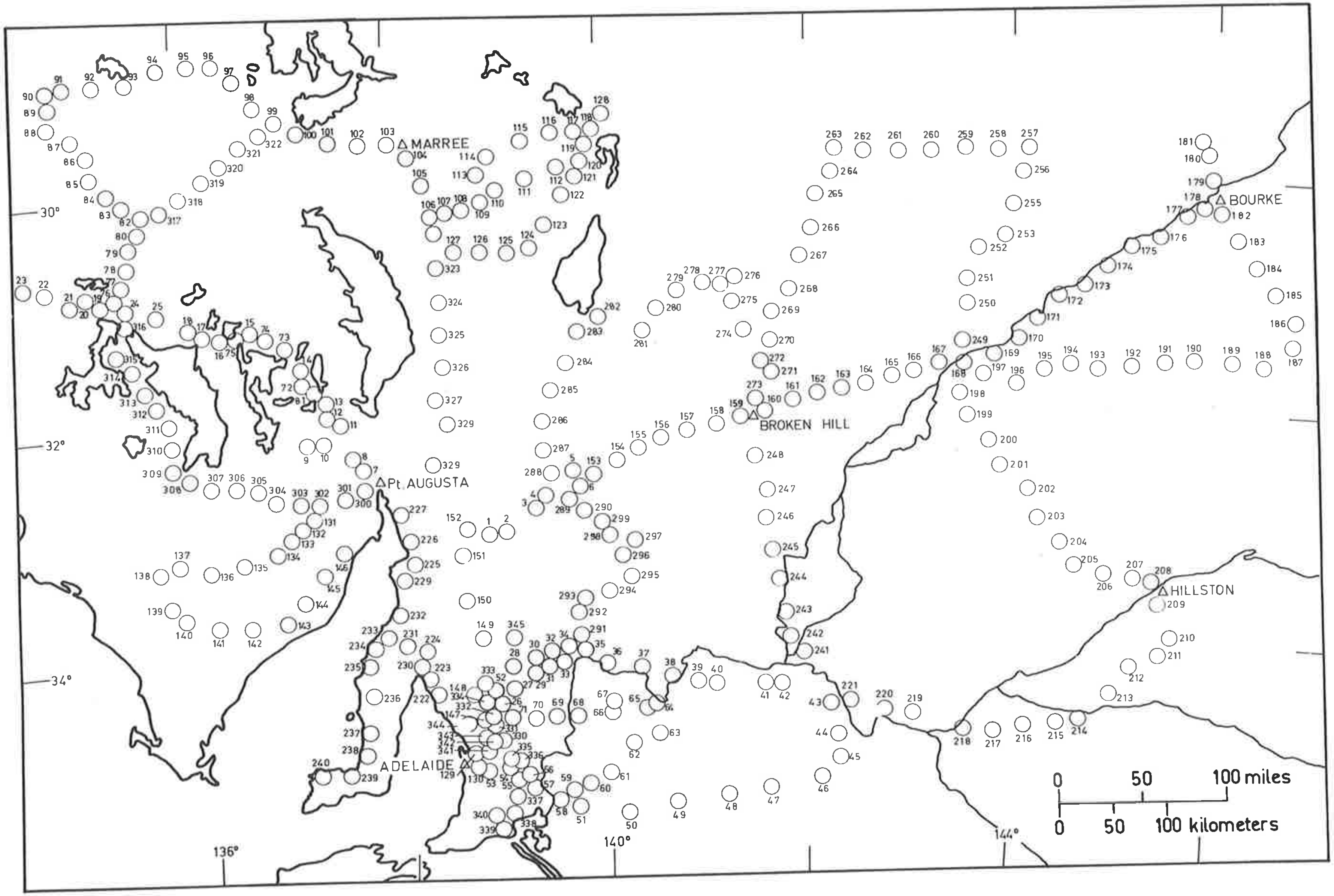
Samples were, in most cases, collected in a planned sequence. There were however a number of reasons why the planned sequence was not carried through. In a few cases adverse weather conditions prevented sampling in some places at the time planned. This meant that sample numbers along any transect, while usually sequential, were not always so. The gaps left in the sampling pattern on one expedition were filled during the next.

Because of the small area of temperate lands in the study area, it was decided to sample this much more intensively (in order to get numbers of statistical significance) than the wide expanses of sub-arid and arid lands. This unequal sampling intensity and somewhat disordered sequence of collecting is apparent in Figure 4.1, which shows the distribution of sample sites, and the number of each site.

Where possible sites were placed at arbitrary intervals along the transects. In the temperate and sub-arid areas, agricultural activities had destroyed virtually all trace of natural vegetation except for minute pockets beside roads, or, more commonly, strips along railway easements. In these areas samples had to be collected from whatever natural vegetation could be found. In some cases in the Mallee region the transects

FIGURE 4.1.

The distribution of sampled locations.
The numbers are those used throughout
the study to refer to the site indicated.



MARREE
BOURKE
BROKEN HILL
Pt. AUGUSTA
ADELAIDE
HILLSTON
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

were planned to follow the railway lines because of the natural vegetation persisting along them in otherwise denuded areas.

This approach lead to a collection of samples with a biased distribution. Road and railway surveyors tended to survey routes along valley floors, rather than over hills, and to skirt round sandhill systems. This tendency was counteracted by some samples deliberately collected from hilly areas and on sand hills to make the sampling as unbiased as was practical.

In all, 345 sites were visited and sampled along approximately 15,000 km of transects. Two of the samples collected (numbers 228 and 254) were lost in transit. Of the 227 locations with soil surface lichens, 118 showed the development of a distinct lichen crust over the soil surface;the rest exhibited only a sparse scatter of lichens over the surface.

3. FLORISTICS OF THE SOIL SURFACE LICHENS

The lichens of the soil crust were eventually classified into 42 taxa. Most of these taxa were at the species level: a number, however, were not. The taxa have, in most cases, been attributed to previously described species, usually in the broad sense of those species. It was believed that arid material ought not to be split into a number of narrowly circumscribed species in the absence of extensive studies on environmental modifications. Generally, the nomenclatural suggestions of Weber (1962, 1967a, 1968) have been followed.

In Appendix 2, a table is presented showing the taxa present at each sampling location. Maps showing the distribution of each species, based on collections made for this study, are presented at the end of this chapter.

(1) Annotated list of taxa

1. *Acarospora schleicheri* (Ach.) Mass.

A species widely distributed on rock and soil throughout the world. This is one of the two yellow species of *Acarospora* recognized by Weber (1968) in his revision of the yellow subgenus of *Acarospora*. This species is not common on soil in the study area, but appears as bright yellow granules scattered on hard soil surfaces.

2. *Acarospora smaragdula* (Wahlenb.) Th. Fr.

A species in the brown sub-group of the genus. Similar material in Australia has been sometimes referred to *A. ferdinandii* (Müll. Arg.) Hue; however, the type of *A. ferdinandii* is a very poor specimen, and cannot be placed in either the brown or yellow sub-genera (W.A. Weber, pers. comm.). *A. smaragdula* is not uncommon an arid and semi-arid soils, appearing as a small plaque (less than

2cm in diameter) usually grey or brownish, sometimes with immersed pruinose apothecia, often two or three in each of the central aereoles. The margins are usually conspicuously lobate.

3. *Acarospora* Mass. species indeterminate.

This form is an eroded thallus that cannot be placed in either subgenus of *Acarospora*. Weber (1962) has studied this type of thalline modification.

4, 5. *Aspicilia calcarea* Mudd.

Aspicilia Mass. is sometimes treated as a section of *Lecanora* Ach. but may be differentiated from *Lecanora* because of its immersed apothecia. Two radically different thallus forms of this species are found in the study area, the typical ashy or white crustose form, and the ashy fruticose form discussed by Weber (1967a), which had been previously referred to a separate genus as *Agrestia cyphellata* Thomson. The two forms may be found occasionally on the same site, with all the linking stages discovered by Weber visible (see plate 1). Because of the striking difference betwean the two forms, they have been maintained as separate taxa throughout this study, the crustose form as *A. calcarea* and, if fruticose as *A. calcarea* mod.* *fruticosa*. Both forms are widespread in the study zone.

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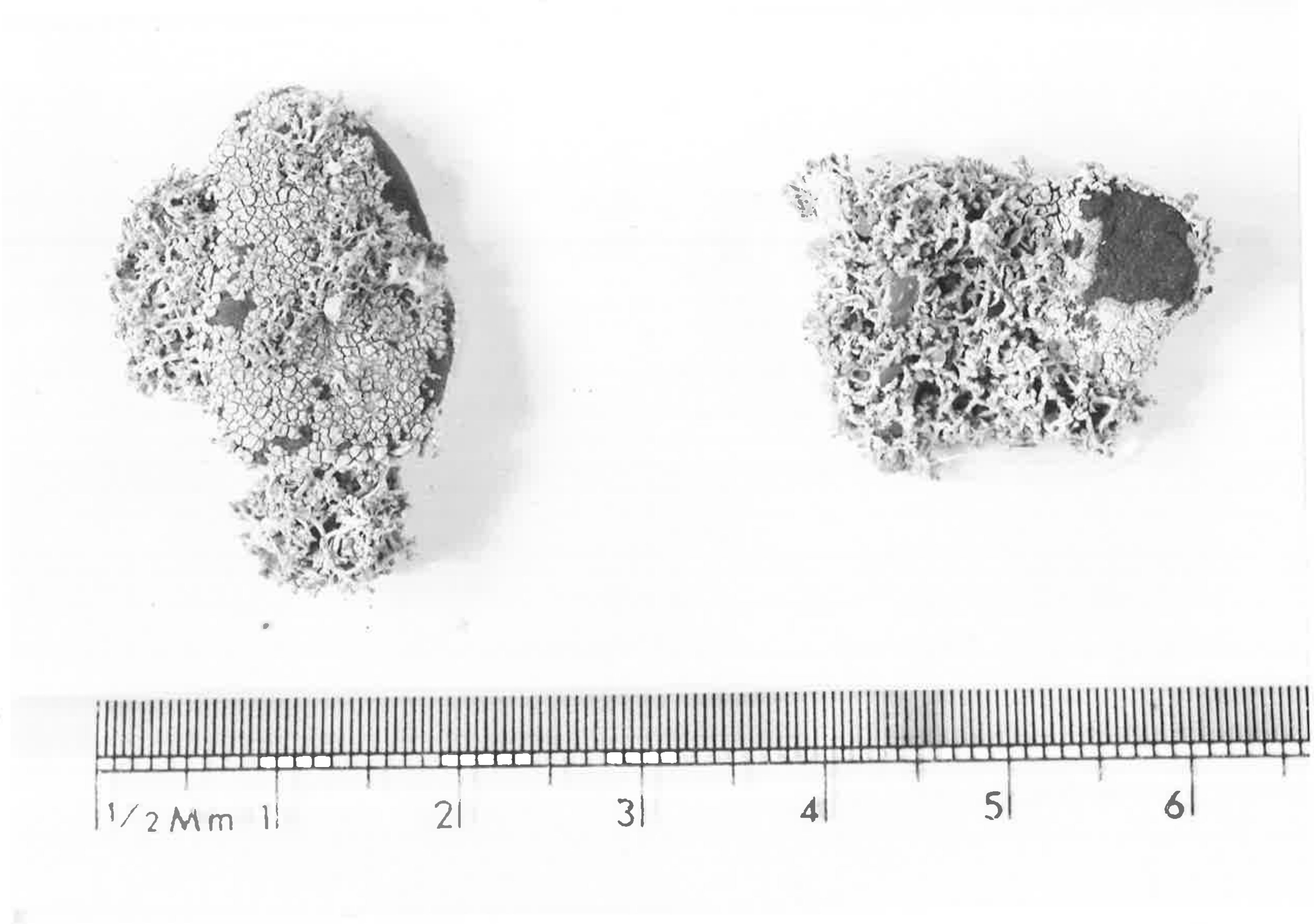
* The term "modification" is used as defined by Weber (1962) "a plant which is the phenotypic product of an interplay between the external environment and the range of expression of the genotype of the plant." It is an extra-legal designation.

PLATE 1.

The crustose form of *Aspicilia calcarea* on pebbles merging with the fruticose modification on soil. The scale is callibrated in half millimetres.


1/2 Mm
1
2
3
4
5
6

6. ? *Biatorella* Th. Fr. species indeterminate.

Material was rarely referred to this genus. That which was, had a severely eroded thallus making the determination doubtful.

7. *Buellia epigaea* Tuck.

A species of widespread arid and sub-arid occurrence around the world. In the study area the thallus is a chalky white, usually crustose with distinct marginal lobes, but occasionally almost sub-fruticose; apothecia are not uncommon. The species is not common in the study area.

8. *Buellia subcoronata* (Müll. Arg.) Malme.

This name has been applied only to Australian material. It is a strong possibility that the species is extra-Australian under a prior name. This species, which has buff-coloured squamules usually a few millimeters in diameter, and erumpent apothecia, has been collected only rarely from arid zone soils. Material collected in the study zone matches the type collection inthe Herbarium of the Botany Department, University of Adelaide.

9. *Caloplaca subpyracella* (Nyl.) Zahlbr.

A species recorded from soil in southern California. The thallus is grey, but often disappears leaving only apothecia, which aresmall (less than 1mm diameter) and have an orange disk with a yellow exciple. This species occurs usually as a few scattered apothecia amongst other lichen thalli, and is easily overlooked when sorting collections.

10. *Caloplaca* Th. Fr. species indeterminate.

This form has a deep orange squamulose thallus, with distinct marginal lobules. Apothecia up to 1.5mm diameter, have a deep orange disk with a paler exciple. This material could prove to be a depauperate form of *Xanthoria* growing on the soil.

11. *Chondropsis semiviridis* (Nyl.) Nyl.

This is the only species in the genus *Chondropsis* (sometimes referred to *Parmelia*). It is limited to Australia and New Zealand. Material from within the study zone shows considerable variation in lobe size. The usually sterile thallus is entirely devoid of attachment to the substrate, and rolls up into a ball when dry. This species is common in the sub-arid zone of the study area.

12. *Cladia aggregata* (Eschw.) Nyl.

This species is widespread in the southern hemisphere, and has been recorded from the northern hemisphere in Japan and the West Indies. The pseudopodetia of material collected from the study area are extremely variable, ranging from imperforate dark brown sterile specimens less than 1cm tall, to much perforate pale green fertile specimens over 5cm tall. The species is common in the temperate part of the study area, but the primary thallus has not been found in that area.

13. *Cladonia foliacea* Schaer.

This species is widely distributed on soils in dry areas. Material from the study area may be referable to *C. foliacea* var. *alicornis* (Lightf.) Schaer. Only well developed (but always sterile) specimens were referred to this species; poorly developed material which may belong there was referred to the form group used for sterile *Cladonia* squamules. The thallus is usually green or grey-brown on the upper surface with a white or grey lower surface. The lower surface is readily seen when the squamules have dried and rolled up at the edges. On hurried examination this species could be confused with *Heterodea müllleri*, with which it sometimes occurs. *H. mülleri*, however, has a dark, rhizoid-clad lower surface. E. Dahl (pers. comm.) believes that all Australian material referred to *Cladonia foliacea* is better referred to the genus *Heterodea*.

14. *Cladonia subsquamosa* Nyl.

A species with much branched podetia, squamulose at the base, always cupless in the study area where it is not common.

15. *Cladonia verticillata* Hoffm.

A distinctive species reported from all continents. The thallus has cupped podetia, usually proliferating from the centres or margins of the cups to make three or more tiers. In the study area the primary thallus commonly persists. Specimens from the study area are usually stunted and distorted, but some fine specimens up to 5cm high have been found.

16. *Cladonia* c.f. *fimbriata* (L.) Fr.

This name is assigned to a form-group used in this study to embrace a wide range of forms apparently close to *C. fimbriata* (L) Fr., which is itself a very variable species. The podetia are erect, variously decorticate powdery or squamulose, sometimes branched, occasionally with abortive cups. The primary thallus commonly persists as squamules. More extensive collections may permit delimitation of species from within the complex. The form is restricted to the humid part of the study zone.

17. *Cladonia* squamules.

This form-grouping was used for all the sterile *Cladonia* squamules found in the study area but which were too small to be certainly determined as *C. foliacea*. It is likely that several species of *Cladonia* were represented in this group, especially depauperate specimens of *C. foliacea,* and probably juvenile forms of *C. verticillata* as well, because *C. verticillata* commonly has a persisting primary thallus in the study area.

18. *Collema ? coccophorus* Tuck.

The genus *Collema* is widespread in arid areas and is notoriously difficult taxonomically. The species in the study area is not certain but it is in section *Synechoblastus* (Trev) Korb. and approximates to *C. coccophorus.* The thallus usually forms a deep olive green or almost black rosette, often partially buried in the soil. Critical study may well reveal that material assigned to this species is in fact a combination of several.

19. *Dermatocarpon lachneum* (Ach.) A.L. Smith.

This name is used in the sense proposed by Weber (1962), including amongst its synonyms *D. desertorum* Tom., *D. hepaticum* (Ach.) Th. Fr. and *D. rufescens* (Ach) Th. Fr.. In the study area this species normally has round, pale-brown squamules with many fine rhizoids below. Occasionally the thallus becomes crenate or darkened. The thalli are difficult to differentiate from those of *Endocarpon pusillum* unless fertile, when the non-septate spores of *Dermatocarpon* are easily distinguished. In addition *E. pusillum* is often grey instead of brown, and is commonly umbilicate rather than having many fine rhizoids as has *D. lachneum*. *D. lachneum* is one of the most common lichens on soil in the study area.

20. *Diploschistes ocellatus* (D.C.) Norm.

This species is known on soil and rock around the world. The species *D. subocellatus* Nyl. ex Cromb. described from Australian material is probably only a colour variant of this normally chalky white form. Found only occasionally in the study area, this species is easily differentiated from the more common *D. scruposus*, by its large (up to 3mm diameter) almost sessile apothecia, which have a prominent thalloid exciple. This species forms a continuous crust over the arid soil, often lying more or less free on the surface, in patches up to 20cm across.

21. *Diploschistes scruposus* (Schreb.) Norm.

This cosmopolitan species is widespread in the study area; its greyish often somewhat mealy thallus has minute (less than 1/2mm. diameter) immersed apothecia, and in some areas covers patches up to 10cm across. It is possible that more than one species has been included under this name, as some material has a very thick proper exciple with a radially striate margin which very nearly closes the apothecium, whereas the species typically has a relatively thin exciple and an open disk. Wind blast could, however, possibly erode the thick exciple in drier areas, leaving the typical *D. scruposus* form; for this reason only one species name has been used.

22. *Endocarpon pusillum* Hedw.

This cosmopolitan species is one of the most common in the study area. The species *E. helmsianum* Müll. Arg. described from central Australia is probably only a luxuriant form of *E. pusillum*. *E. pusillum* is commonly umbilicate with its grey or brown thallus distorted into a more or less crenate form. The squamules are usually fertile, as are those of *Dermatocarpon lachneum*, but the very large multiseptate spores of *E. pusillum* are readily visible under a dissecting microscope, whereas the small, non-septate spores of *D. lachneum* are not.

23. *Fulgensia bracteata* (Hoffm.) Ras.

This species, widespread in America and Europe, is usually sterile in the study area; only very few fertile thalli have been found. The thallus is usually small (about 1cm across), whitish and mealy when dry, and turns a bright citrus yellow when wet. The relationship of this material and *F. subbracteata* (Nyl.) Poelt has not been determined.

24. *Heppia lutosa* Ach.

This very widespread species occurs commonly in the study area, but usually only as depauperate thalli among those of other species; fertile material is rare. The thalli are usually grey-green in colour and form a rosette of rather thick lobes.

25. *Heppia polyspora* Tuck.

H. polyspora is apparently close to *H. australiensis* Müll. Arg., described from central Australia. However, the earlier American name seems to fit the material found and has been adopted, to avoid use of what is probably a synonym. The squamules are small, deep grey-green or brown in colour with a somewhat crenate margin, and with immersed red or red-brown apothecia in each. Fertile material is common.

26. *Heterodea mülleri* (Hampe) Nyl.

This monospecific genus is confined to Australia. The thallus is foliose, with a green or grey-green upper surface and an almost black, more or less pseudocyphellate lower surface. Apothecia are common and marginal. This species is found only in the temperate parts of the study area.

27. *Lecanora atra* (Huds.) Ach.

This species has small (less than 1mm diam.) apothecia with a white thalline margin and a pale, almost flesh-coloured disk, which turns dark brown or almost black in older specimens. The thallus is white, commonly forming a crust up to 5cm across on the soil.

28. *Lecidea coarctata* (J.E. Smith) Nyl.

This species is almost cosmopolitan, especially on hard soil and rocks. In the study area the thalli are usually found on a hard soil surface as small, scattered, white squamules with erumpent apothecia.

29. *Lecidea crystallifera* Tayl.

This species, endemic to Australia, is easily distinguished by its grey upper surface, which is cracked into a mass of solid angles, giving a crystalline appearance. There is a form of lichen in the study area which, though distinguishable from typical *L. crystallifera*, is here included with it. This form appears to be a luxuriant variant of the species, distinguished also by somewhat immersed rather than sessile apothecia. *L. crystallifera* is one of the more common species in the study area.

30. *Lecidea decipiens* (Ehrh.) Ach.

This species is extremely widespread on soils, and is the most common species on soil in the study area. The thallus is composed of small, usually pink squamules. All the shape and colour variants discussed by Weber (1962) occur in the area. In this study *L. crenata* (Tayl) Stiz., *L. coroniformis* (Krph.) Zahlbr. and *Psora concava* B. de Lesd. are regarded as synonyms of *L. decipiens*, following Weber.

31. *Lecidea planata* Müll. Arg.

This species, described from soil in Australia, has a thin greyish-white tesselate thallus encrusting the soil and bears immersed to adnate apothecia. As with many of J. Müller's species of Australian lichens, *L. planata* may well be synonymous with another species of wider distribution.

32. *Lecidea psammophila* (Müll. Arg) Zahlbr.

This species, described from soil in Australia, has cream or greyish-brown squamules with crenate margins, and is commonly fertile in the study area. Müller commented that this species was close to *Psora glauca* Tayl.. Although the type material of *L. psammophila* in the Herbarium of the Botany Department, University of Adelaide, is badly damaged, the material found in the study area matched it.

33. *Lecidea* sp.

This species, found only once, had a crustose thallus of thick, somewhat convex aereoles. The apothecia were sessile upon the squamules. This may be only a form of *L. psammophila* with very crowded squamules.

34. *Parmelia amphixantha* Müll. Arg.

This foliose species occurs on soil in Australia and New Zealand, and is easily distinguished by its relatively narrow dichotomising lobes (1-2mm broad) and sparse black rhizoids below. Material is very rarely fertile. Corralloid branches occasionally develop at the centre of the rosette.

35. *Parmelia australiensis* Cromb.

This species, recorded only for Australia, is similar in appearance to *P. vagans* Nyl. The thallus is quite free of attachments to the soil, its distorted grey-green thallus forming clumps up to 6 or 7cm in diameter lying free on the surface. W.A. Weber, (pers. comm.) suggested that this may only be a detached modification of *P. conspersa*.

36. *Parmelia conspersa* Ach.

This cosmopolitan species usually occurs on rocks, but has been found on hard soil at a number of locations in the study area. On soil the thallus is atypical, the lobes becoming somewhat convex and rather thicker and darker in colour than normal. Individual thalli have been found with lobes on both soil and rock; the lobes on rock show the typical form.

37. *Parmelia molliuscula* Ach.

This widespread species occurs in a wide variety of forms in the study area. One extreme form has lobes so strongly convex, that they are rolled into a cylinder; the other extreme intergrades with *P. conspersa*. Material in the Botany Department, University of Adelaide, determined by J. Müller as *P. congruens* Ach., matches the intermediate forms of *P. molliuscula* found in the study zone. Some of the material referred to this species may be identical with *P. distorta* Kurok.

38. *Parmelia pulla* (Neck.) Ach.

Probably this species is more commonly known as *P. prolixa* (Ach.) Rohl., a later synonym of the name used here. This brown species of *Parmelia* is more common on rocks than soil, but occurs in the study area on firm soils. It is possible that two species are intermixed under this name in the study area.

39. ? *Rinodina orbata* (Ach.) Wainio.

This determination is open to question, only one depauperate dirty-brown thallus being found. The apothecia have a thalloid exciple that sometimes disappears leaving only the black apothecial disk.

40. *Siphula coriacea* Nyl.

The *Siphula* collected from the study area is identical with the collection of *S. caesia* Müll.Arg. held in the Botany Department, University of Adelaide apparently as type material. However there seems to be no real difference between *S. caesia* and *S. coriacea* Nyl., so the older name has been used. The material collected has short, greyish, bullate lobes with somewhat crenate margins. The thalli penetrate deeply (often 2cm) into the soil and stand more or less diagonally out of it, forming rosettes up to 4cm across.

41. *Synalissa* Th. Fr.

Specimens placed in this genus are minute (less than 1mm diam.) thalli, usually aggregated in clumps up to 1cm diameter. During early stages of the study *Synalissa* was confused with *Collema*. The determination is in some doubt, the material perhaps being referable to the genus *Peccania* Forss. Because of its minute size it is probable that this species has been overlooked in collections from some locations in the study area.

42. *Toninia caeruleonigricans* (Lightf.) Th. Fr.

This species, common in arid areas around the world, has small (up to 2mm diam.) bullate squamules, variably pruinose and sculptured. Apothecia are frequently larger than the squamules supporting them. This species shows great variety not only in pruinosity and depth of sculpture, but in size of squamules and apothecia. In the study area almost pure patches of this species occur up to 10cm. across.

(2) A key to lichens in the study area

This key was prepared to allow determination of lichens from soil within the study area. Only material collected for the present study has been used in its preparation.

Lichens from the area, once determined, were re-investigated for useful taxonomic characteristics. Some characters served readily to distinguish taxa; others were less readily discerned or had less taxonomic power. The key was based on the former type of character. Therefore, the microscope, essential in "natural" keys to lichens, is usually not required until late in the key as macroscopic features were emphasized. In most cases, sterile material can be determined from the key.

A glossary of terms used in the key will be found in Fink (1935), hence is not duplicated here.

The key is arranged in three sections, one for lichens with blue-green algae (Section A) and two for lichens with green algae (Sections B and C). One of the sections for lichens with a green algal symbiont (phycobiont) is to allow determination of sterile, whitish crustose specimens (Section C); the other section (Section B), allows determination of all other material. Determinations of sterile white materials are difficult, but the key was shown to correctly place fertile material of the species included.

It must be emphasized that this key ought not to be used with material collected outside the study area, as it need not even indicate a taxonomic affinity, but merely a superficial similarity.

Ultimately, the value of any key is its reliability and ease of use: to this end the key and specimens were submitted to a graduate student who had no prior experience in determining lichens. His experience showed that the key worked easily and reliably.

ARTIFICIAL KEY TO THE SPECIES OF LICHEN ON SOIL IN THE STUDY AREA

I. Phycobiont a blue green alga...............Section A

I. Phycobiont a green alga.................... II

II. Thallus sterile and crustose, white, grey or sordid but not yellow or orange.....Section C

II. Thallus foliose or fruticose or a fertile crust or squamules or any yellow or orange crust...............................Section B

Section A

1. Thallus glistening and gelatinous when wet, colour very dark olive-green. Apothecia sessile. Spores 8 per ascus, thallus almost foliose or microfruticose..... 2

1. Thallus not gelatinous when wet, colour grey-green or brown. Apothecia immersed. Spores many (more than 8) per ascus, thallus squamulose (*Heppia*)................ 3

2. Thallus of moderate size (up to 2cm diam.) squamulose or foliose to fruticose, spores once septate, phycobiont *Nostoc*...*Collema coccophorus*

2. Thallus minute, microfruticose (barely 2mm high) packed into a crust, spores not septate, phycobiont *Gloeocapsa* or *Xanthocapsa* ....*Synalissa* or *Peccania*

3. Thallus a rosette of greyish squamules or lobes, almost foliose at times, apothecia rare, immersed.......................... *Heppia lutosa*

3. Thallus dark olive green, ovate or crenate squamules with a thickened margin, apothecia immersed, usually one per squamule....*Heppia ? polyspora*

Section B

1. Thallus foliose, fruticose, or, if crustose or squamulose, with podetia arising from the primary crustose or squamulose thallus.................................. 2.

1. Thallus crustose or squamulose, but without podetia.. 15.

2. Thallus foliose, but without podetia, either attached to the soil surface, or lying free on the soil surface................................ 3.

2. Thallus fruticose, or with podetia (or pseudo-podetia), the podetia either free or rising from a basal crust or squamules, either attached to the soil, or free on its surface.............. 10.

3. Thallus lying free on the soil surface, or entangled in litter on the surface, but not attached to the soil by rhizoids or hyphae.. 4.

3. Thallus attached to the soil surface at least lightly by rhizoids or hyphae...... 5.

4. The thallus perfectly dichotomous, rolling up into a ball when dry. Lobes green above, yellow below, rhizoids absent......................*Chondropsis semiviridis*

4. The thallus irregular, always contorted and convoluted. Upper surface greyish-green, the dark lower surface usually concealed within the deeply contorted lobes, rhizoids rare..........*Parmelia australiensis*

5. Marginal lobes rolling up from the extremities when dry, exposing the lower surface of the thallus........ 6.

5. Marginal lobes more or less appressed to the soil, never rolling up to expose the lower surface (*Parmelia* sp.).. 7.

6. Thallus green or brown above, dark brown or black below, with dark rhizoids and cyphellae, apothecia marginal.............*Heterodea müllei*

6. Thallus grey or grey-green above, white or grey below, rhizoids absent, cyphellae absent, apothecia not found in the study area..*Cladonia foliacea*

7. Thallus brown or olive-brown above, usually closely adnate to the soil.............*Parmelia pulla*

7. Thallus green or yellow-green above, variably adnate to the soil............................. 8.

8. Thallus neatly dichotomous, lobes narrow (2mm) and entire, lower surface pale with sparse, dark rhizoids........................*Parmelia amphixantha*

8. Thallus much branched, not neatly dichotomous, lower surface brown, rhizoids common and dark............. 9.

9. Lobes rolled into cylinders or somewhat convex......................*Parmelia molliuscula*

9. Lobes flat and appressed, or occasionally much distorted...................*Parmelia conspersa*

10. Thallus of discrete but not fenestrate podetia rising erect from the substrate, with or without basal squamules (*Cladonia* spp.)... 11.

10. Thallus of divaricating often fenestrate pseudopodetia, of anastomosing fruticose or subfruticose lobes, or of short, bullate lobes with bases deeply buried in the soil......... 13.

11. Podetia with well formed cups, proliferating further tiers of these from the centre or margin of the cups. ....*Cladonia verticillata*

11. Podetia either cupless or with more or less abortive cups, not arranged in tiers......................... 12.

12. Podetia short (up to 2cm), usually branching, the branches all in a vertical plane, somewhat distorted, decorticate, squamules usually at the base. ....*Cladonia subsquamosa*

12. Podetia usually quite long, branches not common, but when found, often geniculate, always cylindrical, partly decorticate, with many squamules at the base and up the podetia................*Cladonia* aff. *fimbriata*

13. Thallus of a green or brown divaricating pseudopodetia, hollow and, if fertile, fenestrate. The ends of sterile branches drawn out into a hair. Usually free on soil surfaces as the older portions rot away...*Cladia aggregata*

13. Thallus of white or grey solid lobes, these blunt or anastomosing, but not fenestrate, bases of lobes may be buried in the soil, pass into a crust, or sometimes be free on the surface.. 14.

14. Lobes short, bullate, forming a rosette on the soil surface, the bases of the lobes deeply buried in the soil, pseudocyphellae not found..*Siphula coriacea*

14. Lobes anastomosing, often indistinct, never buried in the soil, but often passing tinto a crust on the soil or nearby pebble, pseudocyphellae common on well developed forms.....................*Aspicilia calcarea* mod. *fruticosa*

15. Thallus or apothecia bright yellow or orange, at least when wet. If apothecia yellow or orange the thallus may be missing, yellow or grey-green or orange.................. 16.

15. Thallus and apothecia never yellow or orange, but may be white, grey, sordid, pink, brown or black................ 19.

16. Thallus of small (usually less than 1mm diameter) bullate, bright citric-yellow granules, often forming a scattered crust on the soil. Apothecia, if present, immersed with many spores per ascus...*Acarospora schleicheri*

16. Thallus of greyish granules, or if yellow, not granular but squamulose or crustose; the thallus is sometimes absent. Apothecia with an orange disk and a paler orange or yellow exciple.................................. 17.

17. Thallus of large, orange squamules, apothecia deep orange with a paler exciple.....*Caloplaca* sp.

17. Thallus missing, crustose or granular, grey, or citric-yellow if wet. Apothecia orange with a yellow exciple................................. 18.

18. Thallus forming a small (1cm diameter) white or pale yellow crust on the soil, turning bright citric-yellow when wet, the surface mealy, marginal lobes not prominent, apothecia rare, but with a deep orange disk and a yellow exciple. ....*Fulgensia bracteata*

18. Thallus greyish, often disappearing, apothecia small (less than 1mm diameter), with an orange disk and yellow exciple....*Caloplaca subpyracella*

19. Thallus squamulose.

[The squamules sometimes packed to apparently form a crust, but the margins then never show marginal lobes, and the crust is never really complete. The squamules may be thin or bullate, entire or crenate, colours include black, sordid white, grey, brown, green or pink]...................................... 20.

19. Thallus crustose.
[The crust sometimes with granules some distance from the general margin, marginal lobes formed at times, the crust sometimes cracking into aereolae. The crust may be quite thick and more or less free from the soil, or very thin and barely distinguishable from the soil, colours vary from white and sordid to grey, grey-green or brown]... 27.

20. Squamules green or grey-green above, when dry rolling up at the edges to show a white lower surface........................*Cladonia* sp. (squamules)

20. Squamules pink, cream, brown or black above, not rolling up at the edges......................... 21.

21. Squamules pink, sometimes with a white margin of varying width...........*Lecidea decipiens*

21. Squamules white, sordid, brown, grey or black, but showing no pink colouration............. 22.

22. Squamules brown or pale grey, with a smooth upper surface, asci in perithecia which may be seen to open through pores in the upper surface......................... 23.

22. Squamules white, sordid, grey or almost black, asci in apothecia not perithecia. 24.

23. Squamules brown, ovate, entire, rhizoids many and fine. The spores are non-septate and small, usually 8 per ascus..............................*Dermatocarpon lachneum*

23. Squamules brown or grey, ovate, sometimes crenate, more or less umbilicate, the rhizoids always thick and long (often several centimetres long) penetrating deep into the soil. The spores are large and muriform, usually two per ascus.......................*Endocarpon pusillum*

24. Squamules dark grey or almost black, often cracked into a shallow, reticulate pattern, more or less pruinose, the squamules bullate. The apothecia may be as large or larger than the squamules supporting them. ....*Toninia caeruleonigricans*

24. Squamules pale, grey or sordid, thin, not bullate. The apothecia small relative to the size of squamule..........25.

25. Squamules grey (or grey-brown at times) the upper surface deeply cracked into solid angles, giving the upper surface a crystalline appearance, the margins entire.................*Lecidea crystallifera*

25. Squamules sordid, the upper surface smooth, the margins entire or crenate...........................26.

26. Apothecia immersed or erumpent, the spores two celled and dark, margins of squamules entire....................*Buellia subcoronata*

26. Apothecia sessile, the spores hyaline, margins of squamules entire or crenate. ....*Lecidea psammophila*

27. The thallus a white, grey, or grey-green crust, apothecia small, (less than 1mm diam) with many spores in each ascus.. 28.

27. The thallus a white, grey or sordid crust with spores 8 in each ascus, the apothecia small or large (up to 3mm diam).. 30.

28. The thallus white, grey-brown or greenish, often heavily pruinose forming thick plaques (less than 3cm diam) with small, but still distinct marginal lobes. The apothecia are immersed in the central aereoles. ....*Acarospora smaragdula*

28. The thallus sordid grey, thin and scurfy and apparently eroded, the margins indistinct, without marginal lobes, apothecia immersed to more or less sessile, depending on the degree of erosion............... 29.

29. A thalloid exciple occurring round the apothecia................*Acarospora* sp.

29. No thalloid exciple present around the apothecia................*Biatorella* sp.

30. Thallus an extensive white or greyish crust, often more or less separate from the soil, the thallus distinctly aereolate, but without marginal lobes, the spores multiseptate (*Diploschistes*).......... 31.

30. Thallus a white or sordid crust, closely attached to the soil, with or without aereolae, or scattered aereolae beyond the thallus margin which may be lobed, spores not septate or once septate......... 32.

31. Apothecia minute (less than 1mm diam) immersed, sometimes almost closed by the exciples, the thallus often grey and mealy................*Diploschistes scruposus*

31. Apothecia larger (up to 3mm diam) adnate, the disk open with an obvious thalloid exciple, the thallus usually white and rather chalky...................*Diploschistes ocellatus*

32. Spores once septate and brown............................ 33.

32. Spores once septate or non septate, but hyaline........... 34.

33. Thallus a very white crust, sometimes almost sub-fruticose, apothecia with a proper exciple. ....*Buellia epigaea*

33. Thallus a sordid crust, rather scurfy, apothecia with a thalloid exciple.............? *Rinodina* sp.

34. Apothecia with a thalloid exciple.................. 35.

34. Apothecia with a proper exciple.................... 36.

35 Apothecia immersed with a bluish pruinose disk, the thallus a rather mealy, granular crust, spores often only two per ascus. ....*Aspicilia calcarea* (crustose form)

35. Apothecia adnate with a brown disk, the thallus a smooth, aereolate crust, the exciple coloured like the thallus, spores usually 8 per ascus.................*Lecanora atra*

36. Apothecia erumpent in a crust of rather scattered, slightly bullate granules. ....*Lecidea coarctata*

36. Apothecia immersed or sessile on a somewhat tesselate, aereolate crust..................... 37.

37. Apothecia more or less sessile or immersed in a rather thin crust..*Lecidea planata*

37. Apothecia sessile on a crust with thick, convex aereoles.........*Lecidea* sp.

Section C

1. Thallus determinate or effigurate, but not with scattered aereolae beyond the margin............. 2.

1. Thallus indeterminate with scattered aereolae beyond the margin.................................... 4.

2. Thallus with distinct marginal lobes ....*Acarospora smaragdula*

2. Thallus of discrete aereolae to the margin, but not with marginal lobes................. 3.

3. Thallus rather thin and mealy, often somewhat greyish, aereolae small (less than 1mm)...............*Diploschistes scruposus*

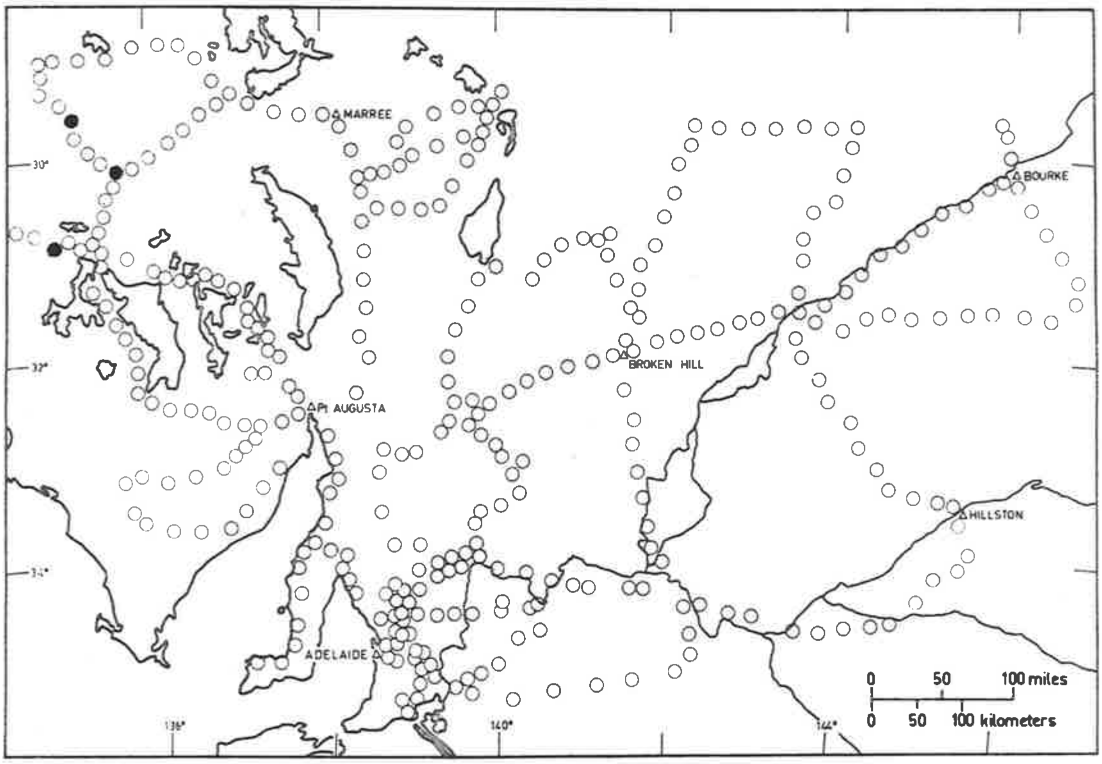
3. Thallus relatively thick, chalky rather than mealy, aereolae often more than 1mm. across..................*Diploschistes ocellatus*

4. Thallus of smooth, bullate, white, discrete globules.....................*Lecidea coarctata*

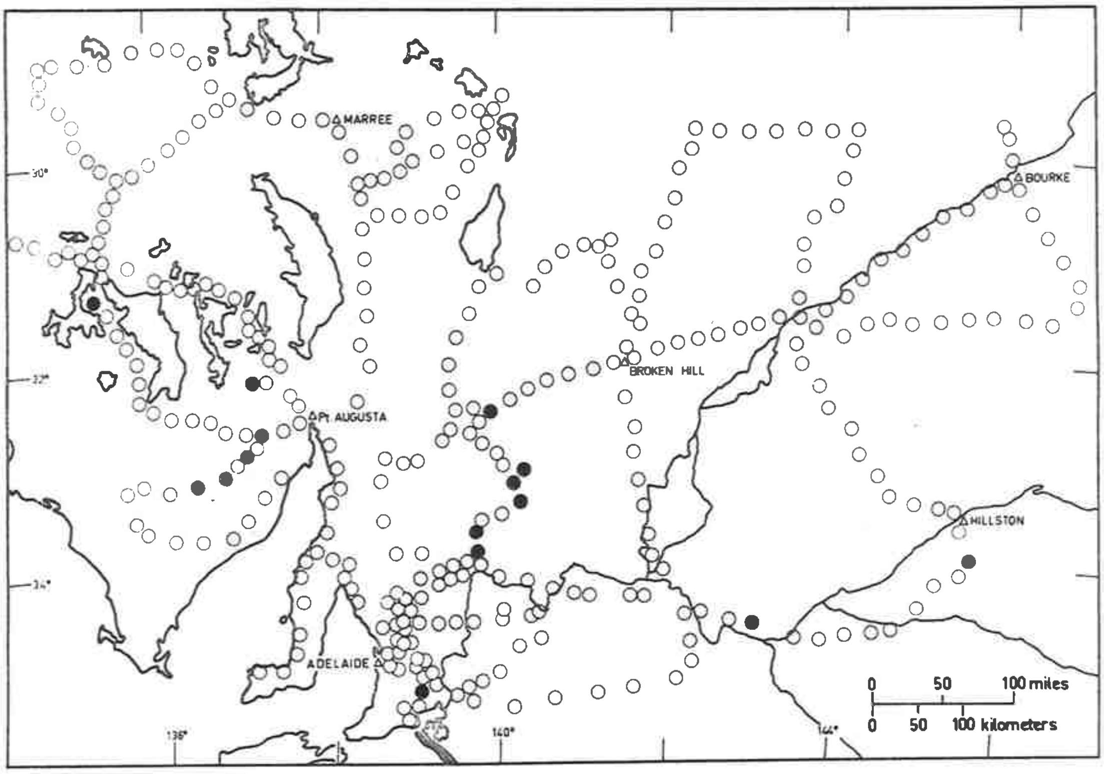
4. Thallus of coalesced whitish or slightly discoloured often mealy aereolae.........*Aspicilia calcarea*

4. DISTRIBUTION MAPS

In the section which follows the distribution of each of the taxa discussed above is mapped. These maps are based only on information collected during the present study, and indicate not only locations at which each taxon was found, but those where the taxon was not found. In all the maps, presence of the taxon named is indicated by filled circles and absence by open circles.



Acarospora schleicheri



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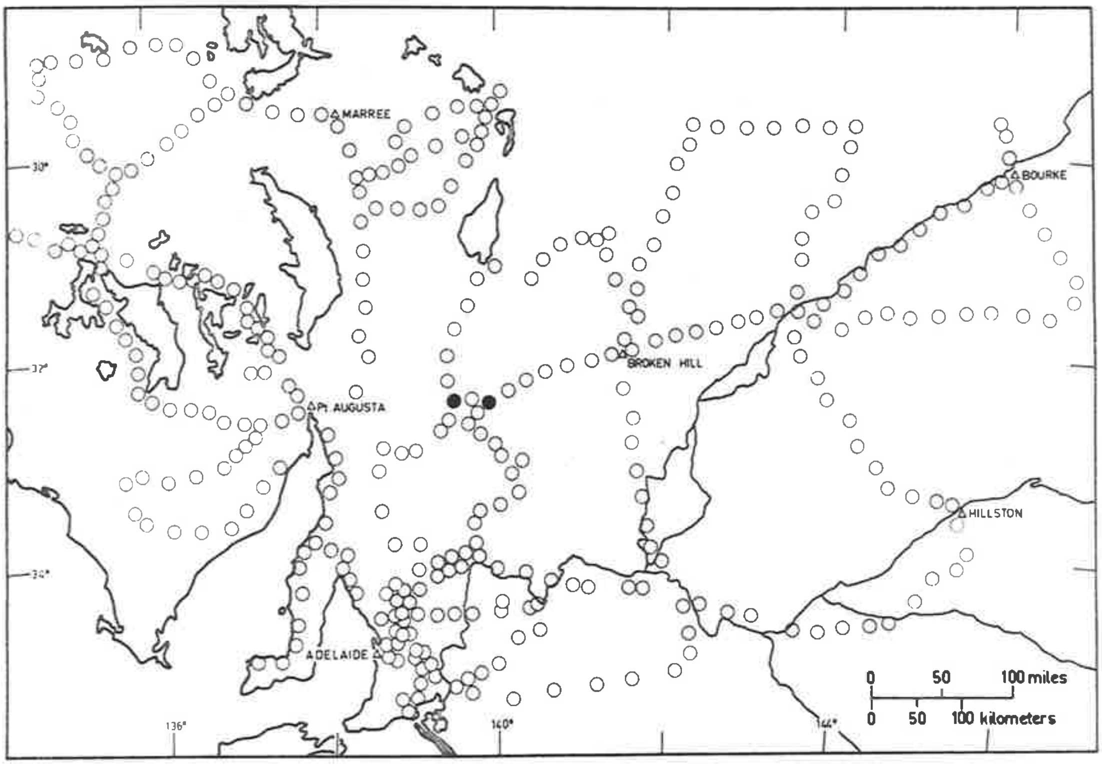

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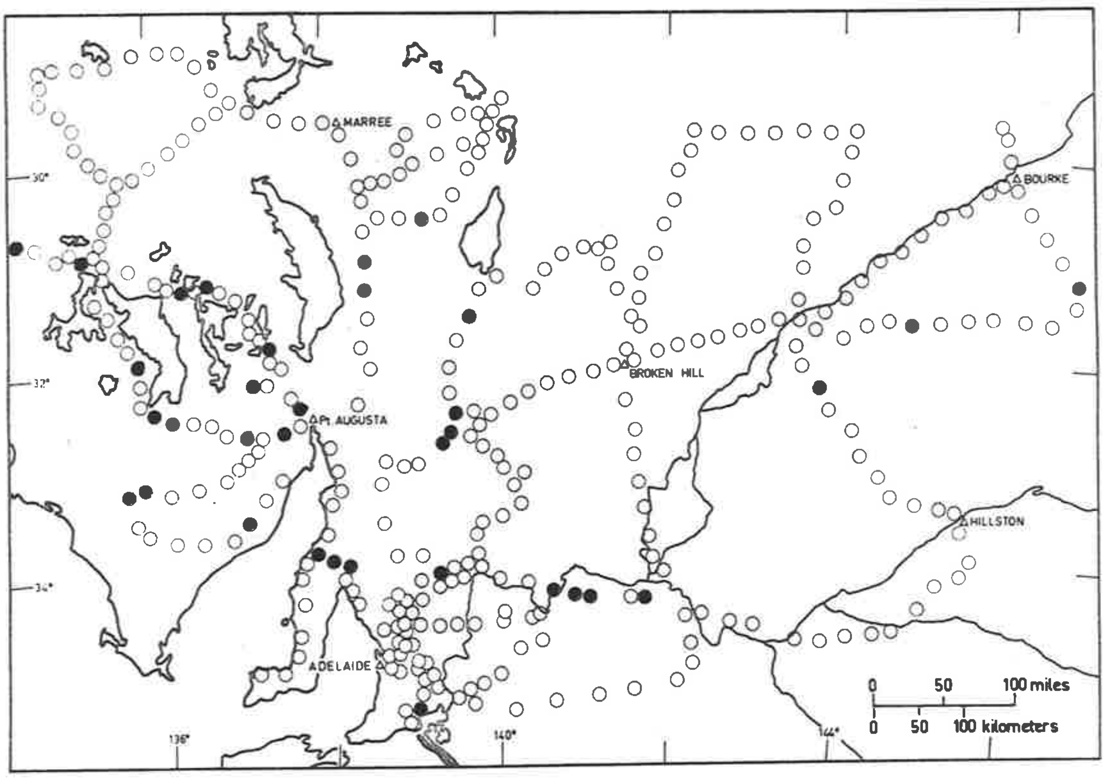

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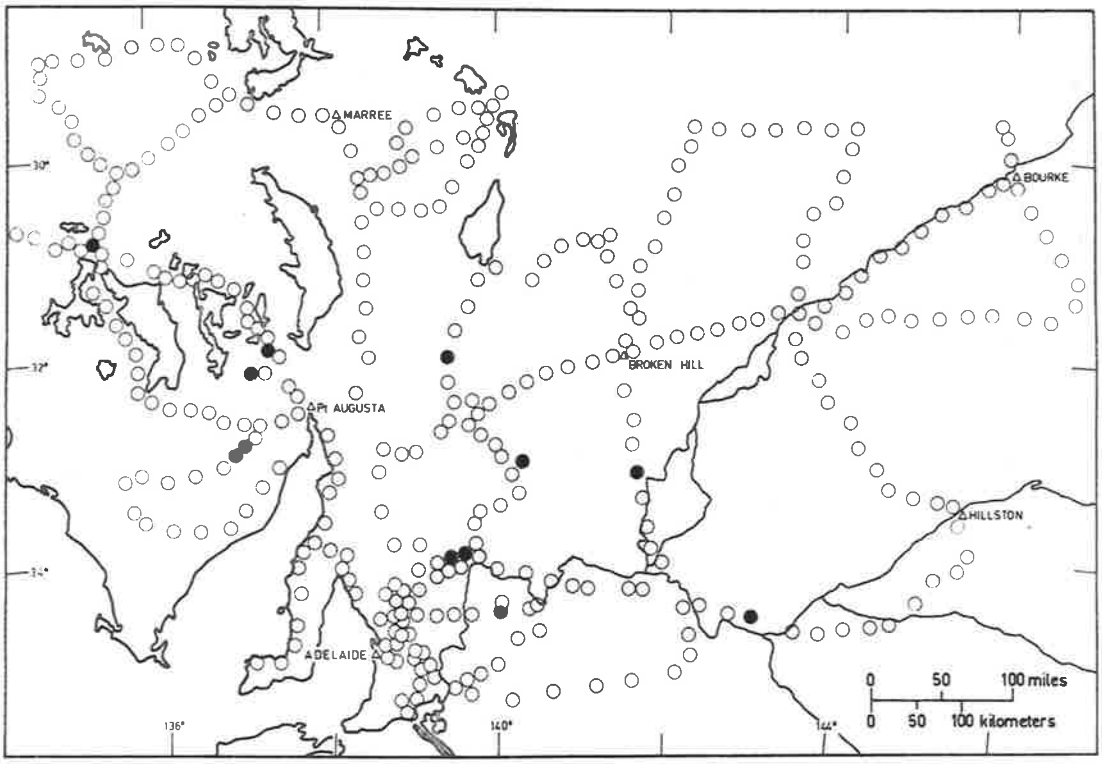
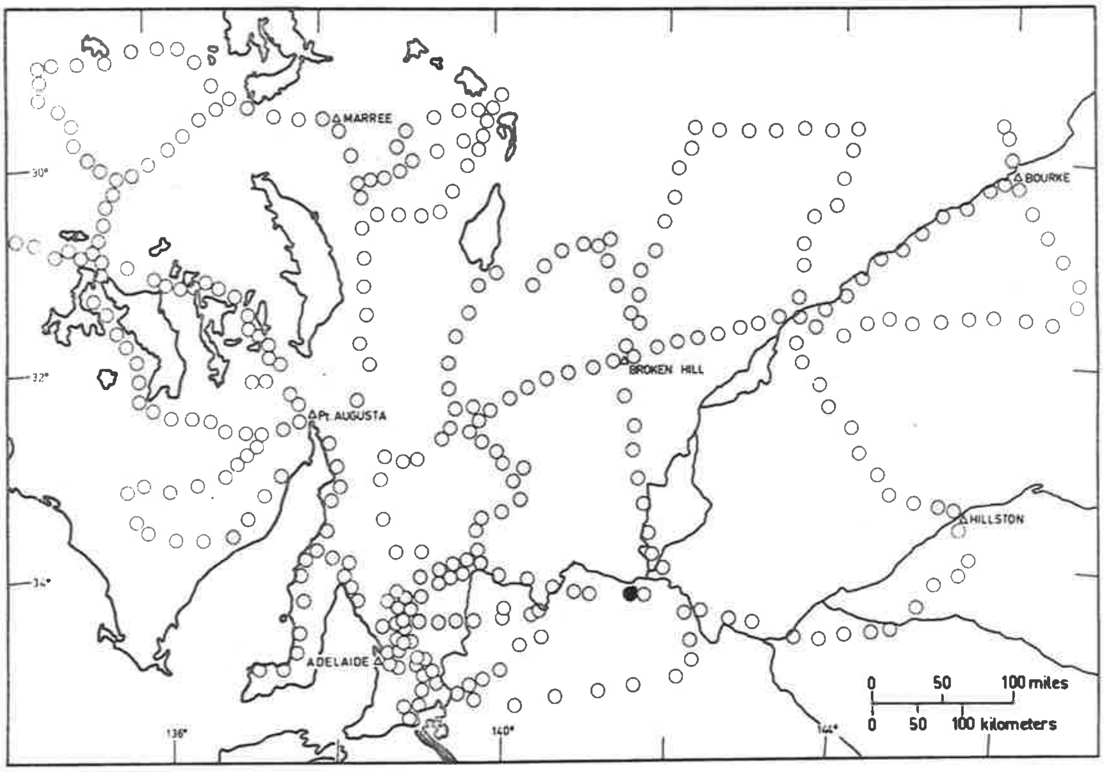
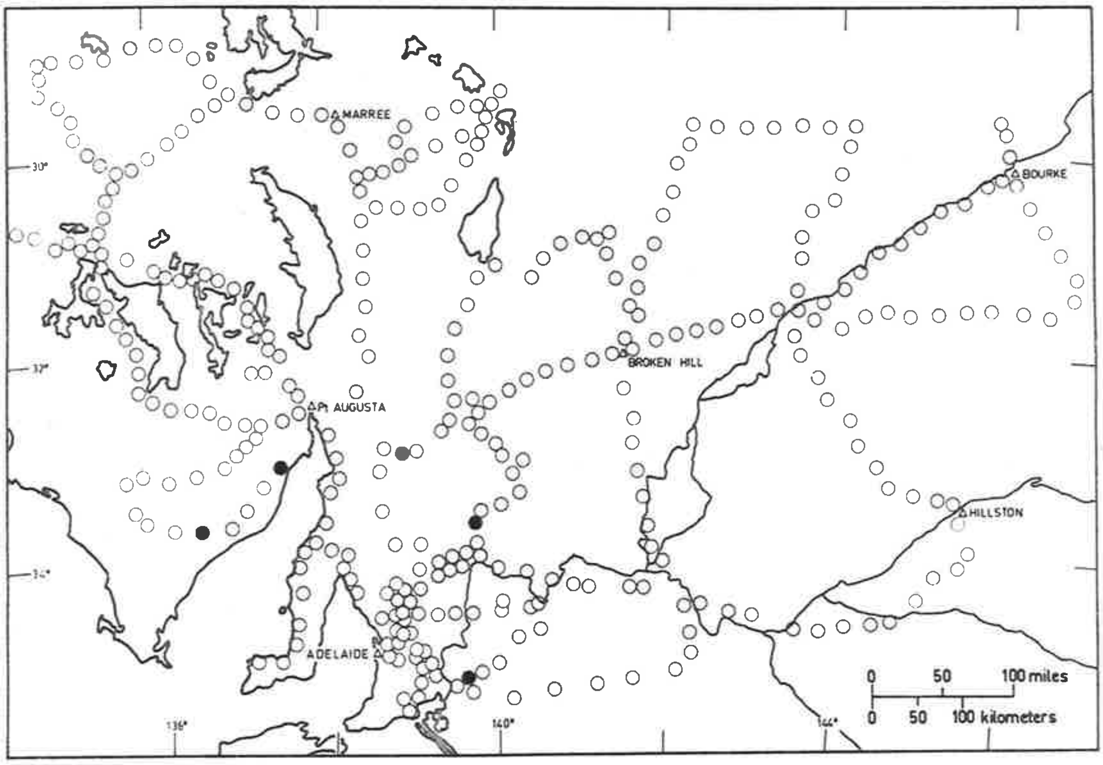


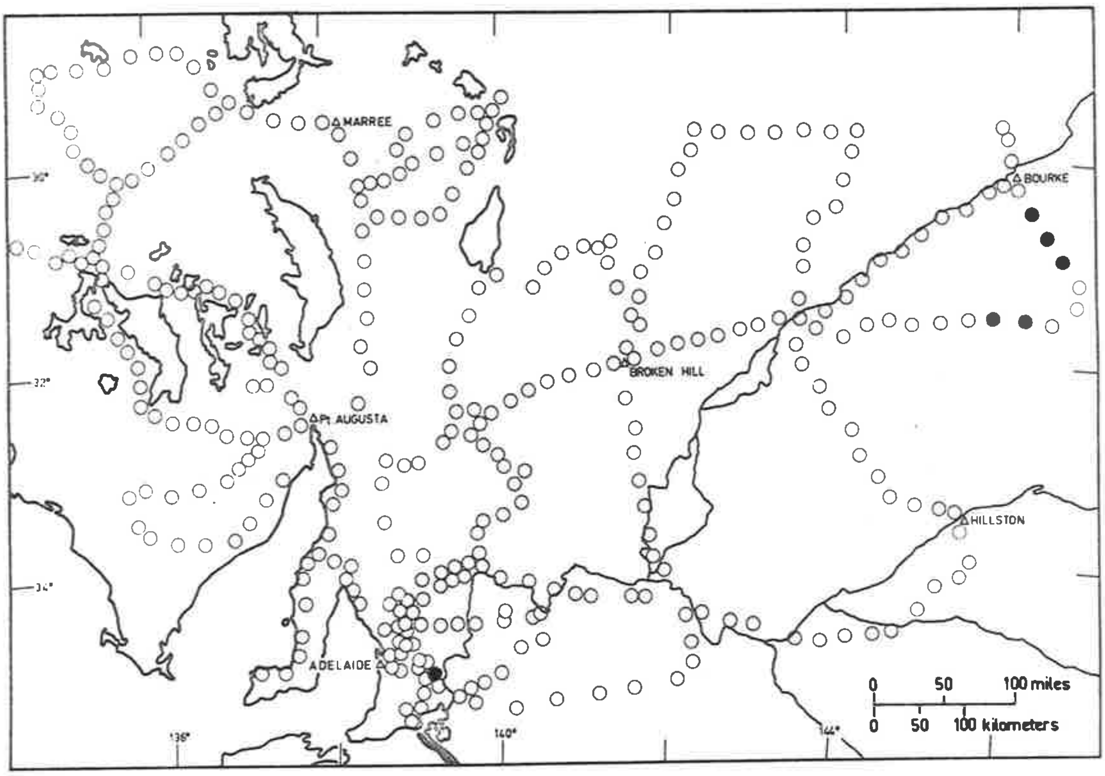
Aspicilia calcarea mod. *fruticosa*



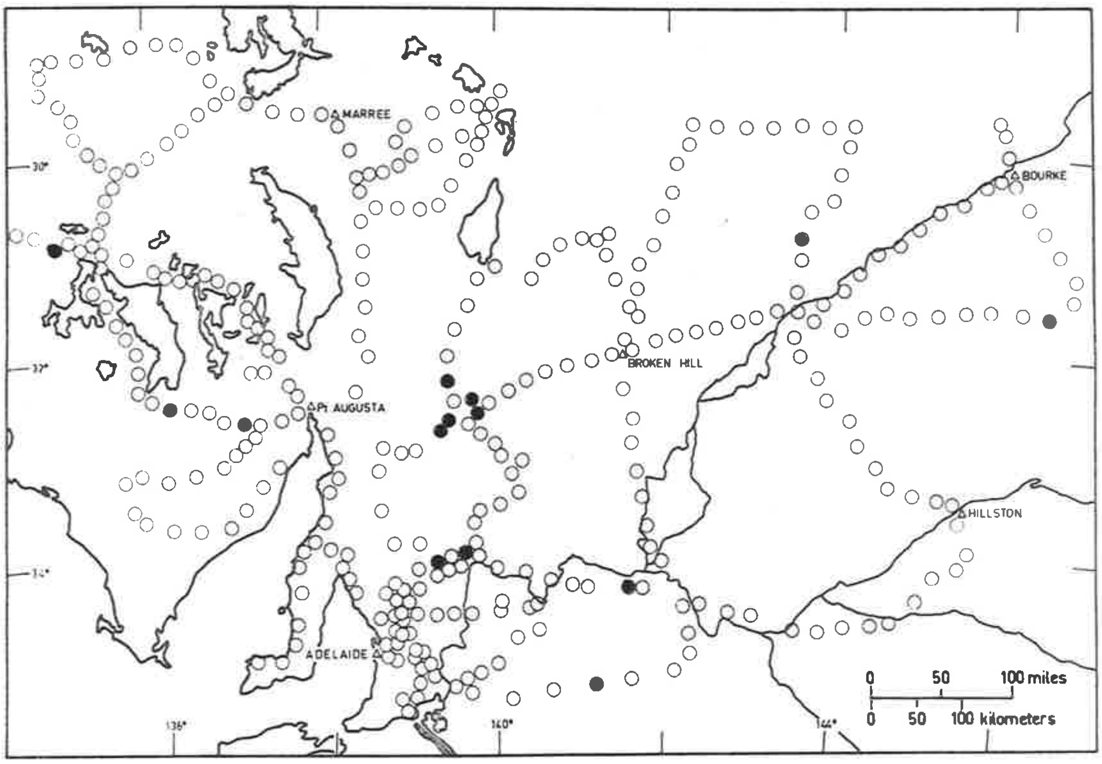
? *Biatorella* sp.



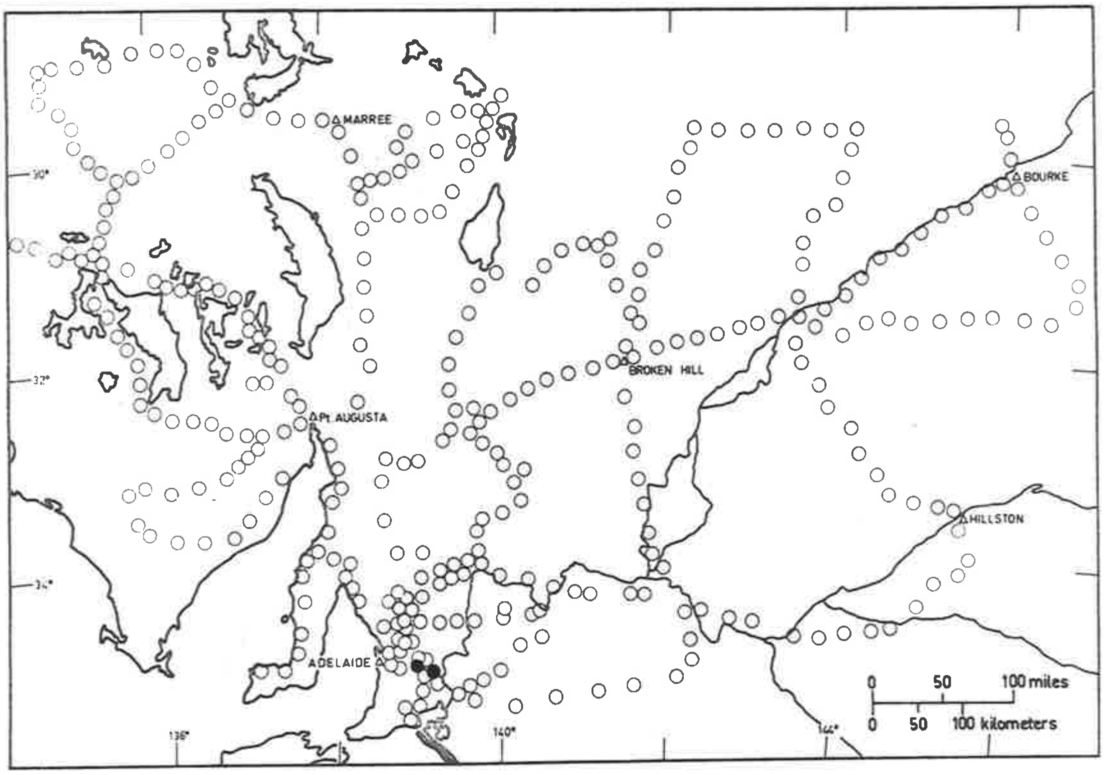
Buellia epigaea



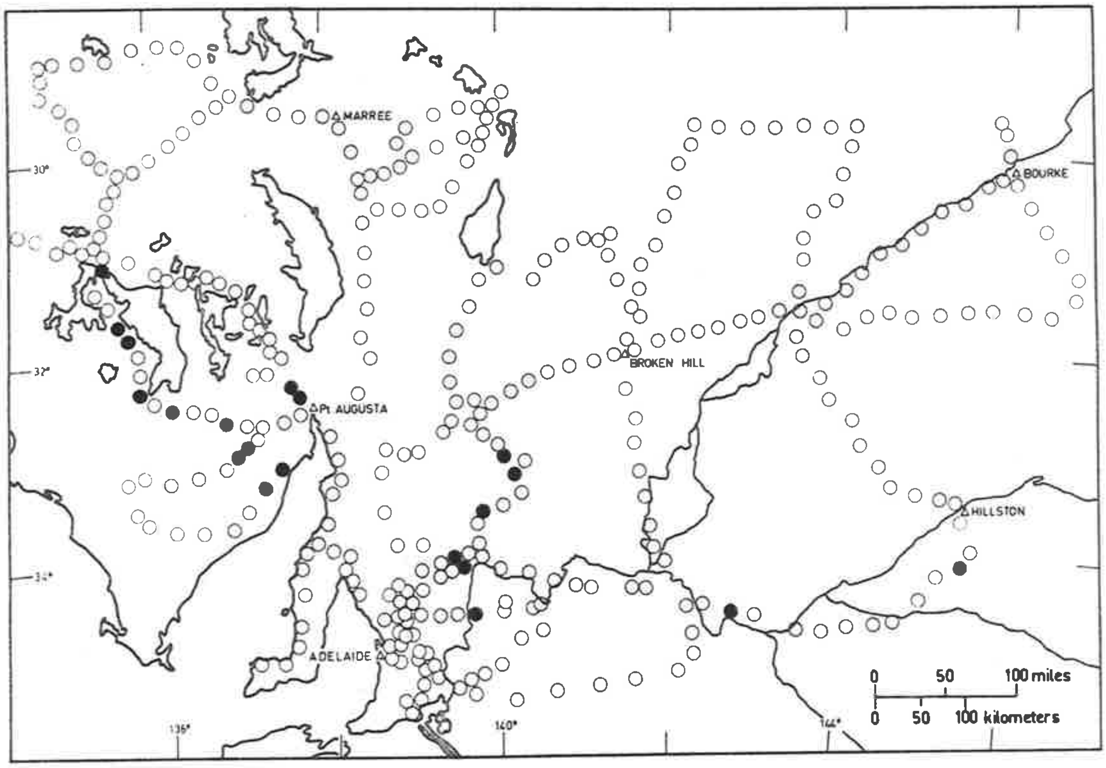
Buellia subcoronata



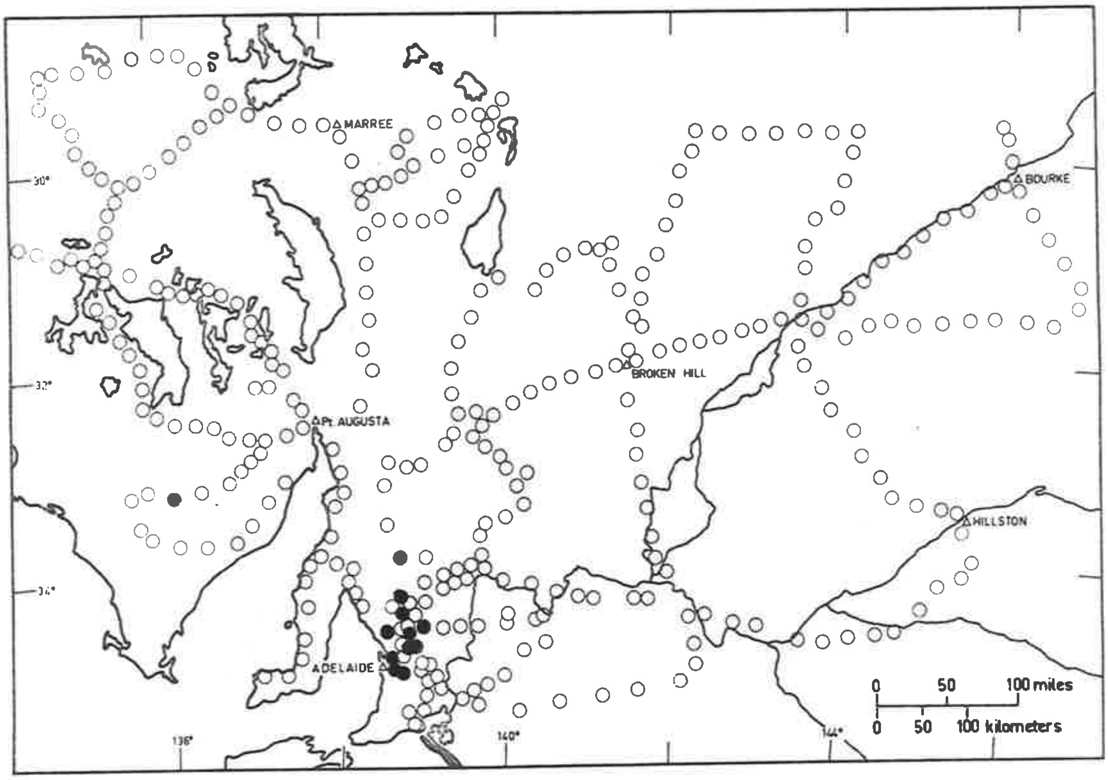
Caloplaca subpyracella



Caloplaca sp.



Chondropsis semiviridis



Cladia aggregata

CHAPTER V

COMMUNITY STRUCTURE AND DISTRIBUTION

Determination of species groupings, and the spatial distribution of these groupings have been dealt with extensively in the literature (Goodall 1962, McIntosh 1967). Before the complete data block from the field study had been assembled an association analysis (Williams and Lambert 1959) was executed, and this indicated a relatively continuous interaction between the species found with no significant negative associations occurring. This suggested that analyses which treated the lichen vegetation as a continuum would be more meaningful than divisive classifications.

With this in mind, the species groupings and distributions were studied by using "Influence Analysis" (Lange 1968) and "Principal Components Analysis" (Orloci 1966). Species were also sorted into regional groups on the basis of the distribution patterns shown in the maps presented in Chapter IV. In this chapter the two numerical approaches and the regional grouping are considered. Results from all three approaches are discussed, and a series of species-groups used in further studies proposed.

1. INFLUENCE ANALYSIS

(1) Method

Influence analysis is a species classification and site ordination technique based on association analysis. It has been used previously by Lange (1968) on heath vegetation and by Barker and Lange (1969) on grazed arid woodland. In this study as no taxon was present in more than half the locations, and only 10 of the 42 taxa occurred in more than 10% of the locations, Influence Analysis computation of interspecific association has been modified.

$Chi_{\text{association}}$ value calculations are based upon those sites in which either or both members of the species-pair in question occurs. This is to avoid generation of spuriously high $chi_{\text{association}}$ values due to mutual absence of the species from most locations. The statistic *chi* was used instead of the more familiar chi^2, as *chi* has a sign, indicating positive or negative association, but chi^2 does not. A computer programme to calculate $chi_{\text{association}}$ values for each species pair and to order the species pairs on *chi* values was written and run on the CDC 6400 computer at the University of Adelaide. Species were then grouped in an agglomerative manner into nodes on the basis of positive interspecific association, starting at the highest attained level of significance, and progressively lowering the significance level for admission into a node until a probability level of 0.001 was reached ($chi_{1\ d.f.} > 3.3$). The number of species which are members of a given nodal group and present at a given site is the influence rating assigned to that site, for the node in question.

(2) Results

A large number of significant interspecific associations were demonstrated by the association analysis (Table 5.1); all were positive. The development of nodes amongst the associated species as the significance level for admission to the nodes was progressively lowered is shown in Figure 5.1. This method of analysis resulted in three nodes at a significance level of $chi > 3.3$ ($p < 0.001$).

The implications of the associations were brought out by examining the field distribution of the interacting species after the approach of Lange (1968). Maps were constructed to illustrate the expression of each node. Using node B as an example, each of the sites studied could be assigned an influence value from zero to eleven according to the number of nodal species it contained. The influence values for each site, for each node and sub-node are listed in Appendix 3. It was apparent that isolines could not be drawn because of variation in the influence values in any area. Therefore, sites were arbitrarily differentiated into "high" influence

TABLE 5.1.

The significant interspecific associations detected by Influence Analysis, grouped to bring significant values close to the principal diagonal. The lettering in the sections indicates the nodal or subnodal group these species belong to.

Group	Species	*Rinodina* sp.	*Biatorella* sp.	*Caloplaca subpyracella*	*Acarospora smaragdula*	*Buellia epigaea*	*Diploschistes ocellatus*	*Aspicilia calcarea* mod. fr.	*Parmelia molliuscula*	*Parmelia australiensis*	*Chondropsis semiviridis*	*Fulgensia bracteata*	*Lecidea crystallifera*	*Lecidea decipiens*	*Toninia caeruleonigricans*	*Cladia aggregata*	*Cladonia fimbriata*	*Cladonia verticillata*	*Cladonia* squamules	*Siphula coriacea*	*Heterodea mülleri*	*Buellia subcoronata*	*Caloplaca* sp.	*Lecanora atra*	*Lecidea coarctata*	*Lecidea psammophila*	*Lecidea* sp.	*Parmelia pulla*	*Cladonia foliacea*	*Parmelia amphixantha*	*Diploschistes scruposus*	*Lecidea planata*
A	*Rinodina* sp.		10.6	3.6																												
A	*Biatorella* sp.																															
A	*Caloplaca subpyracella*																															
B_1	*Acarospora smaragdula*						4.1	3.6																								
B_1	*Buellia epigaea*						3.8		5.3																							
B_1	*Diploschistes ocellatus*							4.8	8.9	6.5	6.5	3.5																				
B_1	*Aspicilia calcarea* mod.fr.									3.8																						
B_1	*Parmelia molliuscula*									6.8	6.8																					
B_1	*Parmelia australiensis*										9.2																					
B_1	*Chondropsis semiviridis*																															
B2	*Fulgensia bracteata*												5.0		3.7																	
B2	*Lecidea crystallifera*													3.5																		
B	*Lecidea decipiens*																															
B	*Toninia caeruleonigricans*																															
C_1	*Cladia aggregata*																4.1	4.6		4.8	6.1											
C_1	*Cladonia fimbriata*																															
C_1	*Cladonia verticillata*																			5.1												3.6
C_1	*Cladonia* squamules																			4.7	3.9				3.6	3.4					3.9	
C_1	*Siphula coriacea*																				4.3									35		
C_1	*Heterodea mülleri*																															
C_2	*Buellia subcoronata*																						4.1	4.6	5.0		6.0					3.7
C_2	*Caloplaca* sp.																							4.1		3.8						
C_2	*Lecanora atra*																									4.2						
C_2	*Lecidea coarctata*																									4.6		5.5				
C_2	*Lecidea psammophila*																															
C_2	*Lecidea* sp.																															
C_2	*Parmelia pulla*																														3.5	
C_3	*Cladonia foliacea*																													4.4		
C_3	*Parmelia amphixantha*																															
C	*Diploschistes scruposus*																															
C	*Lecidea planata*																															

ratings and "low" influence ratings.

Node B had three centres of development, Eyre Peninsula, northern Yorke Peninsula, and in the north of the Murray Basin in South Australia. Isolated high values also occurred elsewhere (Fig. 5.2).

Node C had one major centre of development in the Mount Lofty Range and areas west of the range in the Murray Basin (Fig. 5.3) where it overlapped part of the centre for node B.

Node A, because of low frequency of its species, could not be mapped meaningfully in this way.

If, instead of plotting the distribution of influence values for the terminal nodes, the influence values for the sub-terminal nodes were plotted, a different set of areas of maximal development was obtained. Of the six sub-terminal nodes, five were sufficiently frequent to permit meaningful mapping.

Node B_1 had centres of development on northern Eyre Peninsula, and in the Murray Basin (Fig. 5.4). Node B_2 was diffuse in its expression, being scattered across the south-western part of the study area (Fig. 5.5).

Node C_1 was most strongly expressed in the Mount Lofty Ranges (Fig. 5.6), Node C_2 on the drier eastern slopes of the range and in central New South Wales (Fig. 5.7) whereas Node C_3 developed too diffusely to map, but appeared to be stronger in its development in the Mallee areas of the Murray Basin.

FIGURE 5.1

The development of nodes as *chi* (level of significance) is lowered and new species admitted. The named nodes are discussed in the text, and the species in the nodes listed below with a key to the numbers on the figure.

NODE A

6	*Biatorella* sp.	Sub node A1
39	? *Rinodina orbata*	
9	*Caloplaca subpyracella*	

NODE B

2	*Acarospora smaragdula*	Sub node B1
7	*Buellia epigaea*	
11	*Chondropsis semiviridis*	
35	*Parmelia australiensis*	
37	*Parmelia molliuscula*	
23	*Fulgensia bracteata*	Sub node B2
29	*Lecidea crystallifera*	
30	*Lecidea decipiens*	
42	*Toninia caeruleonigricans*	

NODE C

12	*Cladia aggregata*	Sub node C1
15	*Cladonia verticillata*	
16	*Cladonia fimbriata*	
17	*Cladonia* squamules	
26	*Heterodea mülleri*	
40	*Siphula coriacea*	
8	*Buellia subcoronata*	
10	*Caloplaca* sp.	Sub node C2
27	*Lecanora atra*	
28	*Lecidea coarctata*	
32	*Lecidea psammophila*	
33	*Lecidea* sp.	
38	*Parmelia pulla*	
13	*Cladonia foliacea*	Sub node C3
34	*Parmelia amphixantha*	
21	*Diploschistes scruposus*	
31	*Lecidea planata*	

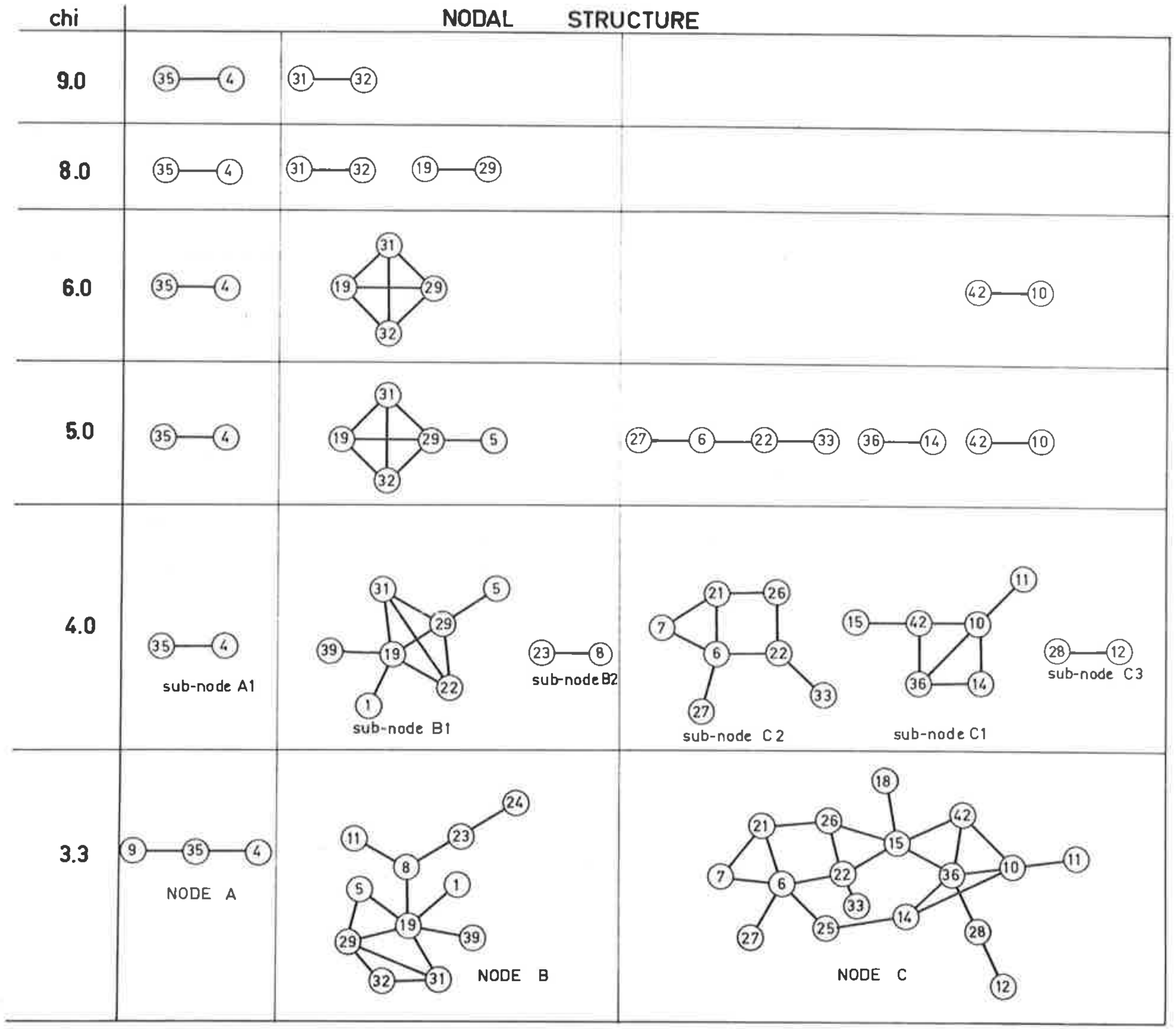
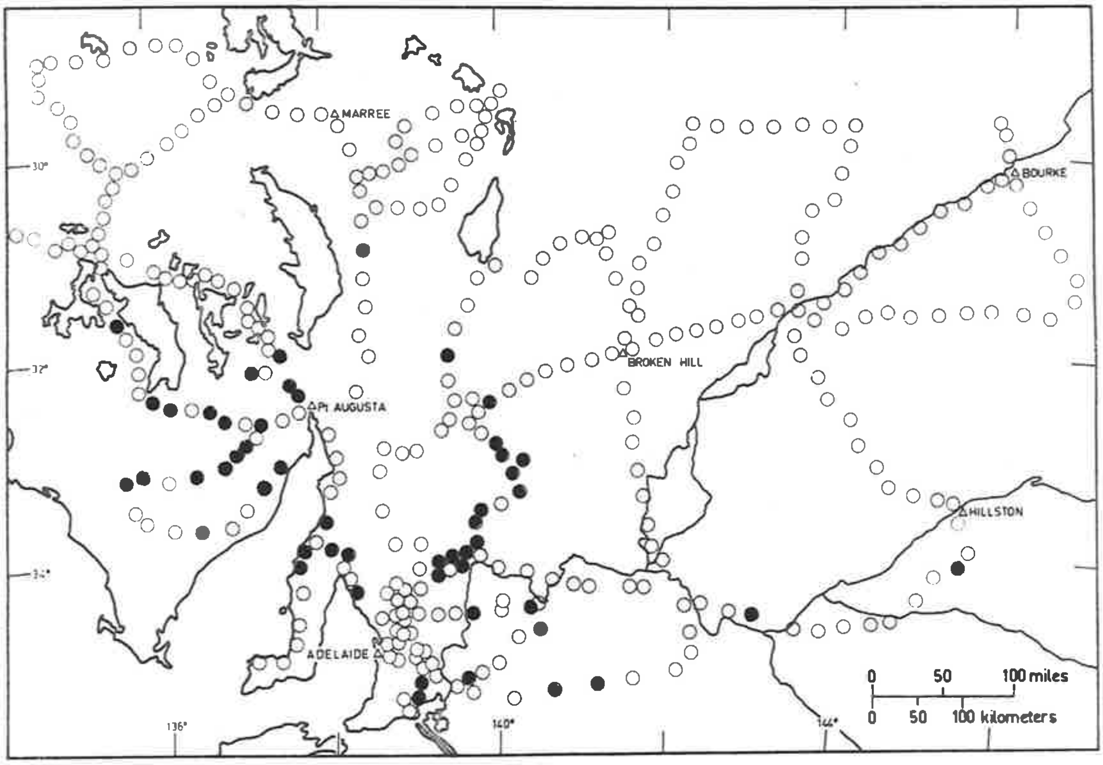

chi
NODAL STRUCTURE
9.0
8.0
6.0
5.0
4.0
3.3
sub-node A1
sub-node B1
sub-node B2
sub-node C2
sub-node C1
sub-node C3
NODE A
NODE B
NODE C

FIGURE 5.2

The distribution of sites with high influence values for node B. Filled circles represent sites with an influence value greater than or equal to four.

FIGURE 5.3

The distribution of sites with high influence values for node C. Filled circles represent sites with an influence value greater than or equal to four.


MARREE
BOURKE
30°
BROKEN HILL
32°
Pt AUGUSTA
HILLSTON
34°
ADELAIDE
0 50 100 miles
0 50 100 kilometers
136°
140°
144°

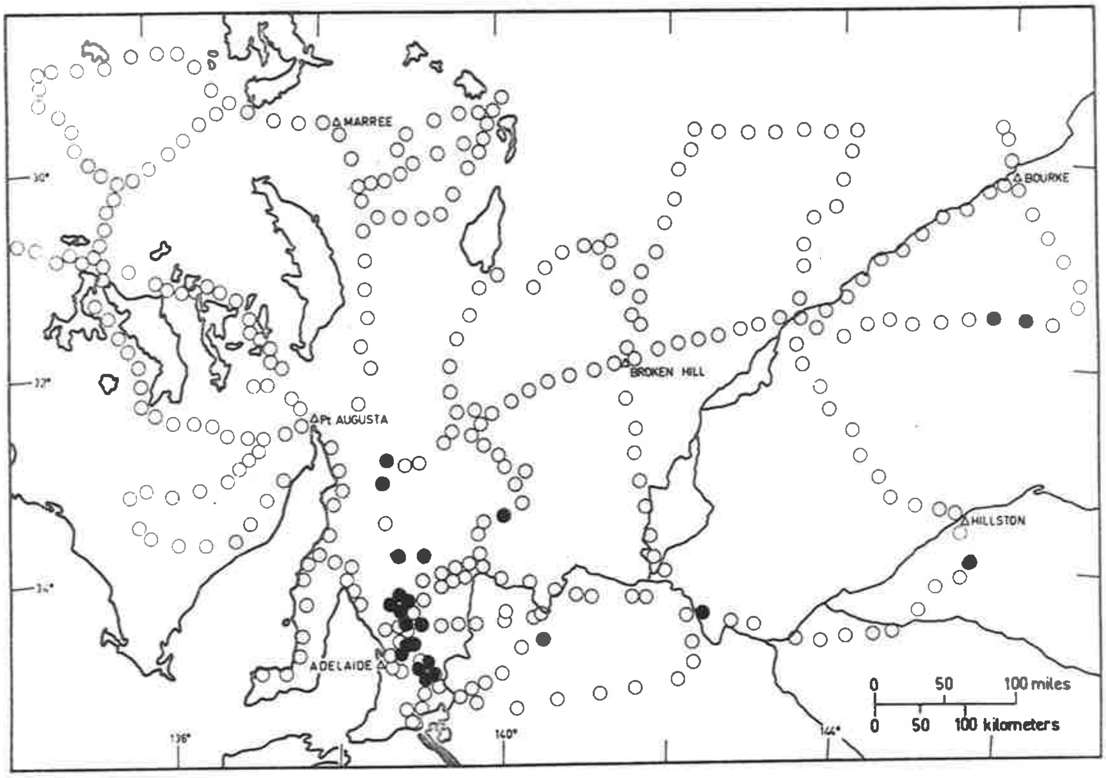
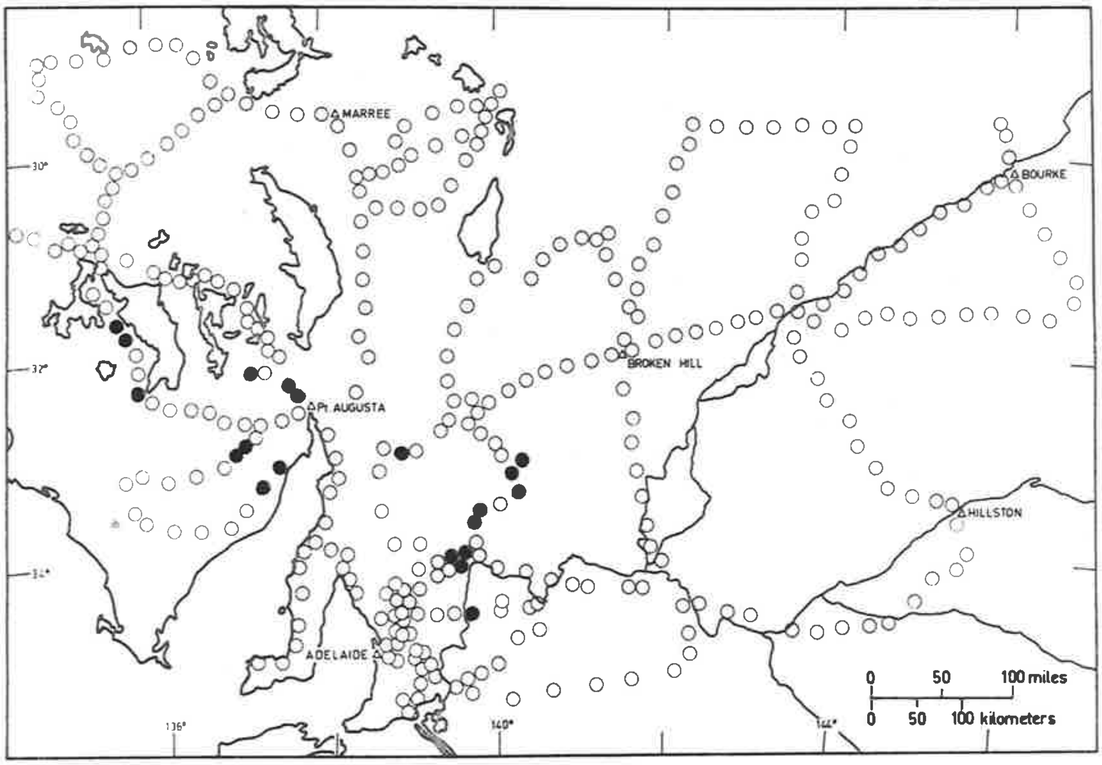

MARREE
BOURKE
30°
BROKEN HILL
32°
Pt AUGUSTA
HILLSTON
34°
ADELAIDE
0 50 100 miles
0 50 100 kilometers
136°
140°
144°

FIGURE 5.4

The distribution of sites with high influence values for node B1. Filled circles represent sites with an influence value greater than or equal to two.

FIGURE 5.5

The distribution of sites with high influence values for node B2. Filled circles represent sites with an influence value of two.


MARREE
BOURKE
BROKEN HILL
Pt. AUGUSTA
HILLSTON
ADELAIDE
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

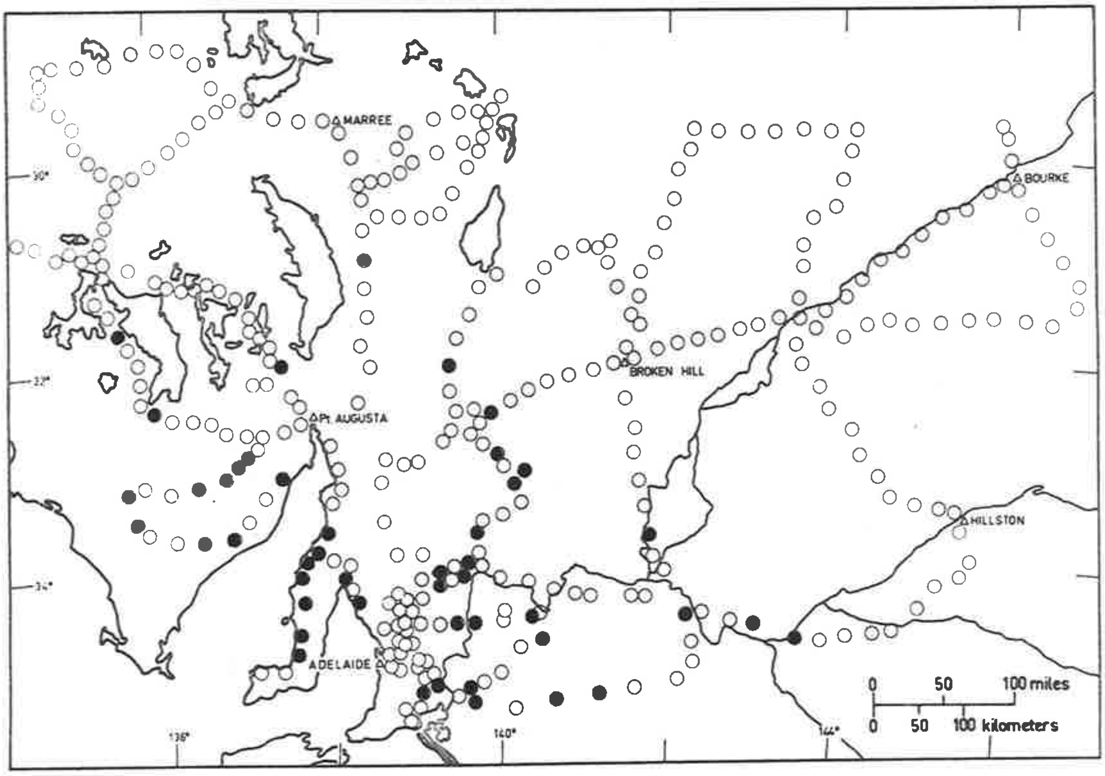
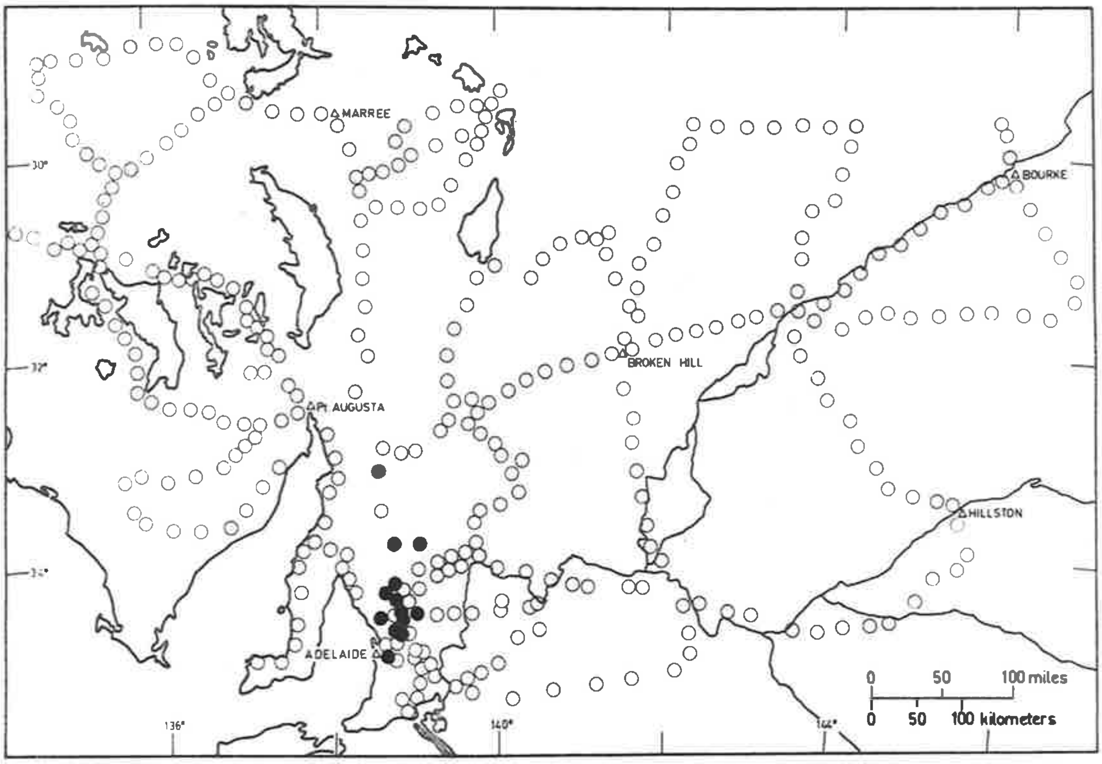

MARREE
BOURKE
BROKEN HILL
Pt. AUGUSTA
HILLSTON
ADELAIDE
30°
32°
34°
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

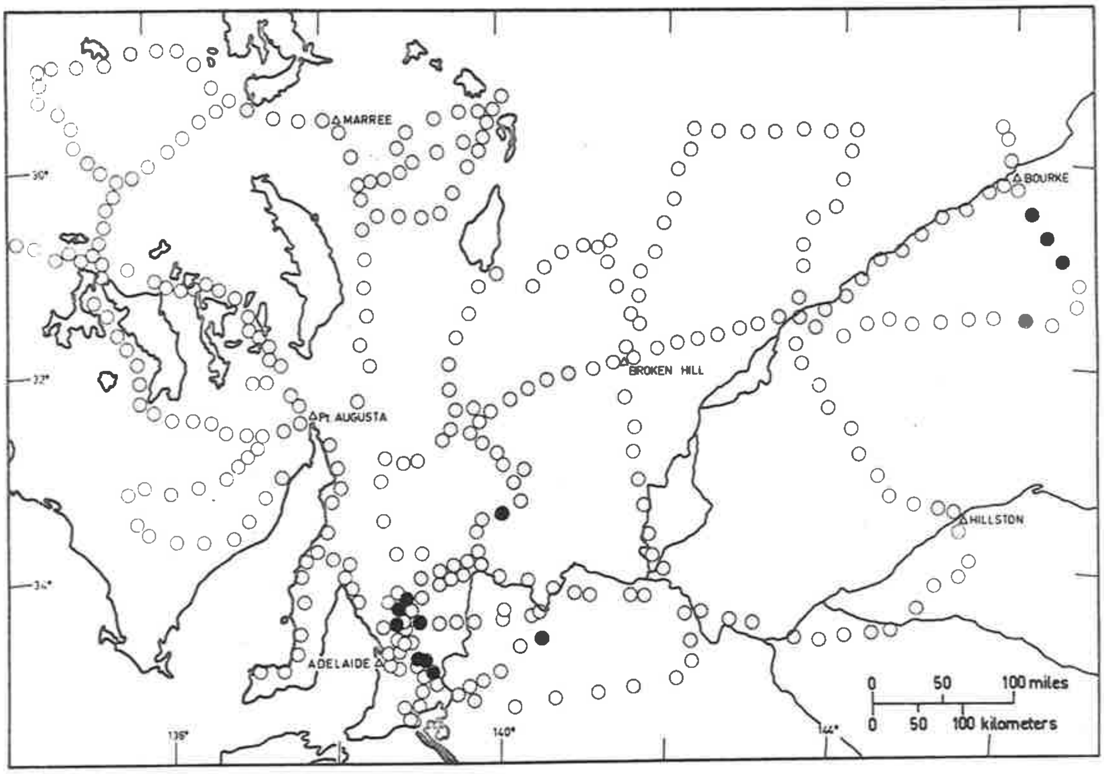
FIGURE 5.6

The distribution of sites with high influence values for node C1. Filled circles represent sites with an influence value greater than or equal to two.

FIGURE 5.7

The distribution of sites with high influence values for node C2. Filled circles represent sites with an influence value greater than or equal to two.


MARREE
30°
BOURKE
32°
BROKEN HILL
Pt. AUGUSTA
HILLSTON
34°
ADELAIDE
136°
140°
144°
0 50 100 miles
0 50 100 kilometers


MARREE
30°
BOURKE
32°
BROKEN HILL
Pt. AUGUSTA
HILLSTON
34°
ADELAIDE
136°
140°
144°
0 50 100 miles
0 50 100 kilometers

(3) Interpretation

The trend in distribution of these nodes appeared to be from node C in the wet areas, intergrading with node B species on the margins of the desert areas, with node A species confined to desert areas. Within Nodes B and C the sub-nodes also seem to reflect a graded series; C_1 confined to the wet areas of the Mount Lofty Ranges, C_2 spreading onto the drier plains, C_3 widespread in the Mallee areas, B_1 relatively restricted on the margins of the arid areas, and B_2 spreading well into the arid areas.

2. PRINCIPAL COMPONENTS ANALYSIS

Principal Components Analysis (P.C.A.) is a mathematically sound method of establishing simultaneous ordinations on many axes. Austin (1968) described P.C.A. as "a mathematical technique for describing the relationships of a set of points (species or stands) in an economical manner". As an approach to vegetation studies it was first used by Goodall (1954), and the theory spelt out more recently by Orloci (1966).

The approach has two limitations that must be borne in mind. First, because the components are mathematical, they need not have any biological significance, although it is widely assumed that they "ought". Second, because the axes are necessarily linear, it is unlikely that they will show a simple relationship to environmental variables, which are not usually linearly related to species variations (Austin 1968). The technique has been shown to be useful on such diverse vegetation as chalk grassland in Britain (Austin 1968), Nigerian savannah (Kershaw 1968), Tropical rain forest in the Solomon Islands (Greig-Smith, Austin, and Whitmore 1967) and on saxicolous bryophytes and lichens (Yarranton 1967a). These studies have, however, all been confined to intensive investigations in small areas. It appears that there is no published account of an attempt to apply P.C.A. to a large scale land survey or biogeographic problem.

(1) Method

The analysis was performed on the CDC 3600 computer in the C.S.I.R.O. Division of Computing Science, Canberra.

The analysis was based on a data block in which the qualitative (0/1) scores were replaced by scores normalized by species frequency, i.e. scores were divided by $\sqrt{r_k}$, where r is the frequency of the k^{th} species. This approach equalizes the importance of rare and frequent species in the analysis, so that common species do not dominate the analysis; this allows relative floristic richness to affect the outcome.

Following Gower (1966) it was possible to derive site ordinations from the species ordinations, because the component values D (for individuals or locations) and C (for attributes or species) are related as follows:

$$D(I) = \frac{1}{\sqrt{\lambda}} \sum_{k}^{m} C(K)\, X(I,K)$$

where λ is the root derived in the first ordination, C the vector from the first ordination, and X the relevant value from the data matrix used to calculate C. I and K indicate respectively the site and species being considered.

The matrices of component loadings produced by P.C.A. were studied, and the loadings for each species or site displayed graphically by plotting its position relative to pairs of components using the components as axes. Only the first 5 components were studied, as it was thought unlikely that further components would be amenable to interpretation.

The component loadings for each site were plotted on to maps, to indicate areas in which poles of the ordination were located.

For convenience in further discussion, the species were placed in groups on the basis of the ordination. They were grouped by arbitrary divisions depending on the sign of the vector loadings they received on the axes being considered, unless an obvious discontinuity occurred in the ordination. The groups were assigned a name, taken from a genus in the group of which only one species was involved in the whole analysis. The component loadings for sites were plotted as graphs, then mapped, and areas with extreme loadings delimited.

(2) Results

(a) Statistical efficiency

The analysis removed 38.7% of the total variance in the data block in the first five components. The efficiency of each of the components is shown in Table 5.2.

Table 5.2

P.C.A. : Efficiency of the first five vectors

Vector	1	2	3	4	5
Efficiency	0.164	0.077	0.056	0.047	0.043

(b) Species ordinations

The component loading calculated for each species for components I-V are tabulated in Appendix 4.1.. In order to illustrate the effect of the components, relationships between four selected separate axis pairs are shown in Figs. 5.8 - 5.11.. Component II was usually used as a basis for these comparisons, as it produced the most clear cut results.

The effect of the components, separately and in combinations, is detailed below.

(i) Component I

This component had the effect of giving high loadings to frequent species (Fig. 5.12); thus, this component approximates to an index of "typicality" of the species.

(ii) Component II

This component differentiated most of the species with high loadings on component I between two poles (Fig. 5.8). One pole was typified by *Siphula coriacea, Lecidea coarctata, L. planata, Cladonia* squamules and *Cladia aggregata* (the *Siphula* pole). The other pole was marked by *Parmelia australiensis, P. molliuscula, Chondropsis semiviridis, Toninia caeruleonigricans* and *Diploschistes ocellatus* (the *Toninia* pole).

(iii) Component III

Component III appeared, like component II, to differentiate the species with high loadings on component I.

However, the most marked effect of component III was to differentiate the species of the *Toninia* pole of component II into two separate groups (Fig. 5.9). One of these groups was typified by *Parmelia australiensis, P. molliuscula, Chondropsis semiviridis* and *Diploschistes ocellatus* (the *Chondropsis* pole) and the second by *Collema ? coccophorus, Aspicilia calcarea* and *Caloplaca subpyracella* (the *Collema* pole).

(iv) Component IV

Component IV differentiated some of the less common or 'atypical' species with low loadings on component I, but not those species with very high loadings. This meant that component IV differentiated the *Siphula* pole derived by axis II into two arms (Fig. 5.10) in a manner similar to that by which component III differentiated the *Toninia* pole. The two poles resulting were typified in one case by *Siphula coriacea, Cladonia* squamules and *Cladia aggregata* (the *Cladia* pole), and the second case by *Lecanora atra, Buellia subcoronata* and *Caloplaca* sp. (the *Lecanora* pole).

When the action of component IV was considered in relation to component III, it was found that four poles were produced (Fig. 5.11). The species composition of these poles was remarkably similar to that of the poles created by the interactions of component II with component III and component IV (Table 5.3). This reflects the relative independence of components III and IV noted above. Some species were, however, placed in different groups on this new combination of axes. *? Biatorella* and *? Rinodina,* formerly placed marginally in the *Siphula* group, were placed in the *Collema* group. *Lecidea coarctata* and *L. planata* were transferred from a marginal position in the *Cladia* group to the *Lecanora* group, and

TABLE 5.3

Showing composition of various species groups as defined by use of different axis pairs. Species are ordered to provide minimal fragmentation of columns.

AXES	I & II		II & IV		II & III		III & IV			
	Siphula group.	*Toninia* group.	*Cladia* group.	*Lecanora* group.	*Chondropsis* group.	*Collema* group.	*Cladia* group.	*Lecanora* group.	*Chondropsis* group.	*Collema* group.
Siphula coriacea	+		+				+			
Cladonia squamules	+		+				+			
Cladia aggregata	+		+				+			
Heterodea mülleri	+		+				+			
Cladonia verticillata	+		+				+			
Diploschistes scruposus	+		+				+			
Parmelia conspersa	+		+				+			
Cladonia subsquamosa	+		+				+			
Endocarpon pusillum	+		+							+
Parmelia pulla	+		+						+	
Lecidea coarctata	+		+					+		
Lecidea planata	+		+					+		
Cladonia fimbriata	+		+				+			
Buellia subcoronata	+			+				+		
Lecidea psammophila	+			+				+		
Caloplaca bolacina	+			+				+		
Parmelia amphixantha	+			+				+		
Lecanora atra	+			+				+		
Lecidea sp.	+			+				+		
Cladonia foliacea	+			+				+		
? *Biatorella*	+			+		+				+
? *Rinodina*	+			+		+				+
Parmelia australiensis		+			+				+	
Diploschistes ocellatus		+			+				+	
Chondropsis semiviridis		+			+				+	
Parmelia molliuscula		+			+				+	
Aspicilia calcarea mod. *fruticosa*		+			+				+	
Fulgensia bracteata		+			+		+			
Acarospora smaragdula		+			+				+	
Buellia epigaea		+			+				+	
Lecidea crystallifera		+			+					+
Toninia caeruleonigricans		+			+					+
Dermatocarpon lachneum		+				+				+
Collema coccophorus		+				+				+
Aspicilia calcarea		+				+				+
Heppia lutosa		+				+				+
Heppia polyspora		+				+				+
Caloplaca subpyracella		+				+				+
Synalissa sp.		+				+				+
Acarospora schleicheri		+				+				+
Acarospora sp.		+				+				+
Lecidea decipiens		+				+				+

Lecidea crystallifera and *Toninia caeruleonigricans* were transferred from a marginal position in the *Chondropsis* group to the *Collema* group.

(v) Component V

This component was unusual in that it segregated two species, *? Biatorella* sp. and *? Rinodina* sp., both with vector loadings greater than + 0.8, from all others. Because of this, this component was not plotted. The next highest loading was + 0.29 for *Caloplaca subpyracella.* All other loadings lay between + 0.183 and - 0.183. It was possible, therefore, to segregate *? Biatorella* sp., *Rinodina* sp. and *Caloplaca subpyracella* into a separate species-group.

(vi) Ordination on three axes

A simultaneous three dimensional ordination based on components II, III and IV was constructed (Fig. 5.13). This clearly illustrated the four separate species groups delimited by use of pairs of axes; two above the plane of axes III and IV, and two below that plain.

FIGURE 5.8

Ordination of species in relation to components I and II, producing a simple dipolar scatter. A key to the species numbers is provided below.

1 *Acarospora schleicheri*
2 *Acarospora smaragdula*
3 *Acarospora* sp.
4 *Aspicilia calcarea*
5 *Aspicilia calcarea* mod. *fruticosa*
6 *? Biatorella*
7 *Buellia epigaea*
8 *Buellia subcoronata*
9 *Caloplaca subpyracella*
10 *Caloplaca* sp.
11 *Chondropsis semiviridis*
12 *Cladia aggregata*
13 *Cladonia foliacea*
14 *Cladonia subsquamosa*
15 *Cladonia verticillata*
16 *Cladonia fimbriata*
17 *Cladonia* squamules
18 *Collema coccophorus*
19 *Dermatocarpon lachneum*
20 *Diploschistes ocellatus*
21 *Diploschistes scruposus*
22 *Endocarpon pusillum*
23 *Fulgensia bracteata*
24 *Heppia lutosa*
25 *Heppia polyspora*
26 *Heterodea müller*i
27 *Lecanora atra*
28 *Lecidea coarctata*
29 *Lecidea crystallifera*
30 *Lecidea decipiens*
31 *Lecidea planata*
32 *Lecidea psammophila*
33 *Lecidea* sp.
34 *Parmelia amphixantha*
35 *Parmelia australiensis*
36 *Parmelia conspersa*
37 *Parmelia molliuscula*
38 *Parmelia pulla*
39 *? Rinodina orbata*
40 *Siphula coriacea*
41 *Synalissa* sp.
42 *Toninia caeruleonigricans*

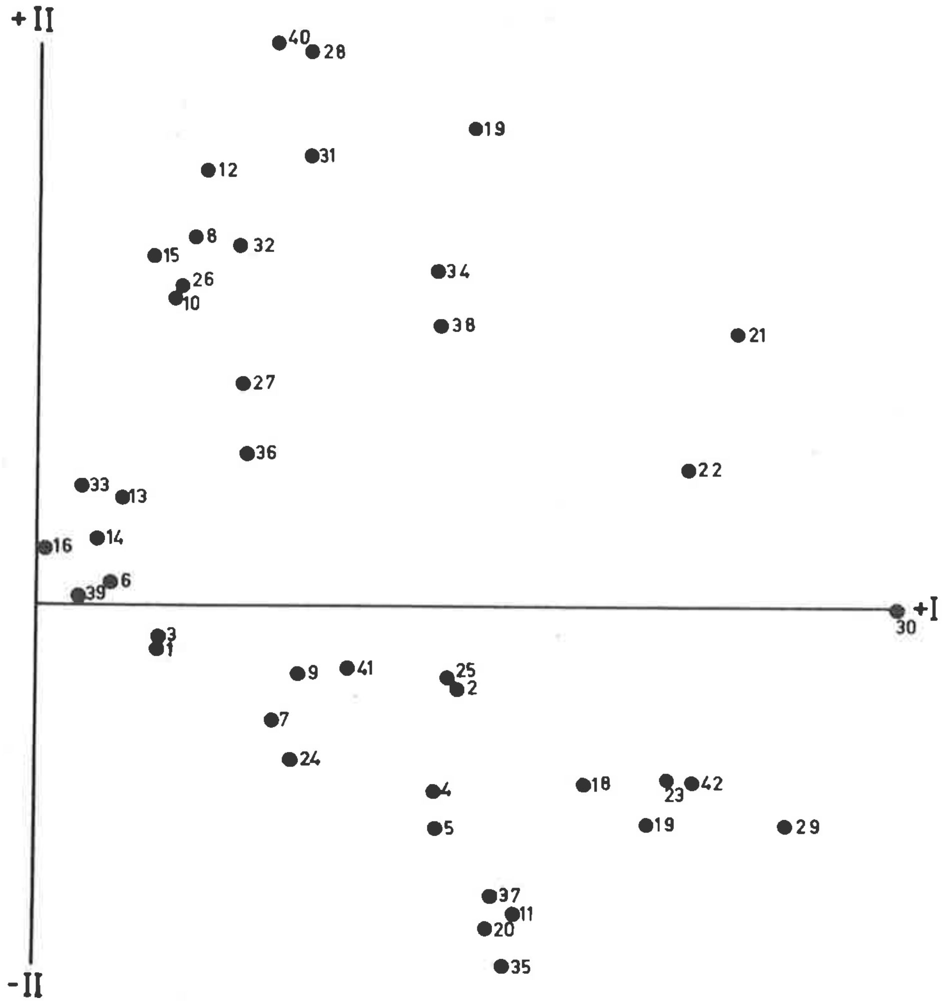

+II
-II
+I
40
28
19
31
12
8
32
15
26
10
34
38
21
27
36
22
33
13
14
16
6
39
30
3
1
9
41
25
2
7
24
4
18
23
42
5
19
29
37
11
20
35

FIGURE 5.9

Ordination of species in relation to components II and III, producing a tripolar scatter. The key to species numbers faces fig. 5.8.

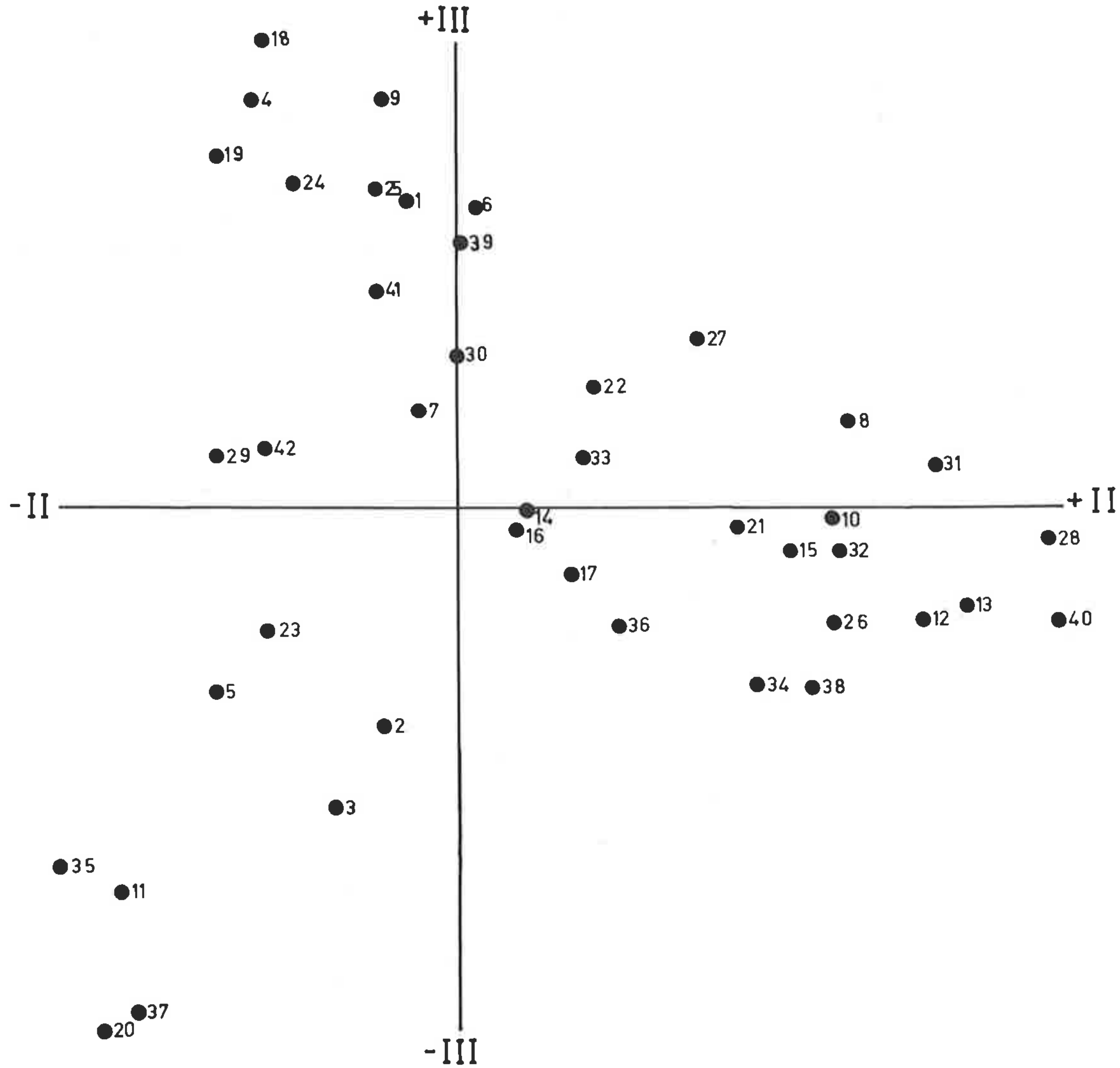
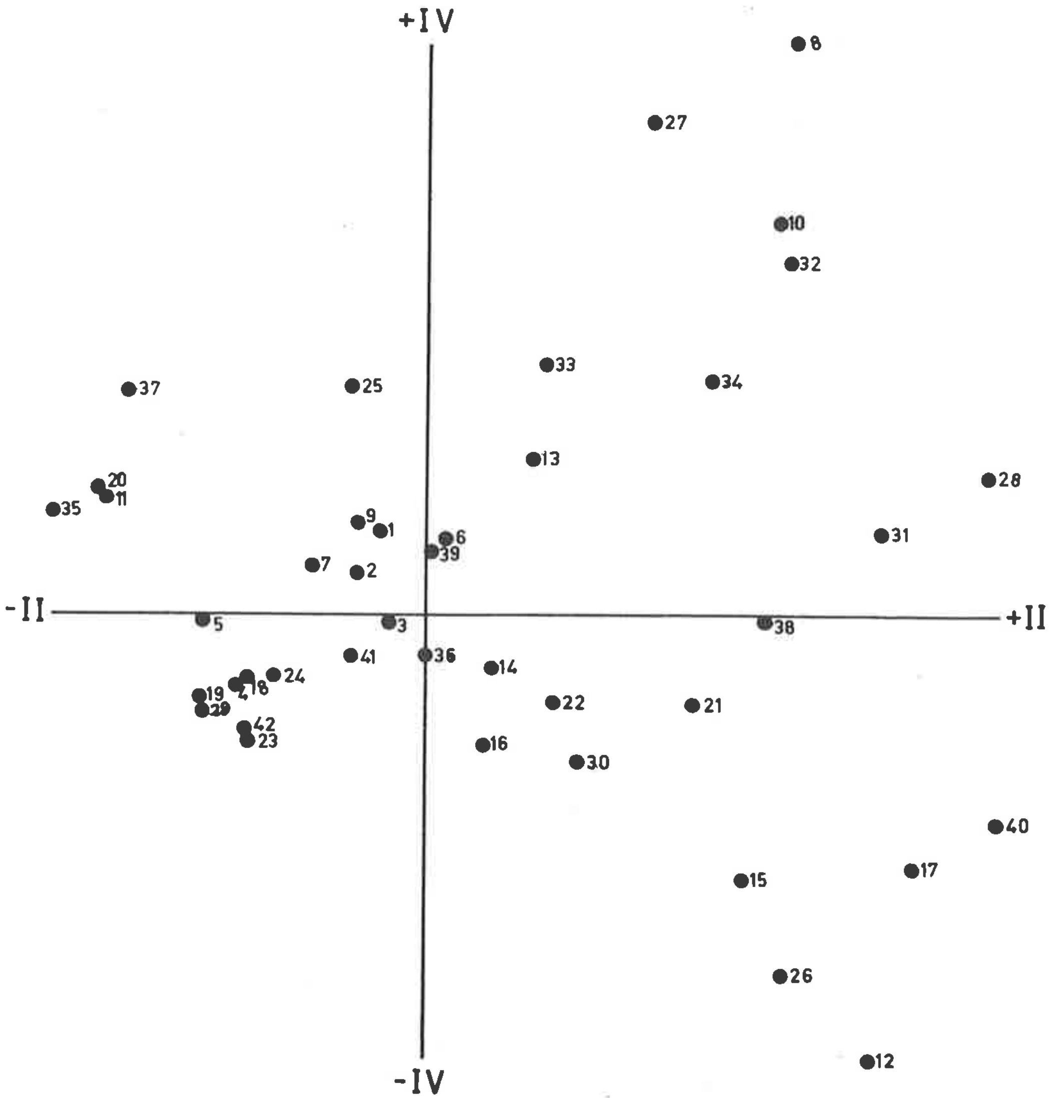

+III
-III
-II
+II
18
4
9
19
24
25
1
6
39
41
30
27
22
7
8
29
42
33
31
14
10
16
21
28
15
32
17
13
23
36
26
12
40
34
38
5
2
3
35
11
37
20

FIGURE 5.10

Ordination of species in relation to components II and IV, producing a tripolar scatter. The key to species numbers faces fig. 5.8.



+IV
-IV
-II
+II
8
27
10
32
33
34
37
25
13
28
20
11
35
9
1
6
39
31
7
2
5
3
38
41
36
14
24
19
4
18
29
22
21
42
23
16
30
40
17
15
26
12

FIGURE 5.11

Ordination of species in relation to components III and IV, producing a tetra-polar scatter. The key to species numbers faces fig. 5.8.

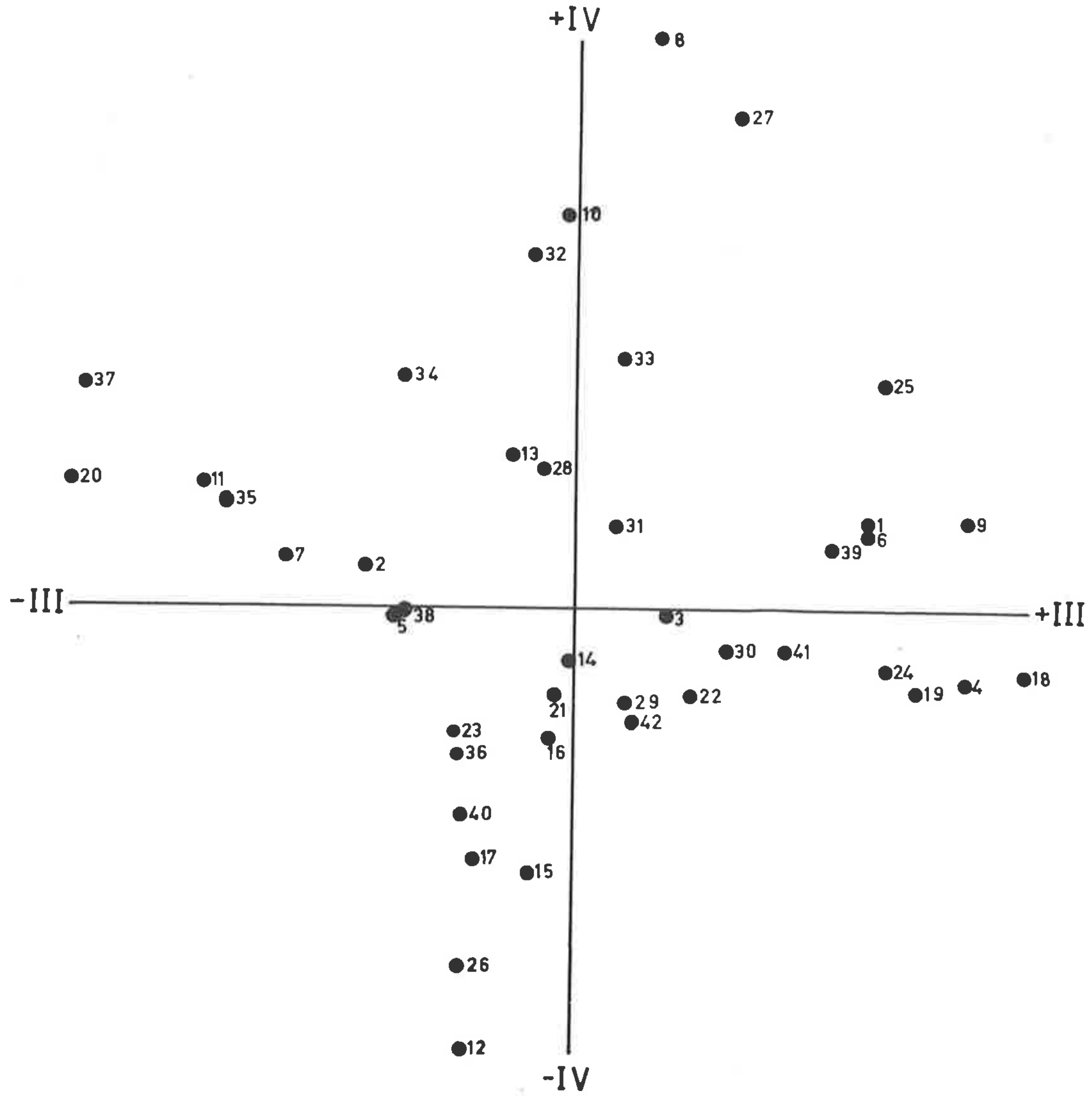
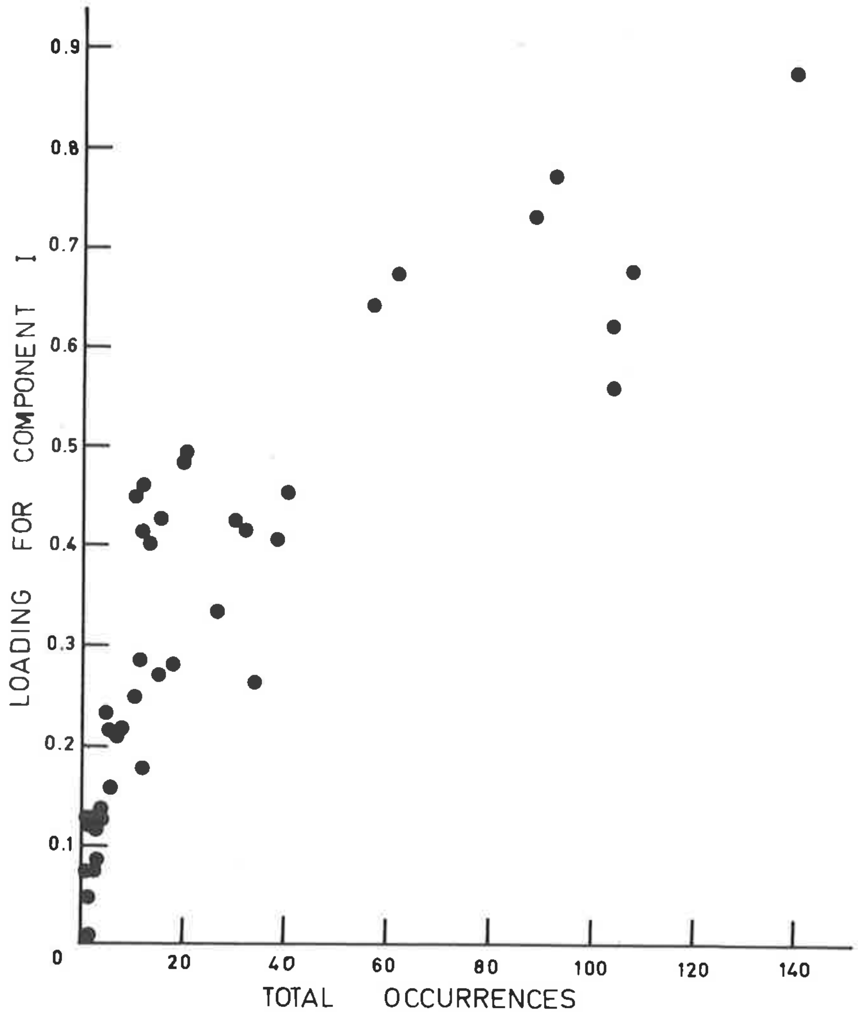

+IV
-IV
-III
+III
8
27
10
32
33
34
37
25
13
28
20
11
35
31
1
9
6
39
7
2
38
5
3
30
41
14
24
18
19
4
21
29
22
42
23
36
16
40
17
15
26
12

FIGURE 5.12

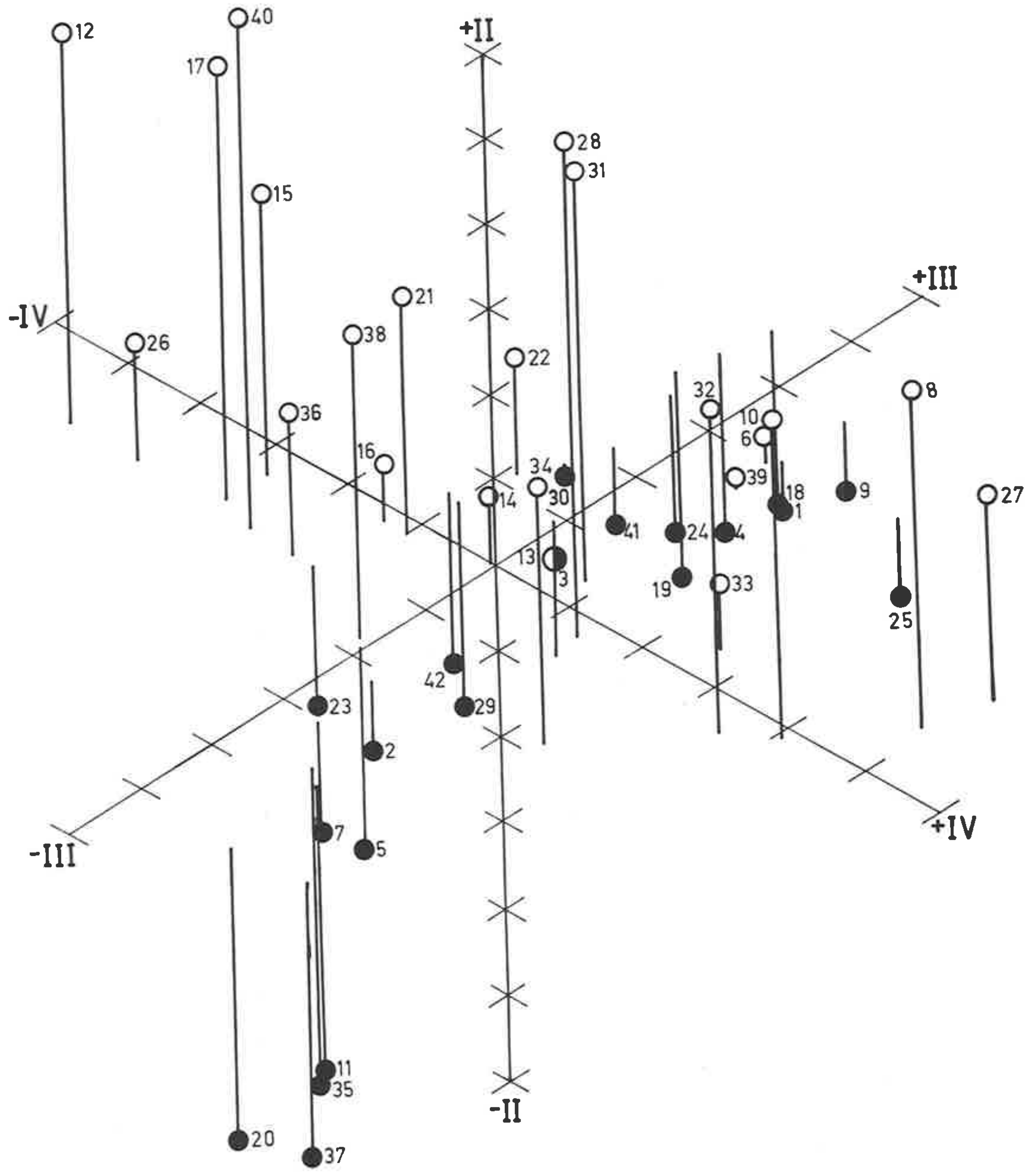
The relationship between the number of occurrences of each species, and the loading of the species for component I.



LOADING FOR COMPONENT I
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
20
40
60
80
100
120
140
TOTAL OCCURRENCES

FIGURE 5.13

Three dimensional ordination of species in relation to components II, III and IV. Filled circles are below the plane formed by axes III and IV, open circles are above that plane: the stalks indicate the projection of the point onto the plane.


+II
-II
+III
-III
+IV
-IV
12
40
17
15
28
31
21
38
26
22
36
16
32
10
6
8
34
39
18
9
27
14
30
41
24
4
1
13
3
19
33
25
42
29
23
2
7
5
11
35
20
37

(c) Site ordinations

The calculated loadings for vectors I-V for each site are included as Appendix 4.2. The relationships between ordinations along four selected axis pairs is shown in Figs. 5.14 - 5.17. The location of sites with extreme loadings for components I - IV are indicated in Figs. 5.18 - 5.21. The effect of the various components is discussed below.

(i) Component I

Extraction of the first, non-centred component is more informative with respect to sites than it is to species. The graphic plot of this component indicated that the sites are relatively homogenous. The points representing each location formed a single, more or less cigar shaped cluster (fig. 5.14) no matter which other component the loadings for component I were plotted against. When mapped, it could be seen that there was a band of high values for the component in the arid and sub-arid region of South Australia tailing off into western New South Wales (Fig. 5.18), indicating the areas in which this "typical" flora was most strongly developed.

(ii) Component II

When component II was plotted against component I a large cluster of sites with negative scores on component II, and a diffuse lobe of sites with positive scores on component II, were produced (Fig. 5.14). The strong positive scores on component II when mapped proved to be concentrated in the Mount Lofty Ranges near Adelaide, and in central New South Wales; strong negative scores were concentrated particularly in the Murray Basin, and in the north of Eyre Peninsula (Fig. 5.19), both in South Australia.

(iii) Component III

Plotting component III against component II produced a tripolar ordination, with a large number of sites in one pole, and diffuse lobes forming the other two (Fig. 5.15). Sites with a strong positive loading for component III (the bulk of sites) were concentrated in the north of the study area, and sites with a strong negative loading for component III were found to be concentrated in the Murray Basin and Eyre Peninsula of South Australia, (Fig. 5.20).

(iv) Component IV

Plotting component IV against component II again produced a tripolar ordination, the mass of sites at one pole, and the other two poles represented by diffuse lobes (Fig. 5.16).

Plotting component IV against component III produced an ordination showing four lobes representing the poles formed in the plots of components II x III and components II x IV (Fig. 5.17). Sites with strong positive loadings for component IV were mostly in central New South Wales; those with strong negative loadings were mostly in the Mount Lofty Ranges near Adelaide (Fig. 5.21).

(v) Component V

Component V produced high loading at only two sites, one north of Bourke in central New South Wales (site 180) and one near Mildura (site 41). These sites had loadings of +5 and +7 respectively: only four other sites had a loading greater than +2 or less than -2 for this component.

(3) Interpretation

The analysis, after indicating the typical lichen flora of the study area, divided the species and sites in a dichotomous manner. Component II appeared to divide the arid floras from the humid floras, each of which was then further divided by component III or IV. Component III appeared to segregate the species and sites of the arid zone into a winter-rainfall arid or sub-arid group, and a more extreme non-seasonal arid group. Component IV apparently divided the more humid sites and species into two groups, one confined to the winter-rainfall areas, the other especially well developed in the summer-rainfall areas.

FIGURE 5.14

Ordination of sites in relation to components I and II, showing a simple dipolar scatter.

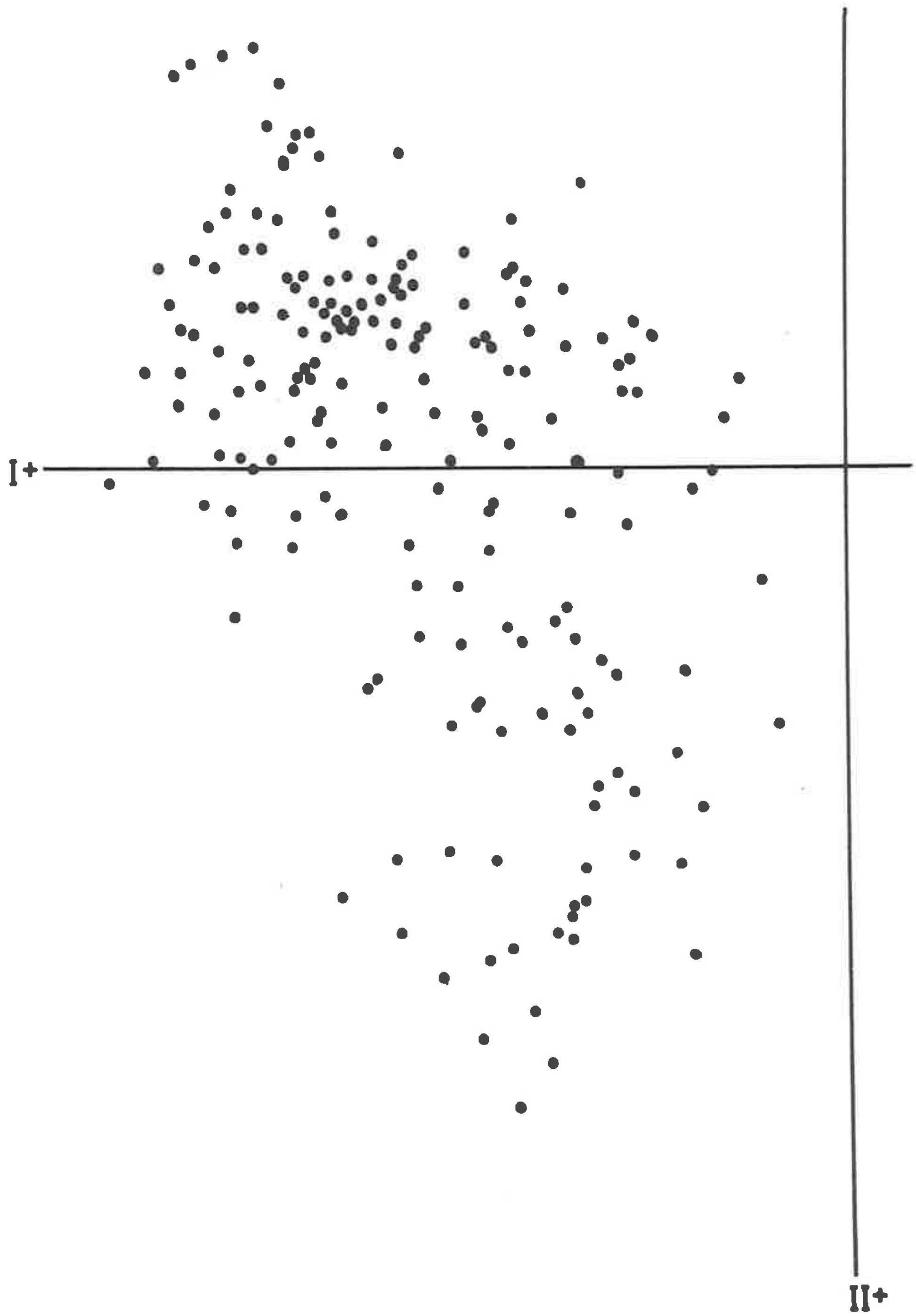

I+
II+

FIGURE 5.15

Ordination of sites in relation to components II and III, showing a tripolar scatter.

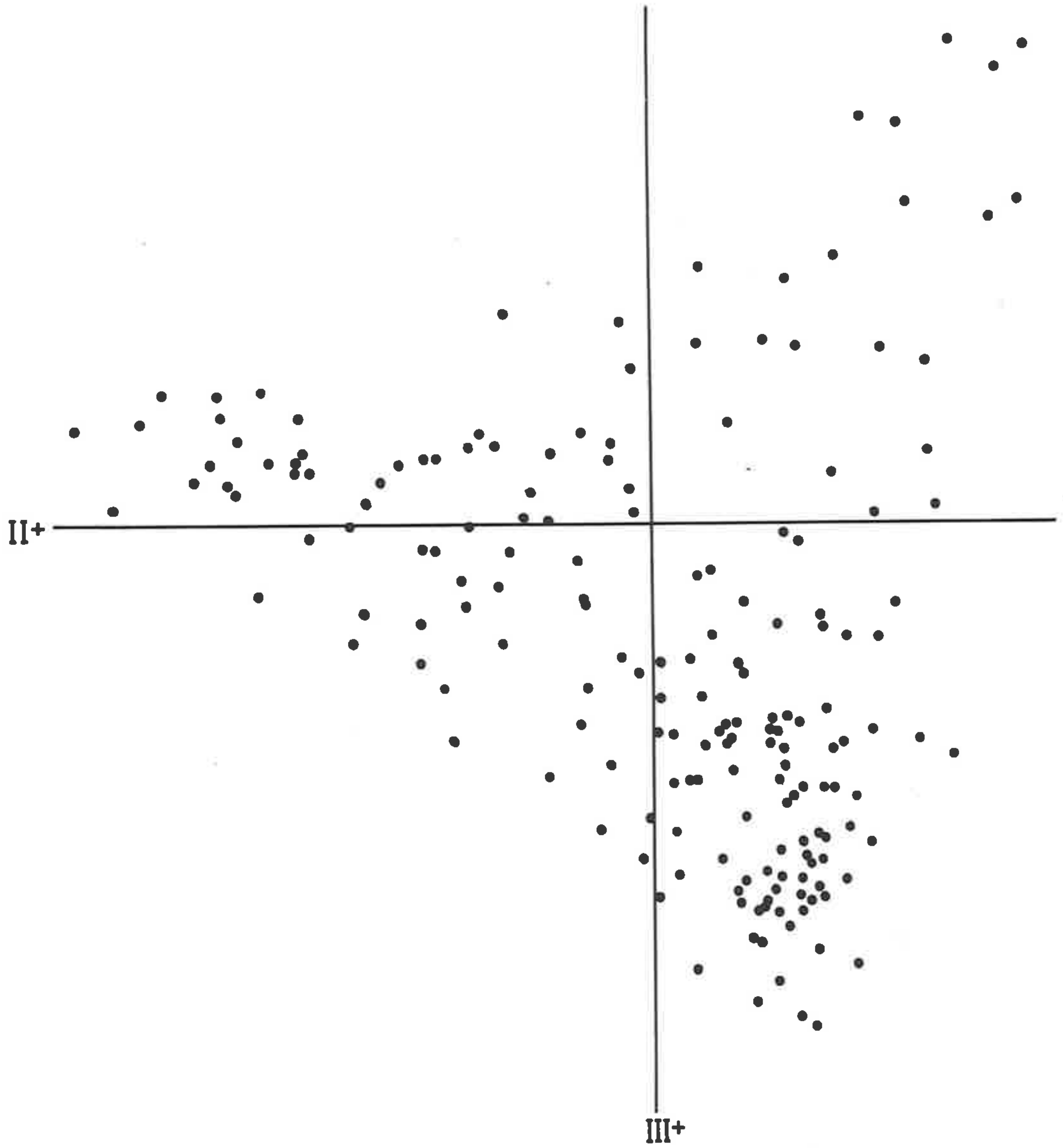

II+
III+

FIGURE 5.16

Ordination of sites in relation to components II and IV, showing a tripolar scatter.

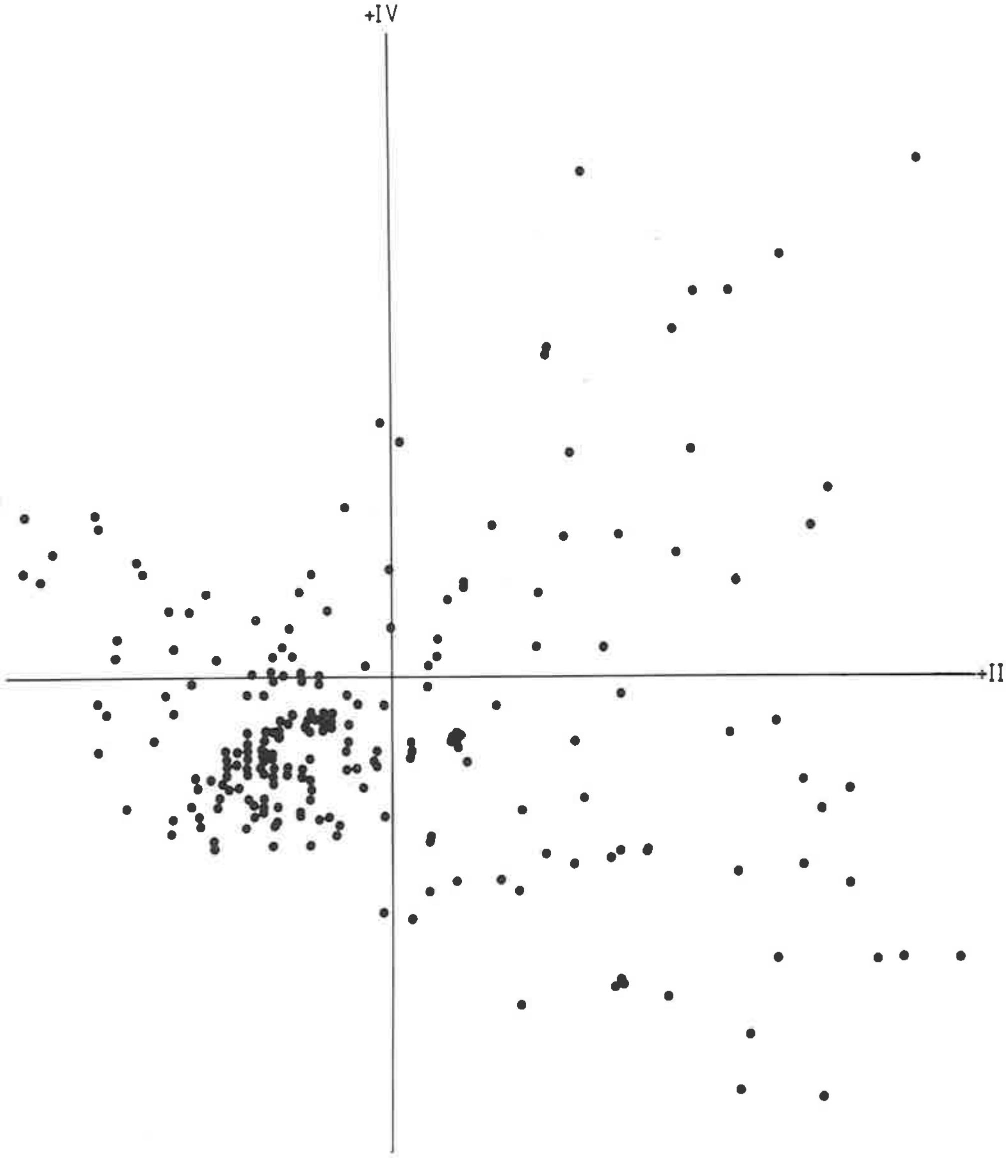

+IV
+II

FIGURE 5.17

Ordination of sites in relation to components III and IV, showing a tetra-polar scatter.

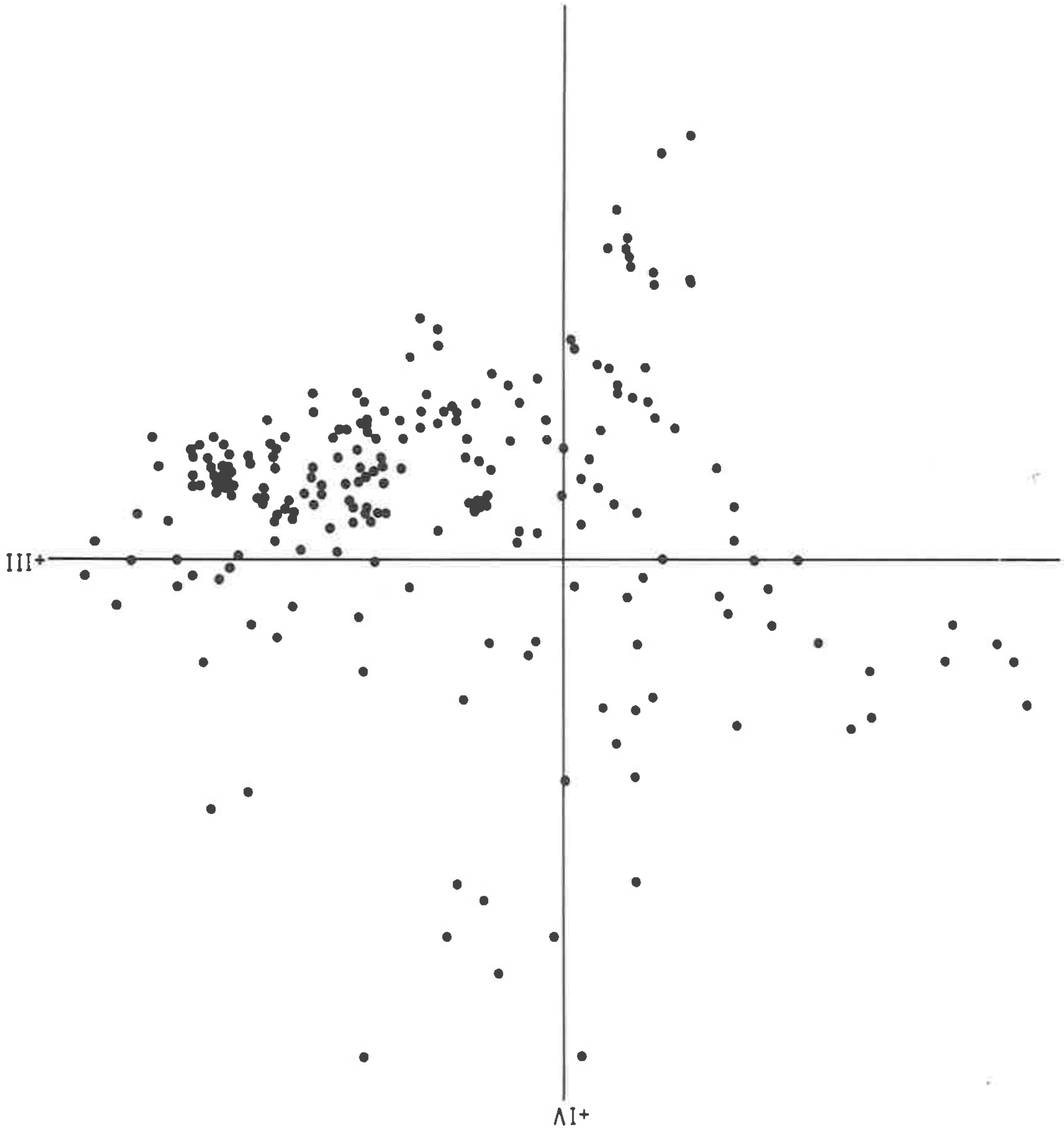
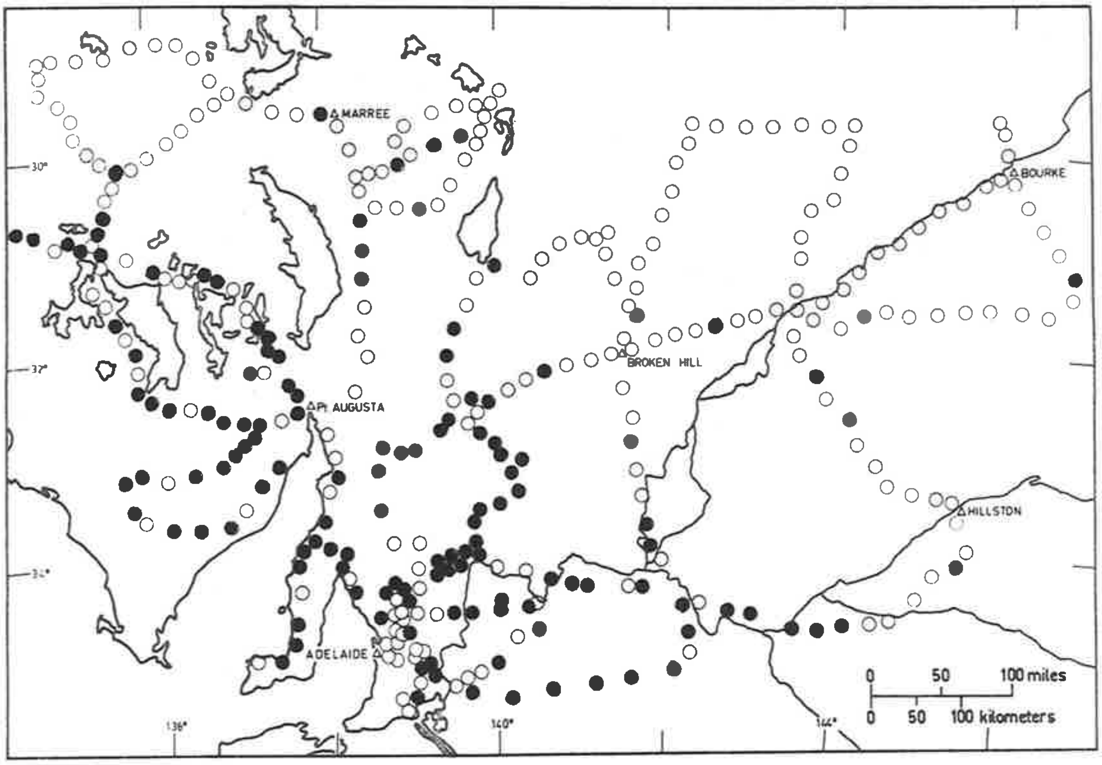

III+
+IV

FIGURE 5.18

The distribution of sites with high loadings on component I. Filled circles represent sites with a loading greater than or equal to four.

FIGURE 5.19

The distribution of sites with high loadings on component II. Filled circles represent sites with a loading on component II greater than or equal to +3, or less than or equal to -3. The sign of the loading is indicated on the enclosing lines.


MARREE
BOURKE
30°
BROKEN HILL
32°
Pt. AUGUSTA
HILLSTON
34°
ADELAIDE
0 50 100 miles
0 50 100 kilometers
136°
140°
144°

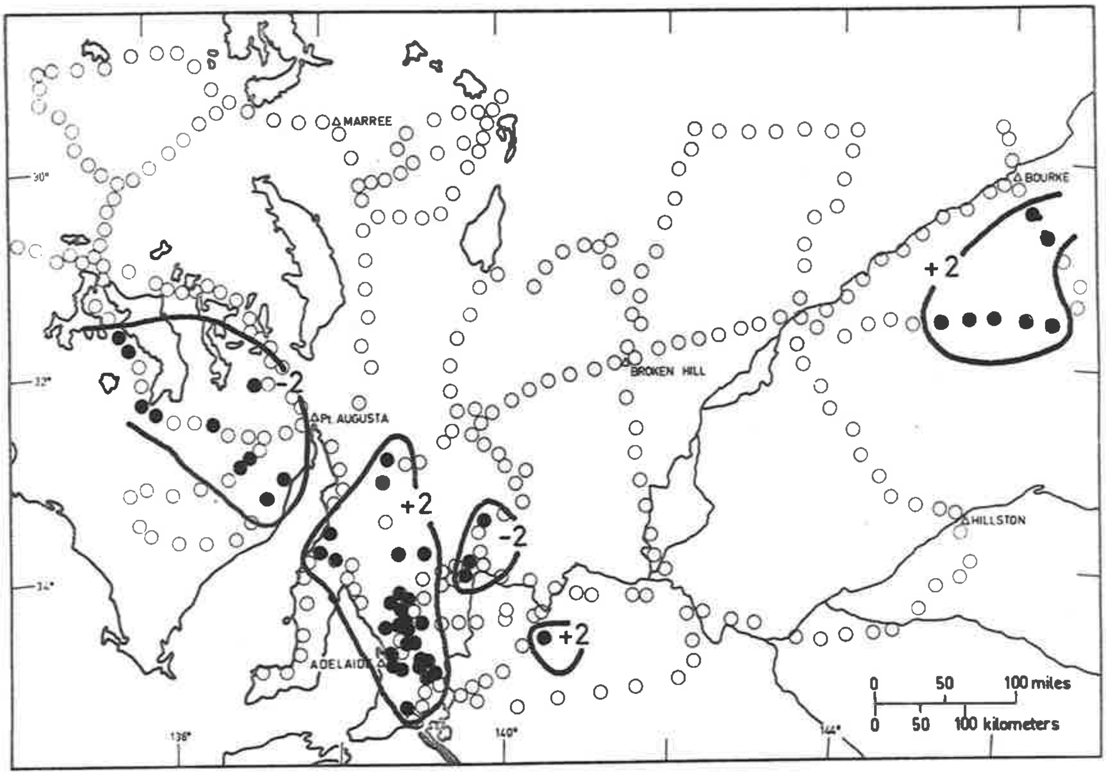
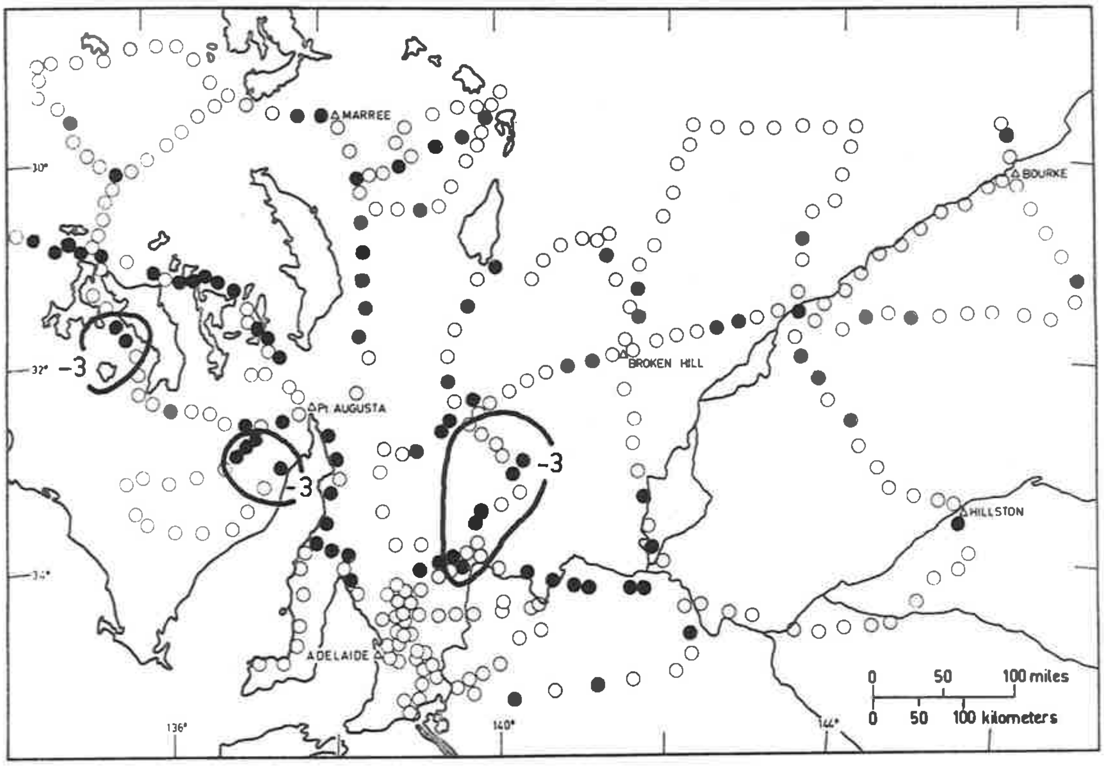

MARREE
BOURKE
30°
+2
BROKEN HILL
32°
-2
Pt. AUGUSTA
+2
-2
HILLSTON
34°
+2
ADELAIDE
0 50 100 miles
0 50 100 kilometers
136°
140°
144°

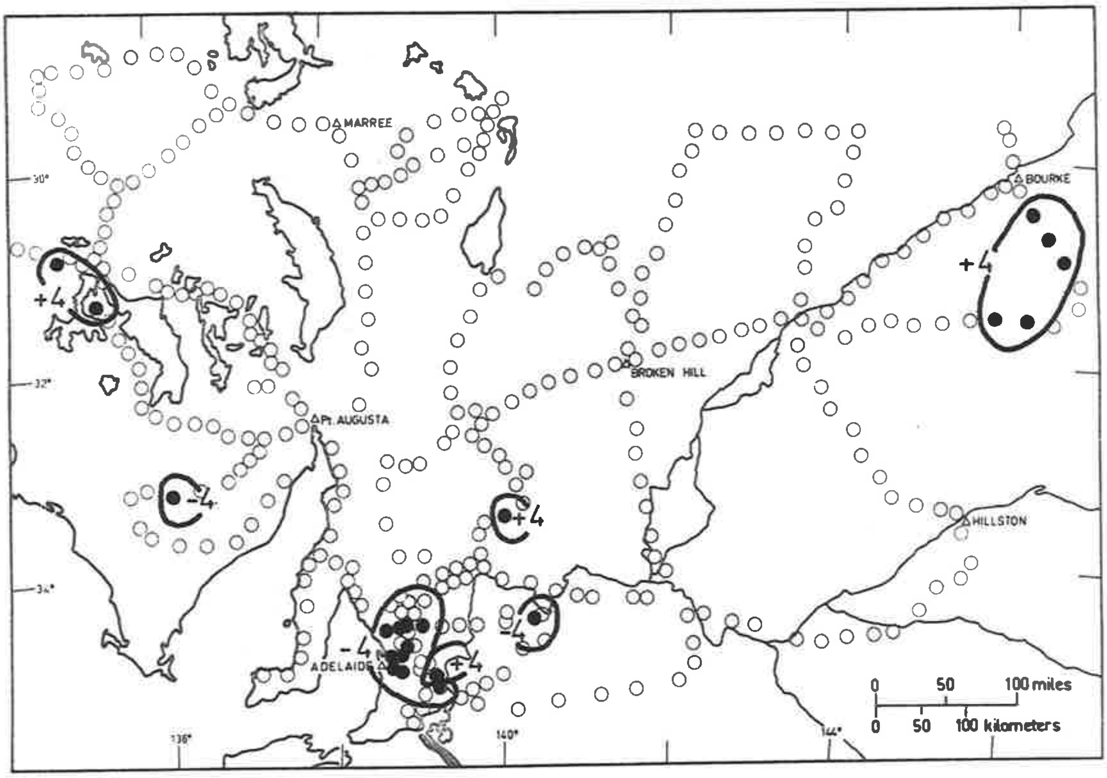
FIGURE 5.20

The distribution of sites with high loadings on component III. Filled circles represent sites with a loading greater than or equal to -3. Sites enclosed within lines are negative, others positive.

FIGURE 5.21

The distribution of sites with high loadings on component IV. Filled circles represent sites with a loading greater than or equal to +3, or less than or equal to -3. The sign of the loading is indicated on the enclosing lines.


MARREE
BOURKE
30°
BROKEN HILL
32°
-3
Pt. AUGUSTA
-3
-3
HILLSTON
34°
ADELAIDE
0 50 100 miles
0 50 100 kilometers
136°
140°
144°


MARREE
BOURKE
30°
+4
+4
BROKEN HILL
32°
Pt. AUGUSTA
-4
+4
HILLSTON
34°
-4
-4
ADELAIDE
+4
0 50 100 miles
0 50 100 kilometers
136°
140°
144°

3. ANALYSIS OF REGIONAL GROUPING

The role of the ecologist is not to discuss statistical or numerical relationships within vegetation, but to reveal the nature of the biological system involved. Numerical approaches are only an aid in that process. In order to provide a biological framework against which to test the numerical studies, a set of species-groups based on regional distribution patterns was established.

To erect the regional species-groups, maps of species distributions and species lists were carefully scrutinized, and the species arranged into groups with a common geographic range. These groups were thus erected on a different basis to that used in the numerical analyses: coincidence of species range rather than frequency of mutual incidence at particular locations. Moreover, the composition of these groups was influenced by impressions gained during the field study.

No "best" grouping can be arrived at in this style, but simply one which seems natural to the worker arranging the species. As a result of this approach, five species-groups with distinctive geographic zonation were delimited quite independently of the numerical analyses. These regional groups are listed below.

Group 1.

Caloplaca sp.
Cladia aggregata
Cladonia subsquamosa
Cladonia verticillata
Cladonia c.f. *fimbriata*
Heterodea müllleri
Parmelia conspersa
Parmelia pulla
Siphula coriacea

Group 2.

? *Biatorella*
Buellia subcoronata
Cladonia squamules
Lecidea coarctata
Lecidea planata
Lecidea psammophila
Lecidea sp.

Group 3.

Aspicilia calcarea
Caloplaca subpyracella
Cladonia foliacea
Heppia polyspora
Lecanora atra
Parmelia amphixantha

Group 4.

Acarospora smaragdula
Aspicilia calcarea
mod. *fruticosa*
Buellia epigaea
Chondropsis semiviridis
Diploschistes ocellatus
Fulgensia bracteata
Lecidea crystallifera
Parmelia australiensis

Parmelia molliuscula
Synalissa sp.
Toninia caeruleonigricans
? *Rinodina*

Group 5.

Acarospora sp.
Acarospora schleicheri
Collema coccophorus
Dermatocarpon lachneum
Diploschistes scruposus
Endocarpon pusillum
Heppia lutosa
Lecidea decipiens

Of these groups, groups 1 and 4 were sharply delineated, as the species had a restricted but relatively continuous distribution, and commonly recurred in groups as listed. Group 1 was more or less confined to the Mt. Lofty Range; group 4 to an arc around the ranges, on Northern Eyre Peninsula and in the Murray Basin.

The species of group 2 and group 3 tended to occur on similar sites, but those in group 3 were absent from the summer-rainfall areas of central New South Wales. Both groups were essentially groups of species that occurred in arid areas, but not in the extremely dry parts.

The species of group 5 were remarkably widely distributed, showing enormous ecological tolerance and occurring throughout the study area. These species seemed to form a basic soil-surface lichen flora, upon which the other groups (group 1 to a lesser extent than the others) were superimposed.

4. ASSESSMENT

(1) Species groups.

*Table 5.4 details the composition of five species-groups (A,B,C,D,E) which, after due consideration of all

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* Table 5.4 will be found in a pocket at the back of the volume.

analyses were concluded to embody the essential distribution pattern of the lichens. This table also shows the high degree of similarity between the groups resulting from the three primary analyses; this correspondence leading to the derivation of the five new groups.

It was apparent from Table 5.4 that Influence Analysis (I.A.) Node C was equivalent to the P.C.A. *Siphula* group (*Cladia* + *Lecanora* groups), and that Node B was equivalent to the P.C.A. *Chondropsis* group. The species not grouped by Influence Analysis mostly belonged to the P.C.A. *Collema* group. I.A. Sub-nodes C_1 and C_2 appeared to be equivalent to the P.C.A. *Cladia* and *Lecanora* groups respectively.

I.A. Sub-nodes B_1 and B_2 were together more or less equivalent to the P.C.A. *Chondropsis* group.

I.A. Node A species were the three species strongly influenced by P.C.A. component V, previously tentatively separated as a species-group.

The regional groups were less in agreement with the P.C.A. groups and I.A. nodes than were those analyses with each other. However, regional group 1 was very similar in composition to the P.C.A. *Cladia* group and I.A. Node C. Regional group 4 was very similar to the P.C.A. *Chondropsis* group and the I.A. Node B. The species of regional group 2 were included in the P.C.A. *Lecanora* or *Cladia* group and in I.A. Node C. Group 3 species were divided between the P.C.A. *Lecanora* and *Collema* groups, and between I.A. Node C (Sub-nodes C2, C3) and the species not grouped by Influence Analysis. Most of the regional group V species were in the P.C.A. *Collema* group, and were ungrouped by Influence Analysis.

Only two species, *Diploschistes scruposus* and *Endocarpon pusillum* were placed in radically different groups by the various methods used for grouping. These two species were placed alternatively in the two extreme groups of an apparent climatic sequence. This was probably a reflection of their wide range of distribution, from the wettest to some of the driest areas studied.

(2) Distribution patterns

The lichens of species-group D, which are almost ubiquitous, form a basic flora for most of the study area. The geographical range of the lichens in species-group D embraced the entire range of species in groups B, C and E, and most of the range of those in species-group A. Species-group A is much less extensive in distribution than species-group D, which it overlaps slightly, but it does not share its range with many of the species of groups B, C and E. Lichens of these latter groups are best understood as bringing regional elaboration to the group D soil surface flora.

With this understanding of two overlapping floras (groups A and D) and three super-imposed groups (groups B, C and E), five geographic regions with respect to lichen floras could be delimited. These regions were:

(1) The Mount Lofty Ranges.
(Group A species predominant, often superimposed on group D species).

(2) Central New South Wales.
(Group B species superimposed on Group D species).

(3) Northern Eyre Peninsula.
(Group C species superimposed on Group D species).

(4) The northern Murray Basin in South Australia.
(As (3) above).

(5) The remainder of the study area.
(Group D species with an admixture of species from groups A, B, C & E).

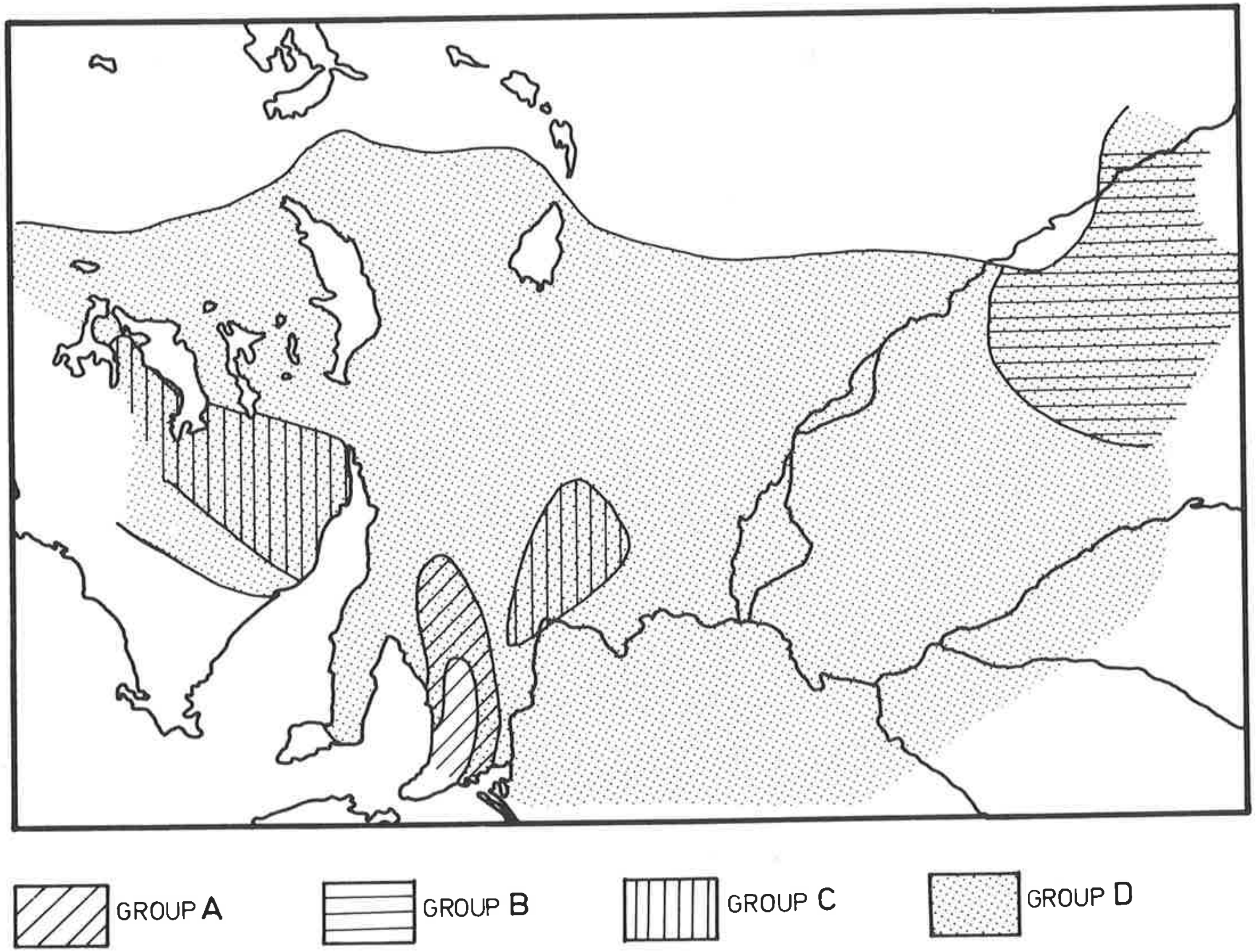
These generalized areas are illustrated in Figure 5.22.

(3) Retrospective comment on procedures

At the beginning of this chapter it was pointed out that in view of what was known about soil surface lichens continuous rather than divisive classifications seemed desirable. Subsequently both of the numerical methods used

FIGURE 5.22

The areas within which species-groups A, B, C, and D, (defined in table 5.4) show maximum development.


GROUP A
GROUP B
GROUP C
GROUP D

reinforced the belief that the data was of a continuous nature. However, the detail of the results proved impossible to map in a continuous manner for two main reasons. The sample locations were too sparsely scattered over the area to cope with the variation (one sample to 3,000 square kilometres) and, a great number of these samples were negative for all species.

In practice there was no option but to condense each continuum into two classes representative of extreme conditions. However, in the final construction of the species-groups, the information from each continuum was invaluable in interpreting the placement of species in those groups.

The essentially similar results produced by two very different numerical approaches indicated that the relationships expressed by them are real: the manner in which they reinforced each other simplified the construction of the final regional analysis.

The numerical analyses drew attention to information not immediately apparent from maps and species lists. The speed and low cost of such studies, coupled with the results produced in the present situation, indicate their value in studies of a biogeographic scale. This is notwithstanding the comment of Moore *et al* (1970) who rejected the use of association analysis on a large scale because of the computing time involved; their programme completed an association analysis on 75 taxa in 20 releves in 10 minutes. In the present study using a more advanced computer an association analysis of 42 taxa in 227 quadrats was completed in 3.66 seconds. Thus, as computer facilities are further developed much larger and more involved analyses will be feasible.

CHAPTER VI

THE RELATIONSHIP BETWEEN DISTRIBUTION AND ENVIRONMENT

1. CHOICE OF ENVIRONMENTAL VARIABLES

Factors affecting the distribution of plants in the arid zone of south eastern Australia can be grouped into three basic types: climatic factors, substrate factors and biotic factors. These are all susceptible to study (Moore 1953a,b). This chapter deals only with those factors of climate and soil which relate to lichen distribution on a broad scale. The effect of an historical biotic influence on the distribution of lichens on a relatively small scale is studied in Chapter VIII.

At the commencement of this study two hypotheses were formulated concerning factors affecting lichen distribution. These were that climate, especially rainfall, would be a significant controlling factor, and that soil type would be a significant but less important factor. From these hypotheses it was predicted that the distribution of taxa and species-groups would coincide with climatic patterns.

Examination of the completed distribution maps of species and species-groups strongly supported the impression gained during the field study that mean annual rainfall, the seasonal distribution of rainfall, and soil type, were closely related to distribution. Examination of data associated with soil maps suggested that several soil variables might be involved; these included pH, nature of the surface, calcium concentration and sodium concentration.

As the collation of environmental data for the study area proceeded, it became apparent that mean maximum temperature for January (the hottest month) was also related to the distribution patterns. This suggested that a single value climatic index reflecting both rainfall and temperature effects would be useful. A range of such indices was available, including those of Thornthwaite (1933, 1948), Prescott (1936, 1949), Davidson (1936) and Prescott and Thomas (1948). Examination of these revealed that the most suitable indices were those of Thornthwaite (1948) and Prescott (1949): these were, however, presented on very small maps, with very little detail. The only suitably detailed map was that produced by Davidson (1936), who used a very crude and rather unsatisfactory index. The use of single value climatic indices was therefore pursued no further.

The relationships between all of the variables discussed above (except single value climatic indices) and the distribution of both lichen species and crusts are discussed below.

2. COLLECTION OF ENVIRONMENTAL DATA

(1) Mean Annual Rainfall

Each site was placed in a mean annual rainfall class using the rainfall map presented as Fig. 3.4. This produced a 5cm class interval with a total range from 10cm to 60cm per annum.

(2) Seasonal incidence of rainfall

Sites were placed into two groups; those with a pronounced winter rainfall maximum and those with either a pronounced summer rainfall maximum, or with more or less uniform rainfall distribution throughout the year.

(3) Soil

Information on the nature of the soil surface was compiled from a study of notes collected at the sampling sites, and from soil maps. The soils were grouped broadly into clays, sands, crusted loam and earth, hard setting loam and earth, amorphous soils and rock pavement.

These soil groupings referred only to the nature of the soil surface, so cannot be equated with the usual soil classifications. Clays were usually riverine or less commonly arid claypans; sands included sand-hills and thin mantles of sand over any other soil.

Soils with a crusted surface and a more friable lower layer were placed in the crusted loam group. Any soil with a hard surface when dry was classed as hard setting. Amorphous soils were usually very fine textured, friable and non-crusting. Rock pavement referred to areas so completely covered with rocks or pebbles ("gibbers") that no soil was visible between the rocks, or, in a few cases, to an extreme form of skeletal soil consisting mostly of fine schistose scree which was restricted to hilly areas.

Chemical characteristics (pH, extracted calcium and sodium) were, because of usually high calcium content of the soil, determined from a saturated soil extract prepared after the method of Richards (1947). A subsample of the soil from each site was ground with a mortar and pestle until it passed a 2mm sieve, and a 50gm portion puddled with water to form a saturated suspension. The suspension was covered and left for 12 hours, then some of the water extracted under pressure. Immediately after extraction the pH of this extract was measured using a glass electrode in circuit with a resistance bridge, and the sample stored under refrigeration. When all extracts had been prepared, sodium content was determined using an EEL flame photometer, and calcium content determined using a Techtron A2 atomic absorption spectrophotometer. 1000 p.p.m. strontium chloride buffer was used to prevent phosphate interference in the calcium determination. Concentrations were calculated in terms of milli or micro-moles of element per gram of soil.

The pH values obtained, with the exception of a single very low value (pH 5.4), ranged between pH 6.5 and pH 8.9. These values were assigned to groups, the class intervals for these groups being 0.4 pH units. The very low value was included in the lowest class (pH 6.5).

The class intervals for calcium and sodium concentrations presented a problem. The range of calcium concentrations encountered was from 100µ moles/gm soil up to 15,150 µ moles/gm soil and the range for sodium concentrations from 32µ moles/gm up to 49,890µ moles/gm soil; in both cases the vast bulk of values were in the lower part of the range. Classes were therefore constructed on a logarithmic scale to ensure more uniform representation of sites in the higher classes.

(4) Normal maximum January temperature

Normal maximum temperature in January was determined for each site by interpolation from Fig. 3.6. This allowed only four classes, with a class interval of 3°C between 26°C and 38°C.

The environmental data relating to each site have been tabulated, and presented as Appendix 5.

3. SELECTION OF METHODS FOR EVALUATING THE RELATIONSHIP BETWEEN DISTRIBUTION AND ENVIRONMENTAL DATA

The relationship between distribution and the environment could be summarized in a number of ways, either qualitative or quantitative. The simplest form would have been to indicate the range for each variable within which each species was found. This could be quantified by calculating the percentage frequency with which a species occurred in each of a number of class intervals for the variable (i.e. number of occurrences of the species at locations falling into that class interval divided by total number of sites falling into that class interval multiplied by 100). This treatment would yield data from which histograms could be constructed to indicate distributional modes for each species with regard to the particular environmental variable.

The relationship illustrated in a histogram could be further quantified by calculation of regression coefficients describing the relation between frequency and the variable studied. It was found, for example, that the relationship between frequency and mean annual rainfall for *Cladonia* squamules took the form:

$$\log_{10} \text{frequency} = (0.11 \times \text{rainfall}) - 0.45,$$

the probability of such a fit being achieved by chance is less than 0.001. Much more complex expressions could have been developed to describe the relationship of other species to rainfall. The biological significance of such expressions are not, however, immediately obvious.

Yarranton (1967b) recommended the use of such regressions in studies of the relationship between species occurrence and the environment. This approach has been applied in a series of studies (Yarranton 1970, Yarranton and Beasleigh 1969). Such an approach, however, pre-supposes that a detailed data block is available.

It was decided to present the relationships between distribution and environmental variables as histograms. No further statistical treatment was attempted because of the low intensity of the data (presence / absence of species without knowledge of frequency or density at each location). This method is highly informative and useful, although less rigorous than the multiple regression approach.

In order to reveal the factors important in influencing species distribution the following argument was invoked.

Species distribution is largely controlled by environmental variation. Thus, if a number of species tend to occur together, it is because they respond in a like way to environmental conditions. Therefore, if the species of a group tending to occur together all show a similar response to any given environmental variable, but a response different to that of other species, the variable either controls, or is correlated with a variable which controls the distribution pattern.

Thus, for example, if it could be shown that all the species of species-group A (defined in Table 5.4), responded in a like manner to rainfall, but in a manner different to that shown by groups B, C and D, it could be claimed that rainfall (or a correlated factor) played an important part in control of the distribution of the species-group.

To determine whether or not species in a species-group responded in a like manner to environmental variables, the following procedure was followed.

The histograms relating species frequency to values of environmental variables were ordered. The order was determined primarily by the modal value of the histogram i.e. the species with its modal value in one extreme class interval was placed first in the ordination, and followed by that with its mode in the next highest interval, and so on. Once the species were arranged in order the species-group to which each belonged was scored beside it. If members of species-groups were placed in close proximity by the environmental ordination, this was taken to indicate that the species in the group responded to that environmental factor in similar ways, i. e. they were either controlled by that factor, or by a closely correlated factor.

If the distribution of a species-group is controlled by the variable being considered, it would be expected that the centre of development of that species-group would be related to the pattern of the environmental variable being considered. This would allow a check on the conclusions reached on the basis detailed above.

4. THE FREQUENCY HISTOGRAMS

In this section the relationships between species frequency and the set of environmental variables are presented, and some remarks about the nature of the frequency distributions across the range of environment made. Causation of the pattern is considered in a later section.

(1) Frequency distribution in relation to mean annual rainfall

Distribution of species varied widely in relation to rainfall. Two species, *Endocarpon pusillum* and *Lecidea decipiens* occurred at sites in each of the rainfall classes. *Diploschistes scruposus* and *Cladonia* sp. squamules occurred at sites in all but the driest class, *Dermatocarpon lachneum* and *Lecidea crystallifera* occurred at sites in all but the wettest class. The most restricted range was that of *Diploschistes ocellatus*, which occurred only at sites with a rainfall between 15cm and 25cm. Other species with very restricted ranges were *Chondropsis semiviridis* and *Aspicilia calcarea* mod. *fruticosa* which occurred only in the classes between 15cm and 30cm.

In Fig. 6.1 the frequency histograms for the more common species are ordered by the mode of the histogram, those with modes in high rainfall classes appearing at the top left hand side of the figure, those with modes in low rainfall classes at the bottom right hand side. In this figure the broad rainfall tolerance of most species was apparent. The histograms have a more or less smooth outline, usually without marked discontinuities. The 10cm to 15cm per annum, or driest class, was the only one in which all lichens were notably less frequent.

(2) Frequency in relation to seasonal rainfall incidence

The frequency of common species for sites in summer and winter rainfall areas was calculated (Table 6.1). Many species did not occur at all in areas with summer rainfall, and most others had a markedly higher frequency in areas with winter rainfall. Two species, *Buellia subcoronata* and *Lecidea planata*, were more frequent in areas with summer rainfall than in areas with winter rainfall; the frequency of *Lecidea psammophila* was virtually the same in both rainfall regions.

(3) Frequency in relation to soil extract pH

The relationship between frequency and pH is illustrated in Fig. 6.2 in which the frequency histograms for each species are arranged with their modes in ascending order of pH value. From Fig. 6.2 it is apparent that most histograms exhibit definite pH modes, although *Lecidea decipiens* and *Heppia polyspora* occur with a more or less uniform frequency across the whole pH range.

TABLE 6.1

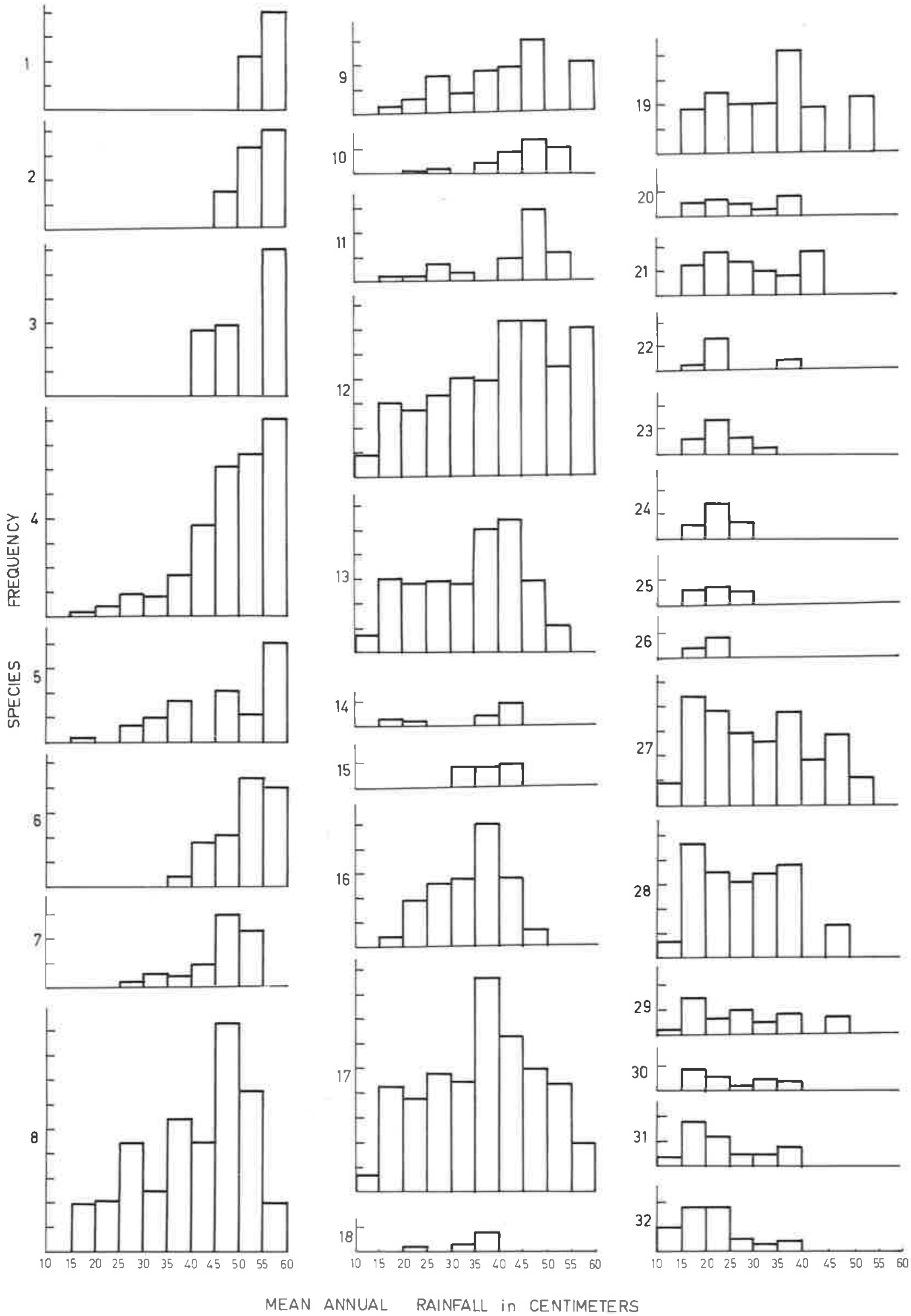
The frequency of species in areas with predominant summer and winter rainfall

Species	Summer Rain	Winter Rain
Acarospora smaragdula	0	6.3
Aspicilia calcarea	3	14.6
Aspicilia calcarea mod. *fruticosa*	0	5.0
Buellia epigaea	0	2.1
Buellia subcoronata	5	0.4
Caloplaca subpyracella	2	5.4
Chondropsis semiviridis	0	8.4
Cladia aggregata	0	5
Cladonia squamules	1	16.1
Collema coccophorus	13	37.2
Dermatocarpon lachneum	13	37.5
Diploschistes ocellatus	0	4.2
Diploschistes scruposus	4	35.4
Endocarpon pusillum	12	39.6
Fulgensia bracteata	0	21.2
Heppia lutosa	11	18.3
Heppia polyspora	7	9.6
Heterodea mülleri	0	1.6
Lecanora atra	1	2.1
Lecidea coarctata	2	3.8
Lecidea crystallifera	2	37.8
Lecidea decipiens	11	54.1
Lecidea planata	7	4.6
Lecidea psammophila	2	2.1
Parmelia amphixantha	3	10.0
Parmelia australiensis	0	8.4
Parmelia conspersa	0	2.8
Parmelia molliuscula	0	5.0
Parmelia pulla	0	5.4
Siphula coriacea	0	4.2
Synalissa sp.	2	10.0
Toninia caeruleonigricans	2	26.7

FIGURE 6.1

Histograms showing the relationship between species-frequency (Y-axis) and mean annual rainfall (X-axis). The scale divisions on the Y-axis are 10% frequency intervals. A key to the species treated in each histogram is provided below.

1. *Heterodea mülleri*
2. *Parmelia conspersa*
3. *Siphula coriacea*
4. *Cladonia* squamules
5. *Lecidea planata*
6. *Cladia aggregata*
7. *Lecidea coarctata*
8. *Diploschistes scruposus*
9. *Parmelia amphixantha*
10. *Lecidea psammophila*
11. *Parmelia pulla*
12. *Endocarpon pusillum*
13. *Lecidea crystallifera*
14. *Lecanora atra*
15. *Buellia subcoronata*
16. *Fulgensia bracteata*
17. *Lecidea decipiens*
18. *Buellia epigaea*
19. *Toninia caeruleonigricans*
20. *Acarospora smaragdula*
21. *Aspicilia calcarea*
22. *Parmelia molliuscula*
23. *Parmelia australiensis*
24. *Chondropsis semiviridis*
25. *Aspicilia calcarea* mod. *fruticosa*
26. *Diploschistes ocellatus*
27. *Dermatocarpon lachneum*
28. *Collema coccophorus*
29. *Synalissa* sp.
30. *Caloplaca subpyracella*
31. *Heppia polyspora*
32. *Heppia lutosa*



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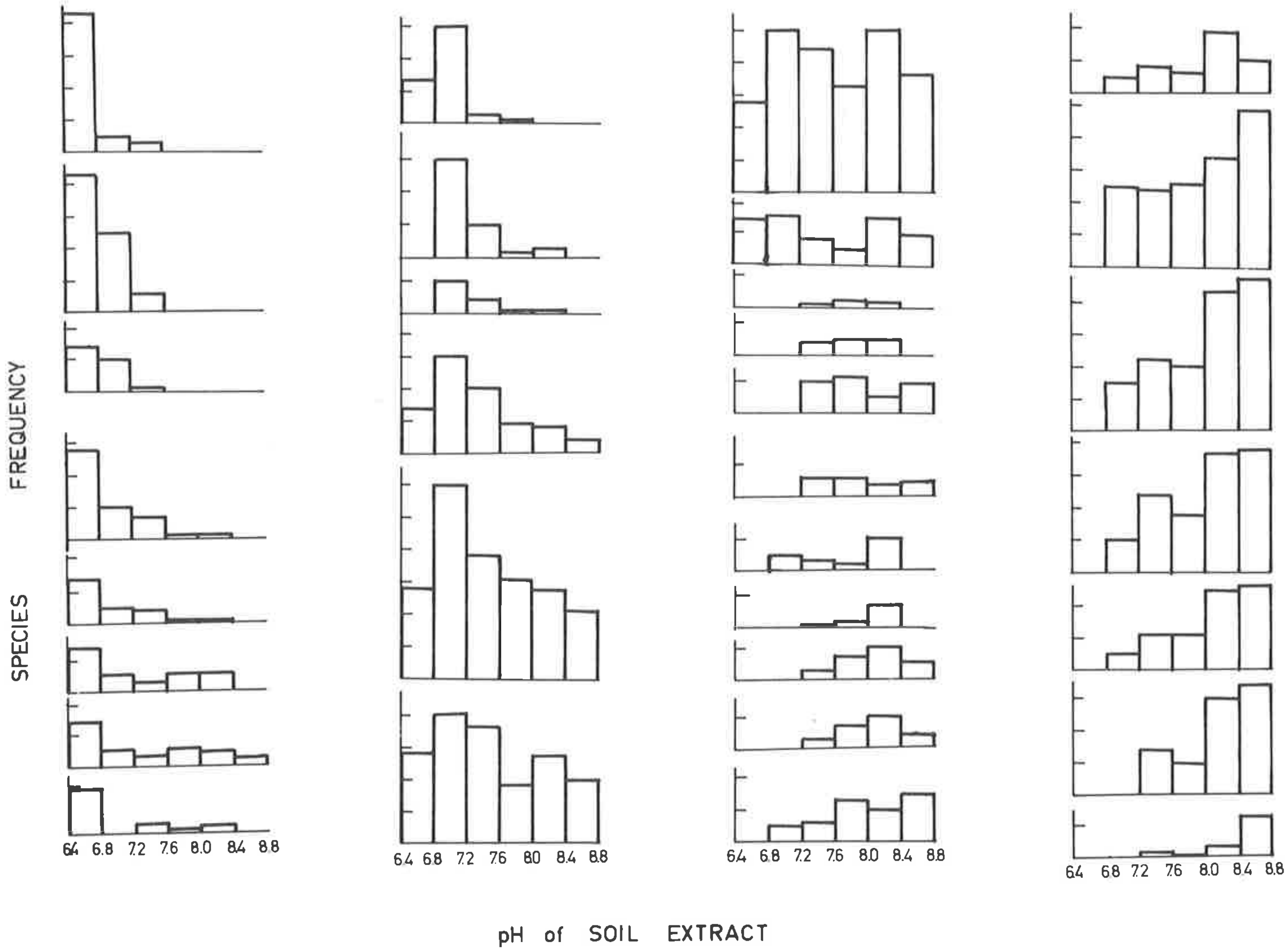
MEAN ANNUAL RAINFALL in CENTIMETERS

FIGURE 6.2

Histograms showing the relationship between species-frequency (Y-axis) and pH of the soil extract (X-axis), The scale divisions on the Y-axis are 10% frequency intervals. A key to the species treated in each histogram is provided below.

1. *Buellia subcoronata*
2. *Cladia aggregata*
3. *Heterodea mülleri*
4. *Lecidea coarctata.*
5. *Lecidea psammophila*
6. *Parmelia amphixantha*
7. *Parmelia pulla*
8. *Lecanora atra*
9. *Siphula coriacea*
10. *Lecidea planata*
11. *Parmelia conspersa*
12. *Cladonia* squamules
13. *Endocarpon pusillum*
14. *Diploschistes scruposus*
15. *Lecidea decipiens*
16. *Heppia polyspora*
17. *Buellia epigaea*
18. *Parmelia molliuscula*
19. *Caloplaca subpyracella*
20. *Synalissa* sp.
21. *Acarospora smaragdula*
22. *Diploschistes ocellatus*
23. *Parmelia australiensis*
24. *Chondropsis semiviridis*
25. *Heppia lutosa*
26. *Aspicilia calcarea*
27. *Dermatocarpon lachneum*
28. *Collema coccophorus*
29. *Lecidea crystallifera*
30. *Fulgensia bracteata*
31. *Toninia caeruleonigricans*
32. *Aspicilia calcarea* mod. *fruticosa*


SPECIES FREQUENCY
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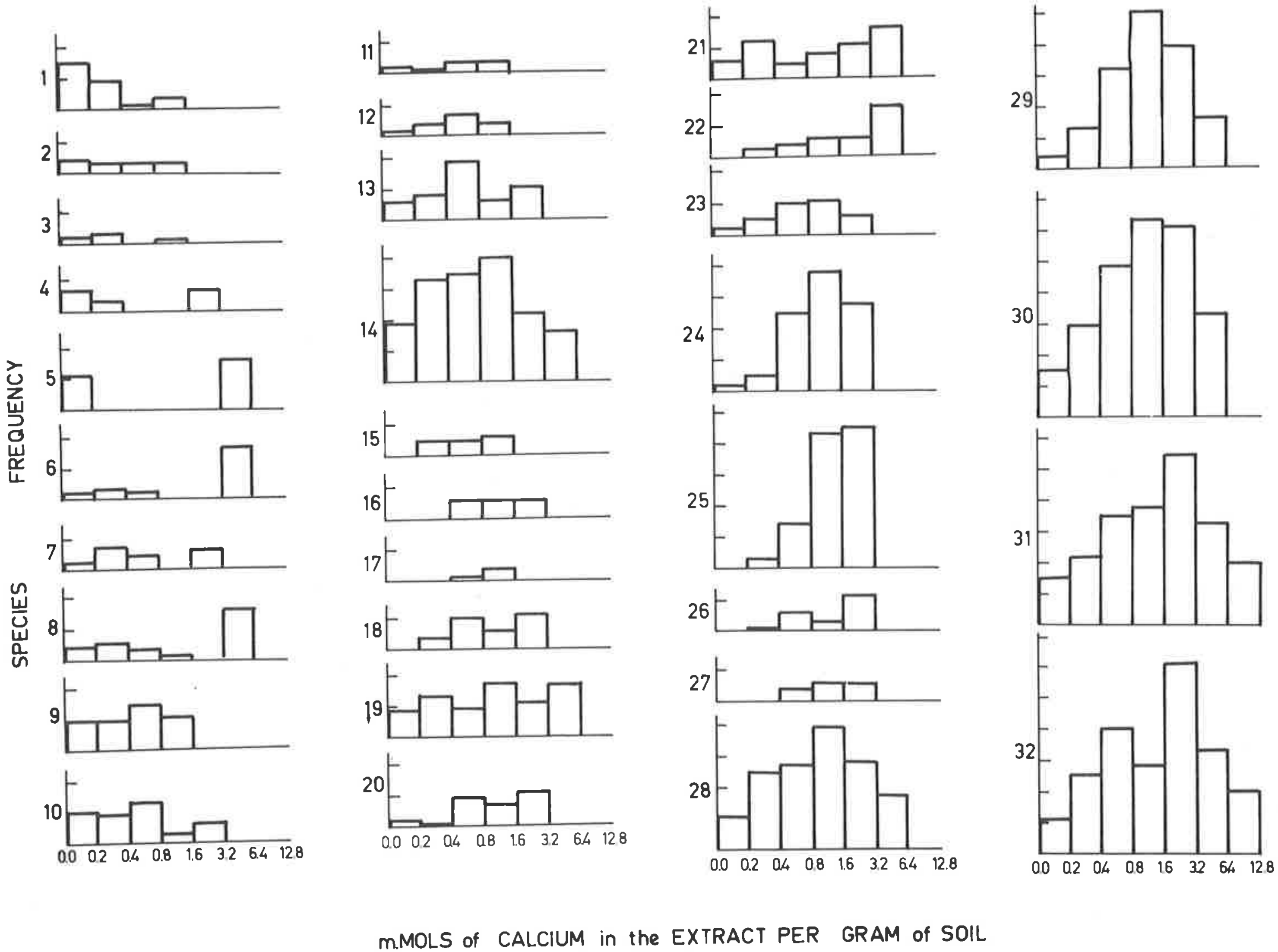
pH of SOIL EXTRACT

FIGURE 6.3

Histograms showing the relationship between species-frequency (Y-axis) and calcium concentration (X-axis). The scale divisions on the Y-axis are 10% frequency intervals; the class intervals on the X-axis are logarithmic. A key to the species treated in each histogram is provided below.

1. *Lecidea planata*
2. *Siphula coriacea*
3. *Heterodea mülleri*
4. *Lecidea psammophila*
5. *Buellia subcoronata*
6. *Lecanora atra*
7. *Cladia aggregata*
8. *Lecidea coarctata*
9. *Heppia lutosa*
10. *Heppia polyspora*
11. *Parmelia conspersa*
12. *Caloplaca subpyracella*
13. *Aspicilia calcarea*
14. *Endocarpon pusillum*
15. *Acarospora smaragdula*
16. *Aspicilia calcarea* mod.*fruticosa*
17. *Buellia epigaea*
18. *Chondropsis semiviridis*
19. *Parmelia australiensis*
20. *Cladonia* squamules
21. *Parmelia amphixantha*
22. *Parmelia pulla*
23. *Synalissa* sp.
24. *Toninia caeruleonigricans*
25. *Fulgensia bracteata*
26. *Parmelia molliuscula*
27. *Diploschistes ocellatus*
28. *Diploschistes scruposus*
29. *Lecidea crystallifera*
30. *Lecidea decipiens*
31. *Dermatocarpon lachneum*
32. *Collema coccophorus*



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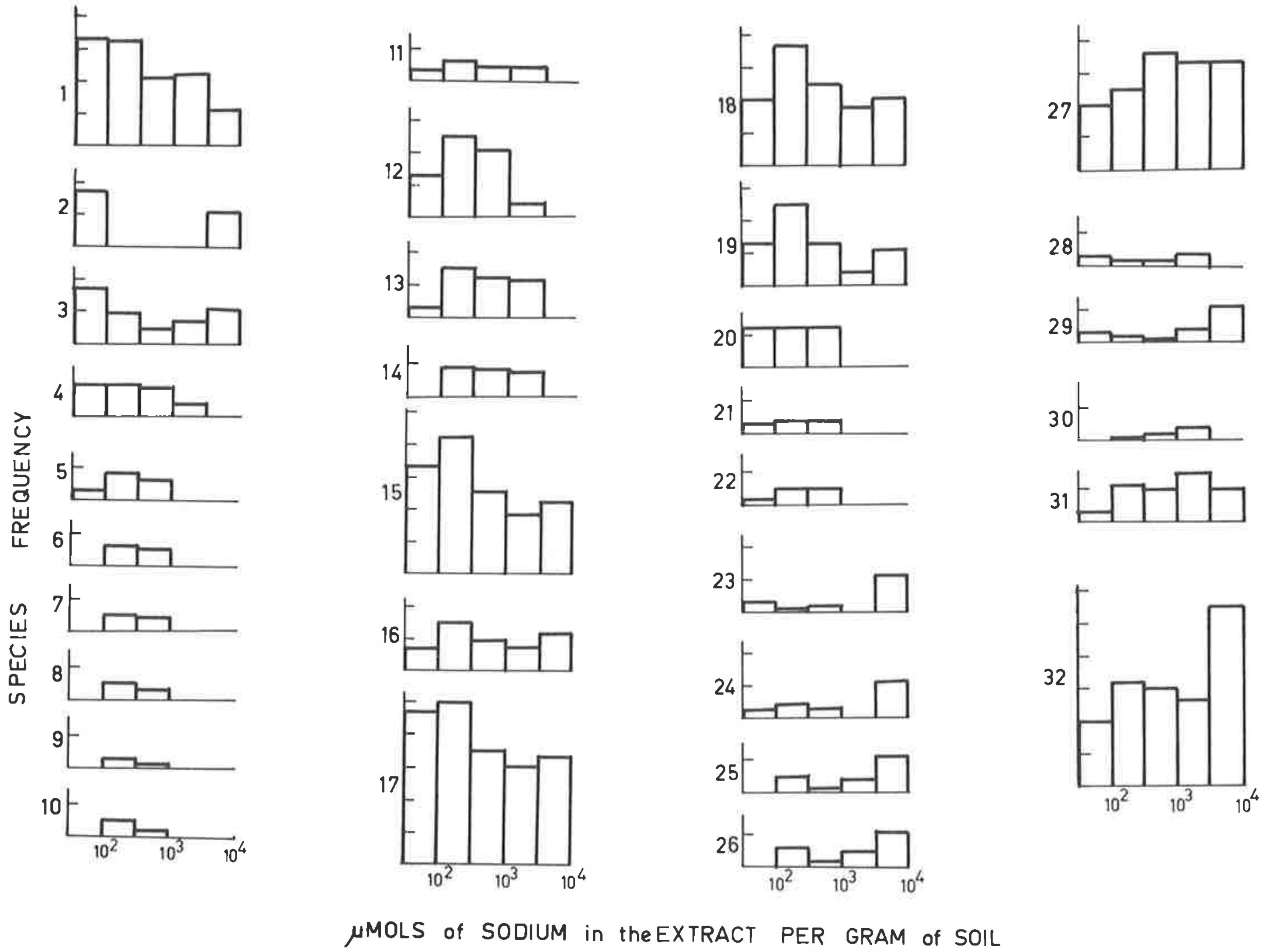
m.MOLS of CALCIUM in the EXTRACT PER GRAM of SOIL

FIGURE 6.4

Histograms showing the relationship between species-frequency (Y-axis) and sodium concentration (X-axis). The scale divisions on the Y-axis are 10% frequency intervals; the class intervals on the X-axis are logarithmic. A key to the species treated in each histogram is provided below.

1. *Diploschistes scruposus*
2. *Buellia subcoronata*
3. *Parmelia amphixantha*
4. *Heppia polyspora*
5. *Chondropsis semiviridis*
6. *Caloplaca subpyracella*
7. *Cladia aggregata*
8. *Aspicilia calcarea* mod. *fruticosa*
9. *Buellia epigaea*
10. *Diploschistes ocellatus*
11. *Acarospora smaragdula*
12. *Toninia caeruleonigricans*
13. *Cladonia* squamules
14. *Synalissa* sp.
15. *Endocarpon pusillum*
16. *Aspicilia calcarea*
17. *Lecidea decipiens*
18. *Lecidea crystallifera*
19. *Fulgensia bracteata*
20. *Parmelia australiensis*
21. *Parmelia molliuscula*
22. *Lecidea planata*
23. *Lecanora atra*
24. *Lecidea coarctata*
25. *Siphula coriacea*
26. *Parmelia pulla*
27. *Dermatocarpon lachneum*
28. *Parmelia conspersa*
29. *Lecidea psammophila*
30. *Heterodea mülleri*
31. *Heppia lutosa*
32. *Collema coccophorus*



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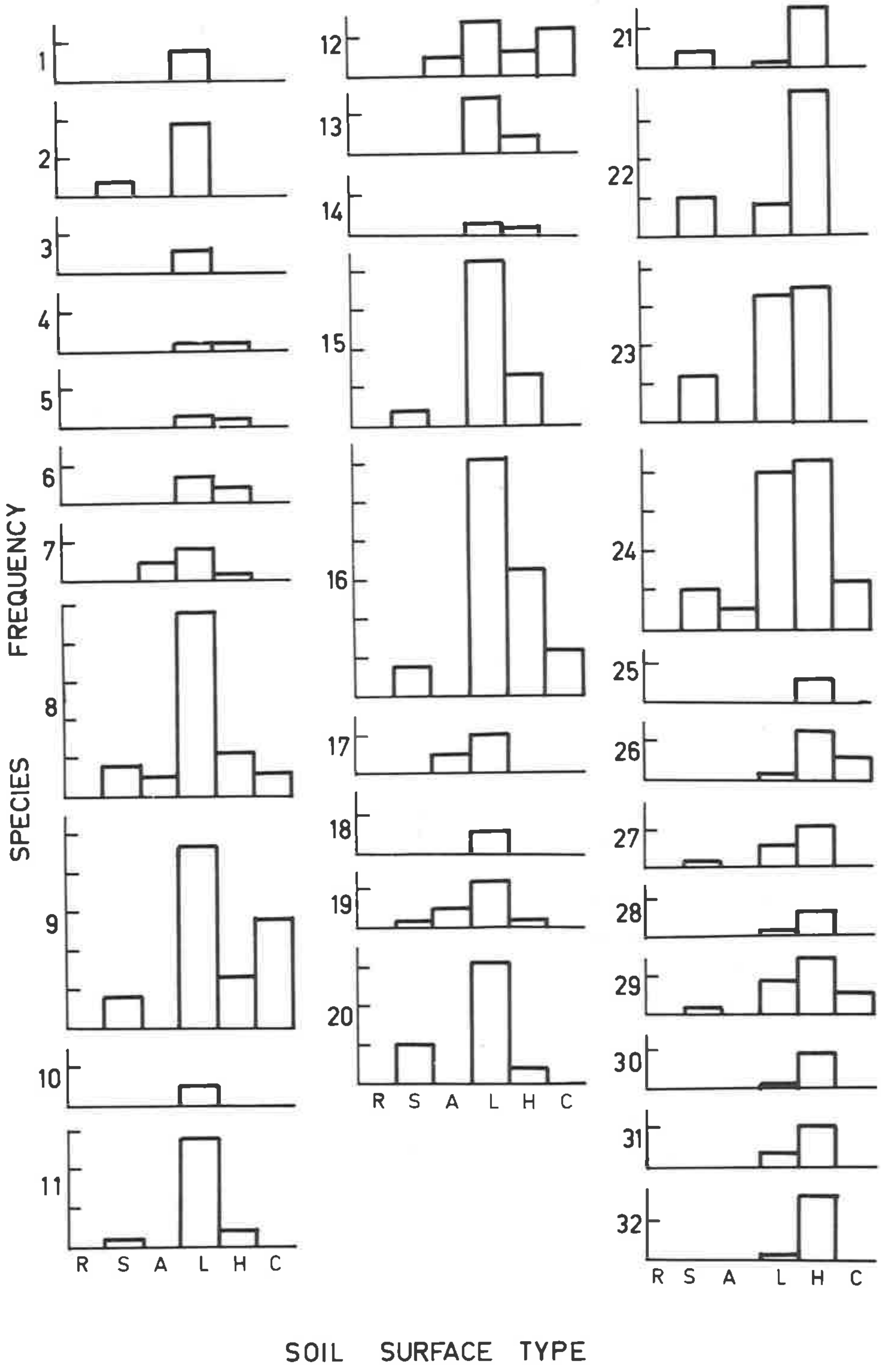
µMOLS of SODIUM in the EXTRACT PER GRAM of SOIL

FIGURE 6.5

Histograms showing the relationship between species-frequency (Y-axis) and nature of the soil surface (X-axis). The scale divisions on the Y-axis are 10% frequency intervals. The letters on the X-axis refer to Rock, Sand, Amorphous, Loam, Hard-setting and Clay surfaces respectively. A key to the species treated in each histogram is provided below.

1. *Cladia aggregata*
2. *Cladonia* squamules
3. *Diploschistes scruposus*
4. *Endocarpon pusillum*
5. *Heterodea müllerí*
6. *Lecidea coarctata*
7. *Lecidea planata*
8. *Lecidea psammophila*
9. *Parmelia amphixantha*
10. *Parmelia conspersa*
11. *Parmelia pulla*
12. *Siphula coriacea*
13. *Acarospora smaragdula*
14. *Aspicilia calcarea*
15. *Aspicilia calcarea* mod. *fruticosa*
16. *Buellia epigaea*
17. *Buellia subcoronata*
18. *Caloplaca subpyracella*
19. *Chondropsis semiviridis*
20. *Collema coccophorus*
21. *Dermatocarpon lachneum*
22. *Diploschistes ocellatus*
23. *Fulgensia bracteata*
24. *Heppia lutosa*
25. *Heppia polyspora*
26. *Lecanora atra*
27. *Lecidea crystallifera*
28. *Lecidea decipiens*
29. *Parmelia australiensis*
30. *Parmelia molliuscula*
31. *Synalissa* sp.
32. *Toninia caeruleonigricans*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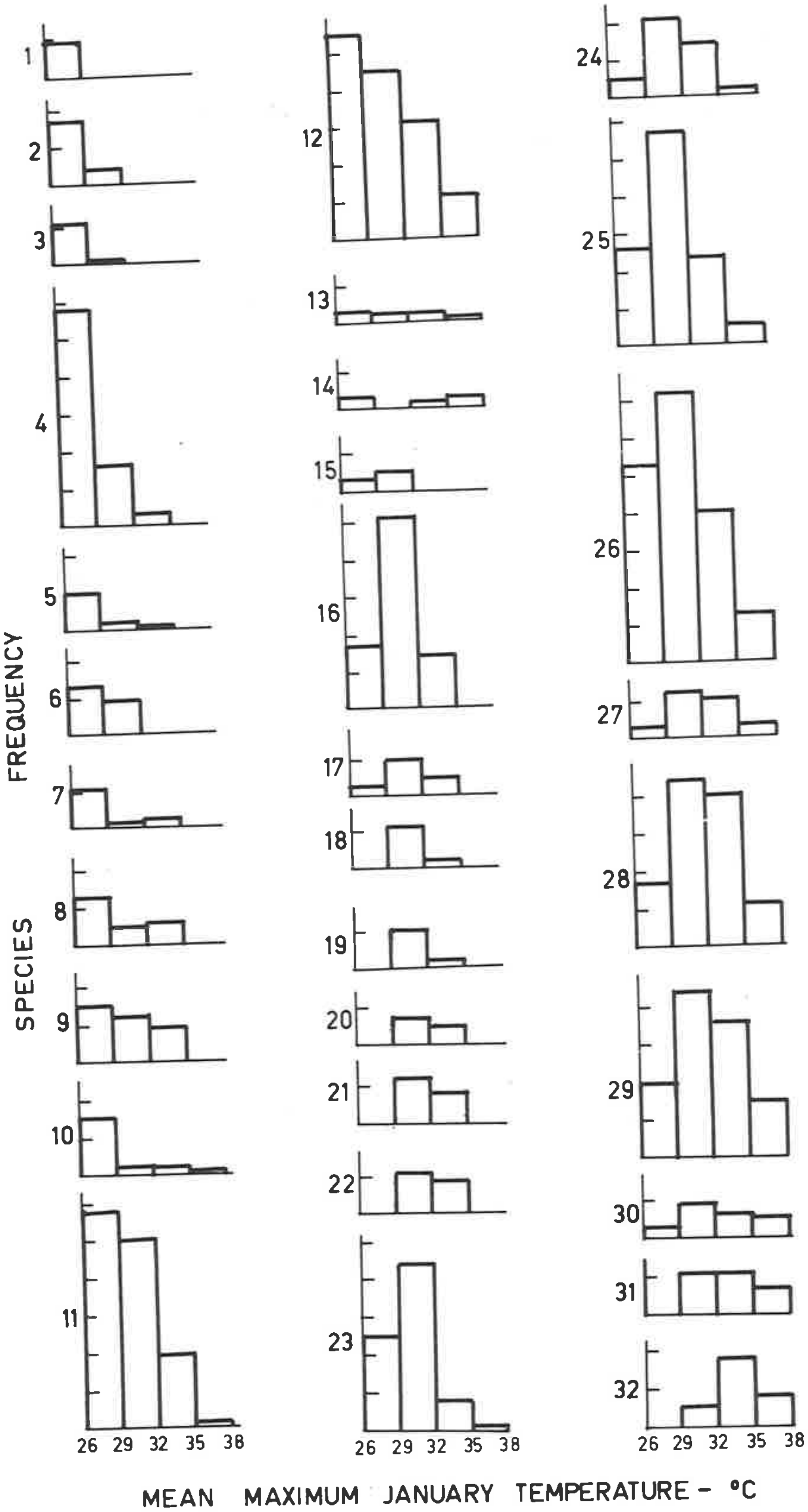
SOIL SURFACE TYPE

FIGURE 6.6

Histograms showing the relationship between species - frequency (Y-axis) and mean daily maximum temperature for January (X-axis). The scale divisions on the Y-axis are 10% frequency intervals. A key to the species treated in each histogram is provided below.

1. *Heterodea müller*
2. *Siphula coriacea*
3. *Cladia aggregata*
4. *Cladonia* squamules
5. *Parmelia conspersa*
6. *Parmelia pulla*
7. *Lecidea psammophila*
8. *Lecidea planata*
9. *Parmelia amphixantha*
10. *Lecidea coarctata*
11. *Diploschistes scruposus*
12. *Endocarpon pusillum*
13. *Lecanora atra*
14. *Buellia subcoronata*
15. *Buellia epigaea*
16. *Toninia caeruleonigricans*
17. *Acarospora smaragdula*
18. *Parmelia molliuscula*
19. *Diploschistes ocellatus*
20. *Aspicilia calcarea* mod. *fruticosa*
21. *Chondropsis semiviridis*
22. *Parmelia australiensis*
23. *Fulgensia bracteata*
24. *Aspicilia calcarea*
25. *Lecidea crystallifera*
26. *Lecidea decipiens*
27. *Synalissa* sp.
28. *Collema coccophorus*
29. *Dermatocarpon lachneum*
30. *Caloplaca subpyracella*
31. *Heppia polyspora*
32. *Heppia lutosa*



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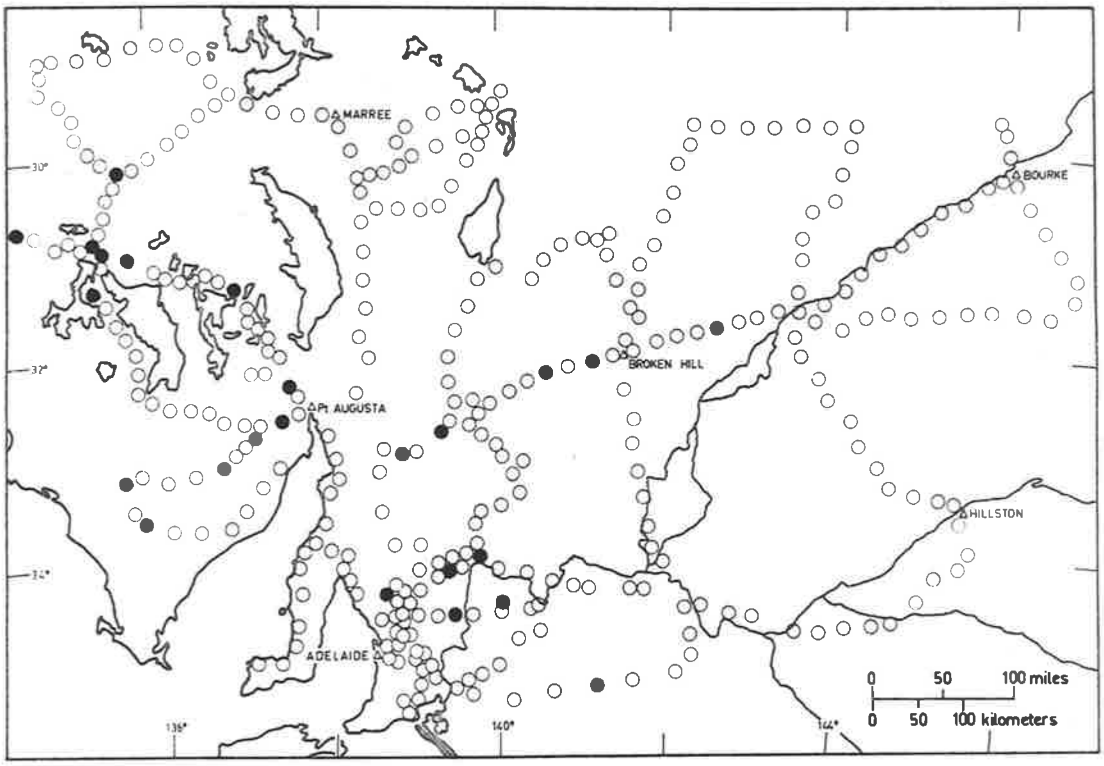
MEAN MAXIMUM JANUARY TEMPERATURE - °C

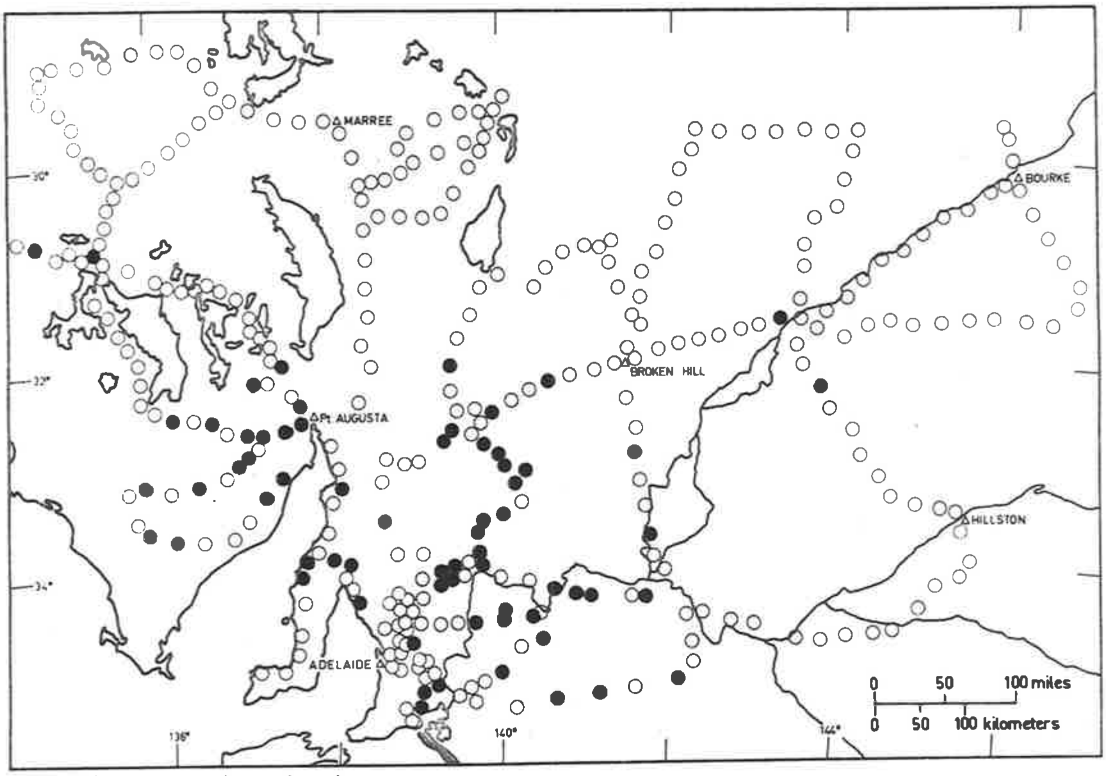
FIGURE 6.7

Histogram showing the relationship between the frequency of lichen-crust formation (Y-axis) and selected environmental variables (X-axis). The scale divisions on the Y-axis are 10% frequency intervals. A key to the environmental variable treated in each histogram is provided below: further explanation of each appears either in the text or in the preceding figures dealing with the relationship between species-frequency and environmental variables.

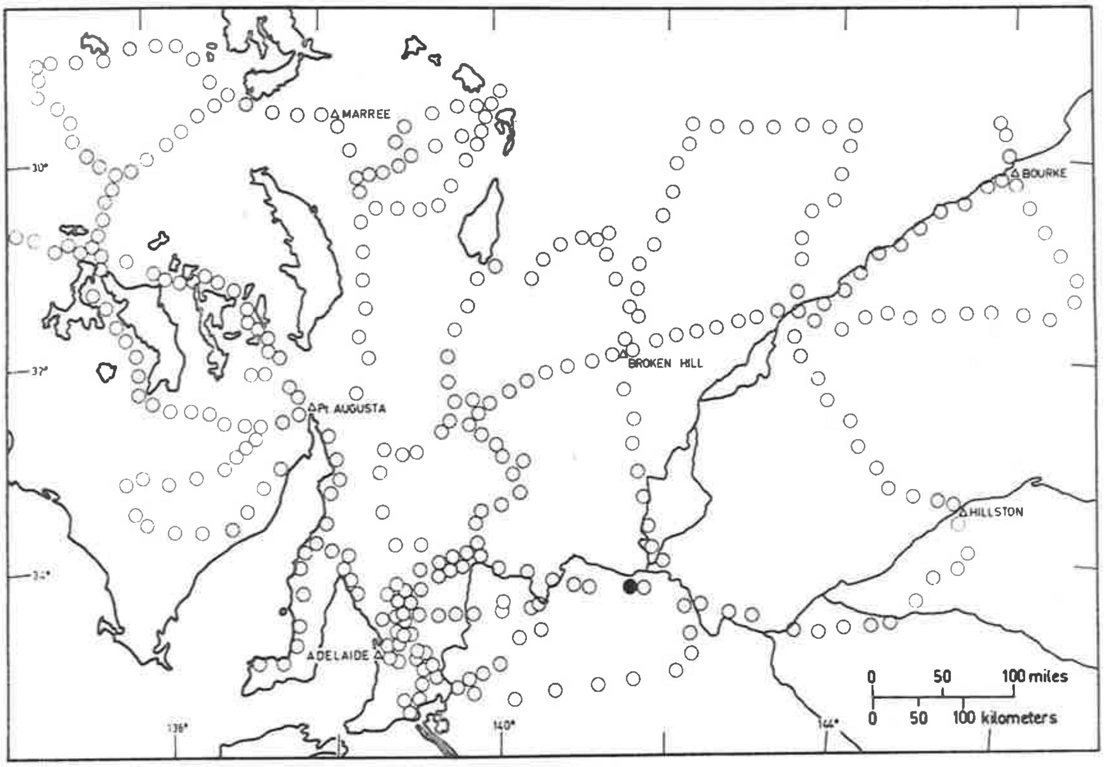
1. Mean annual rainfall.
2. pH of the soil-extract.
3. Extracted calcium / gram of soil.
4. Extracted sodium / gram of soil.
5. Nature of the soil surface.
6. Mean daily maximum temperature for January.



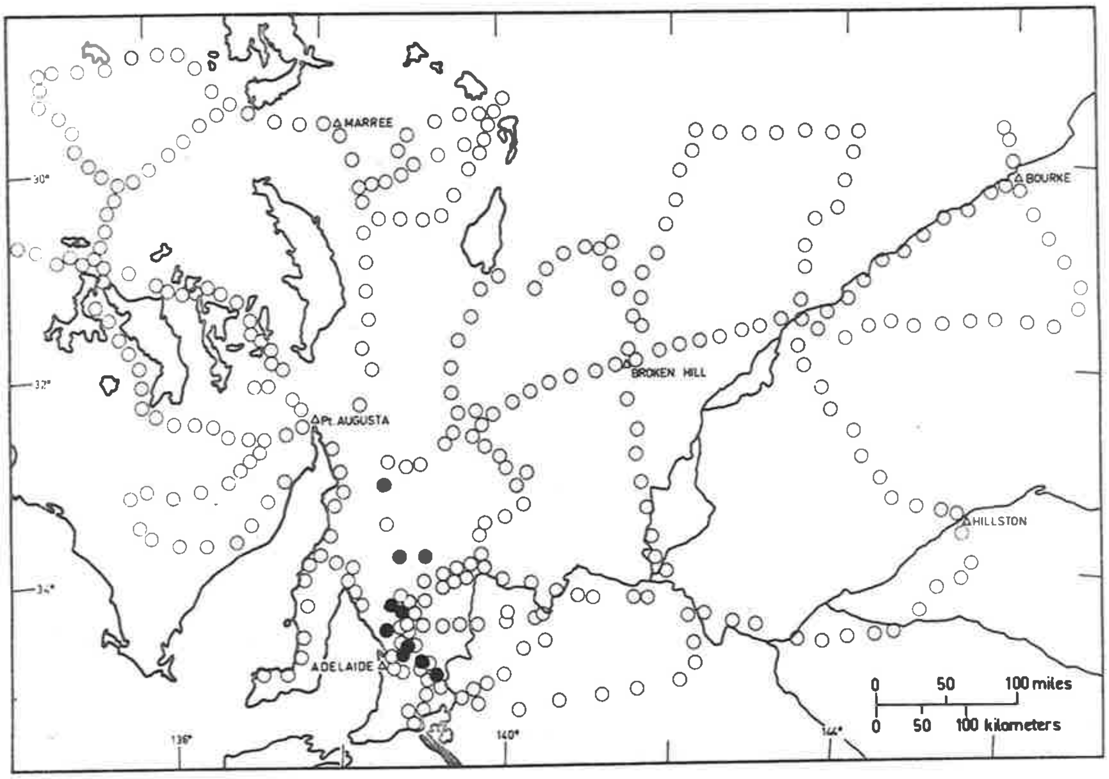
Synalissa sp.



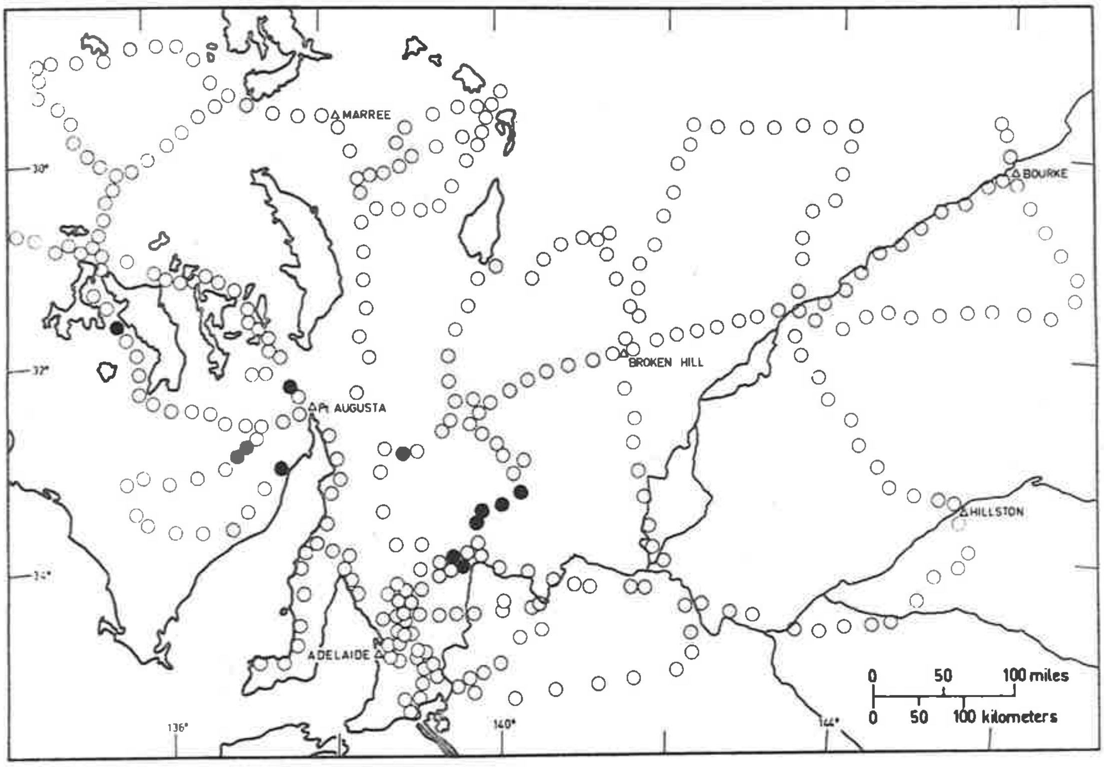
Toninia caeruleonigricans



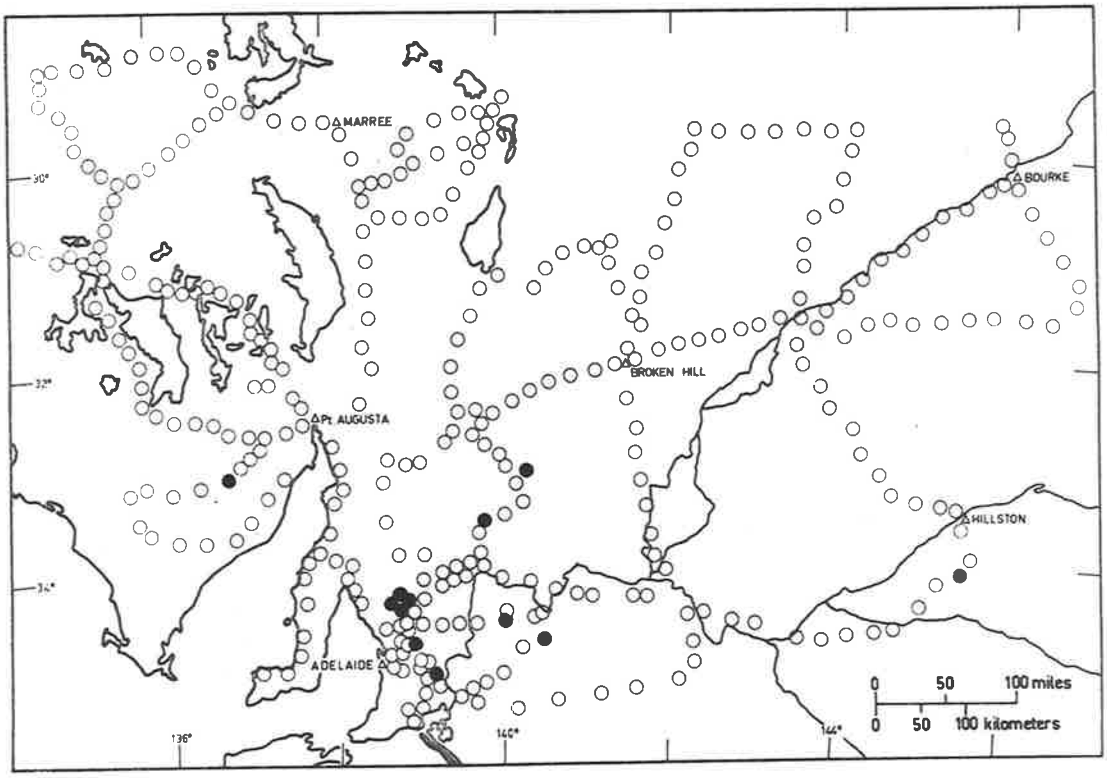
? Rinodina orbata



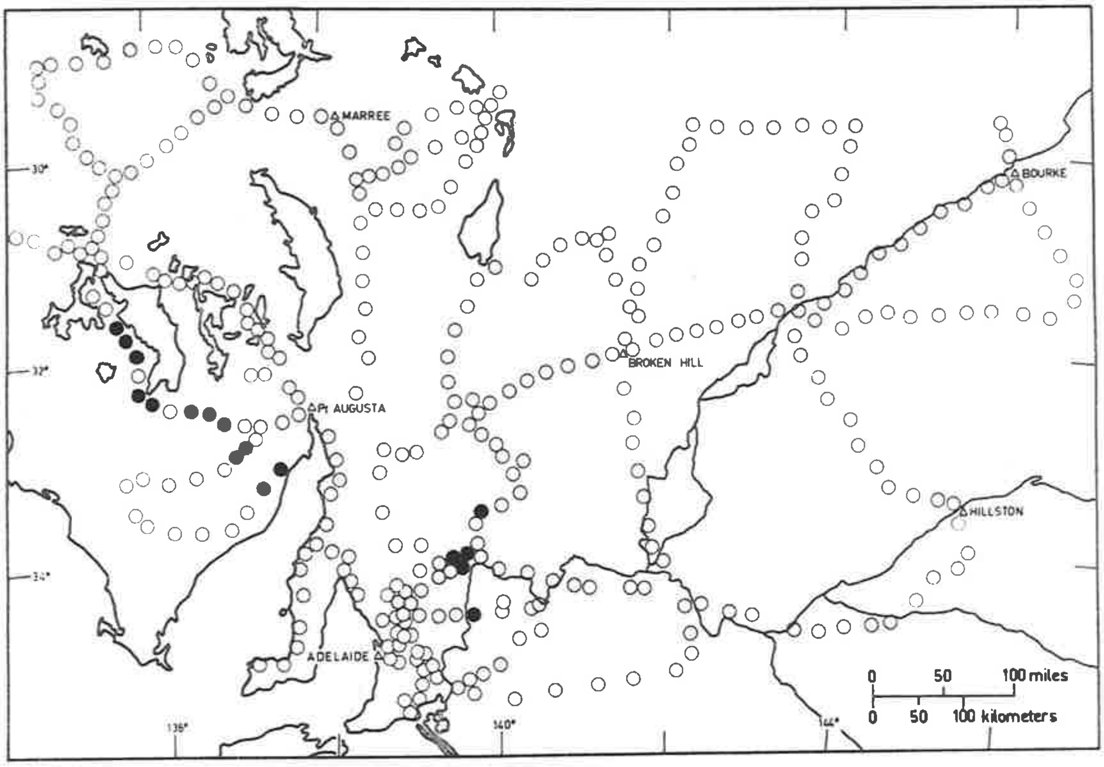
Siphula coriacea



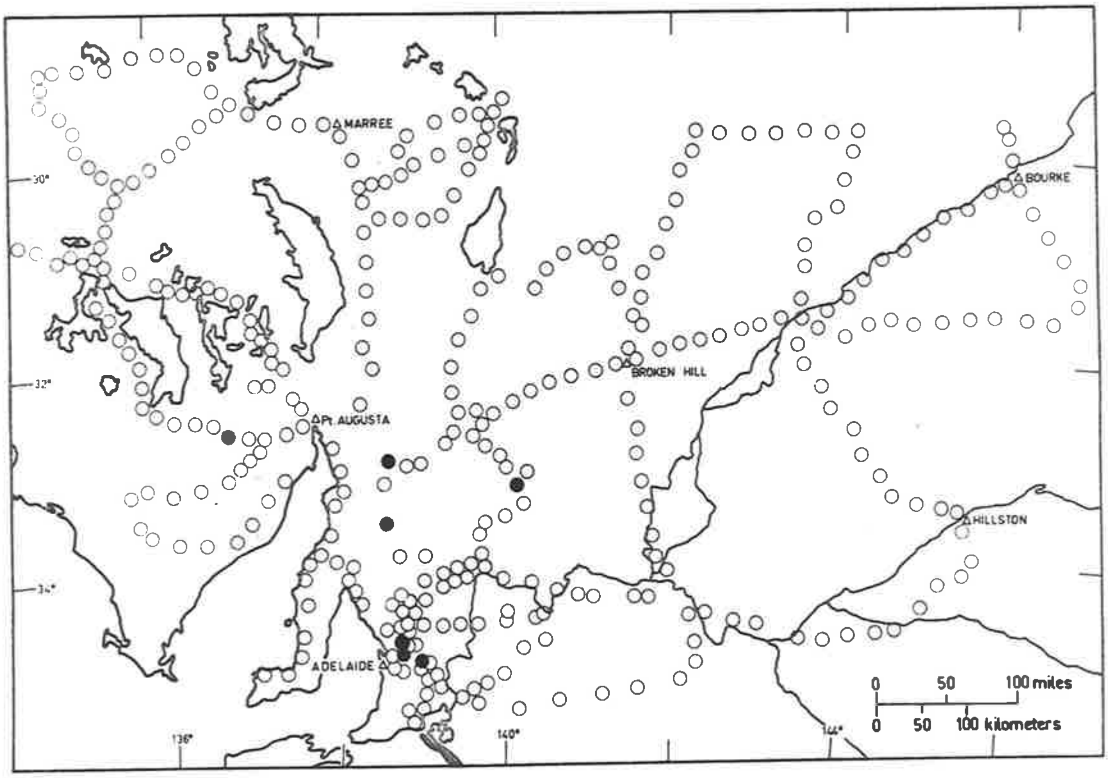
Parmelia molliuscula



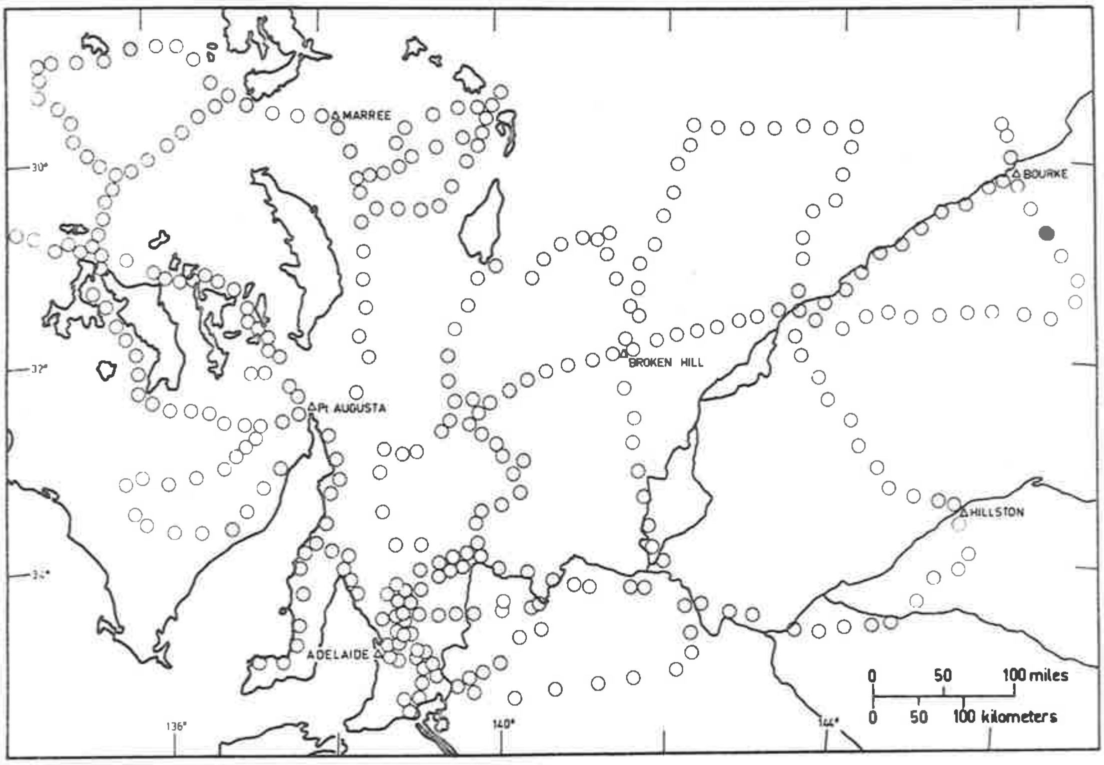
Parmelia pulla



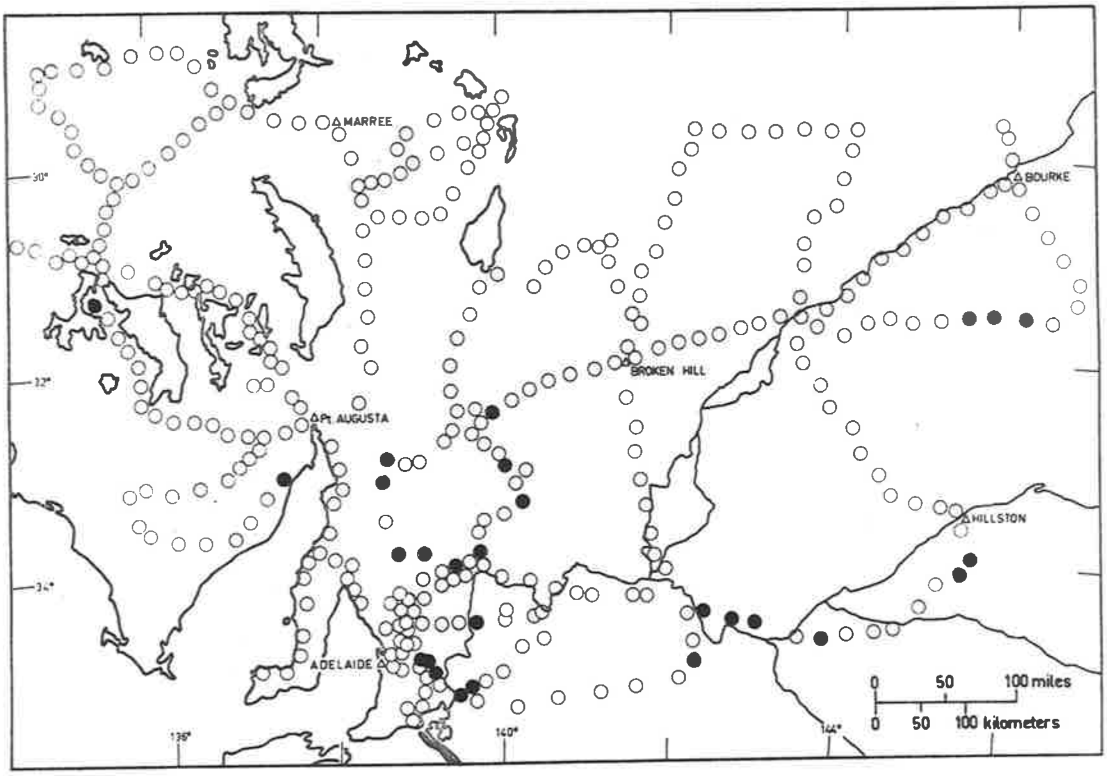
Parmelia australiensis



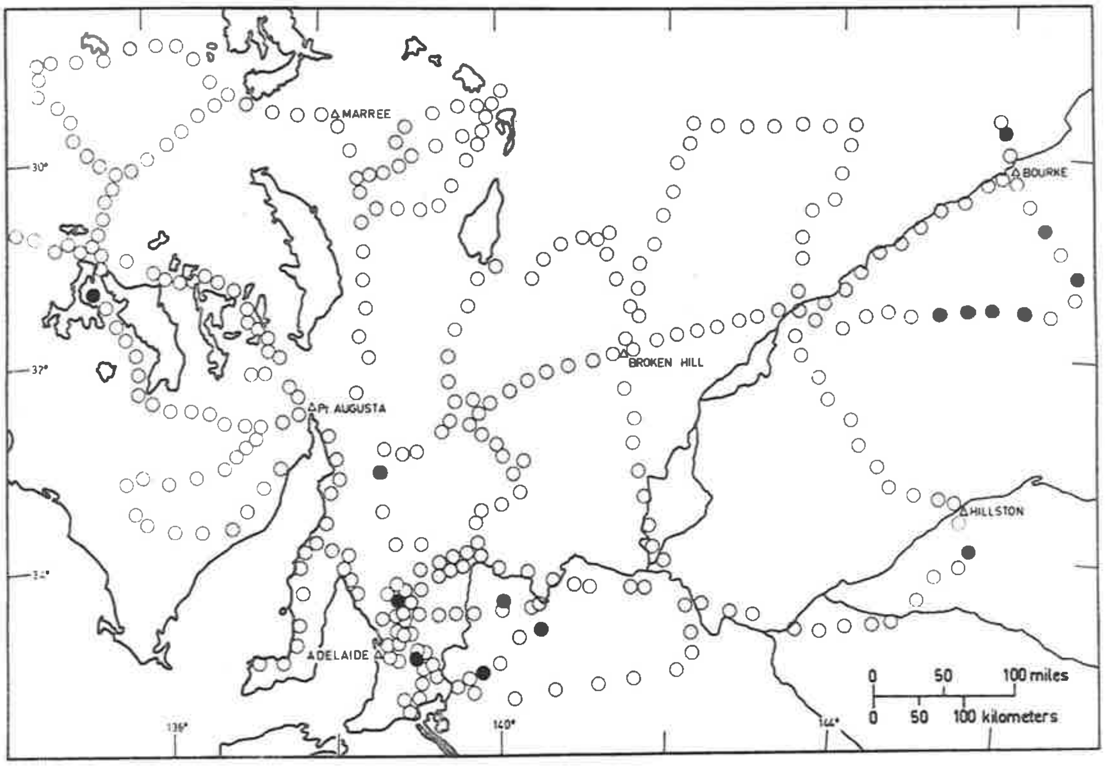
Parmelia conspersa



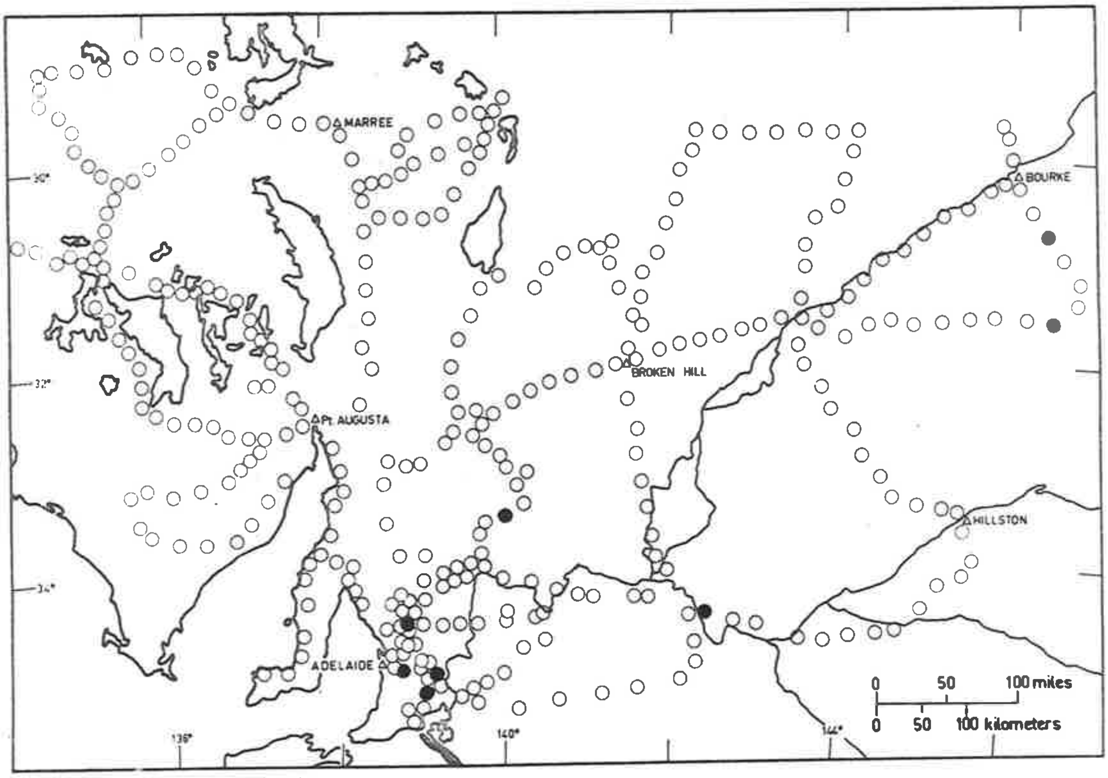
Lecidea sp.



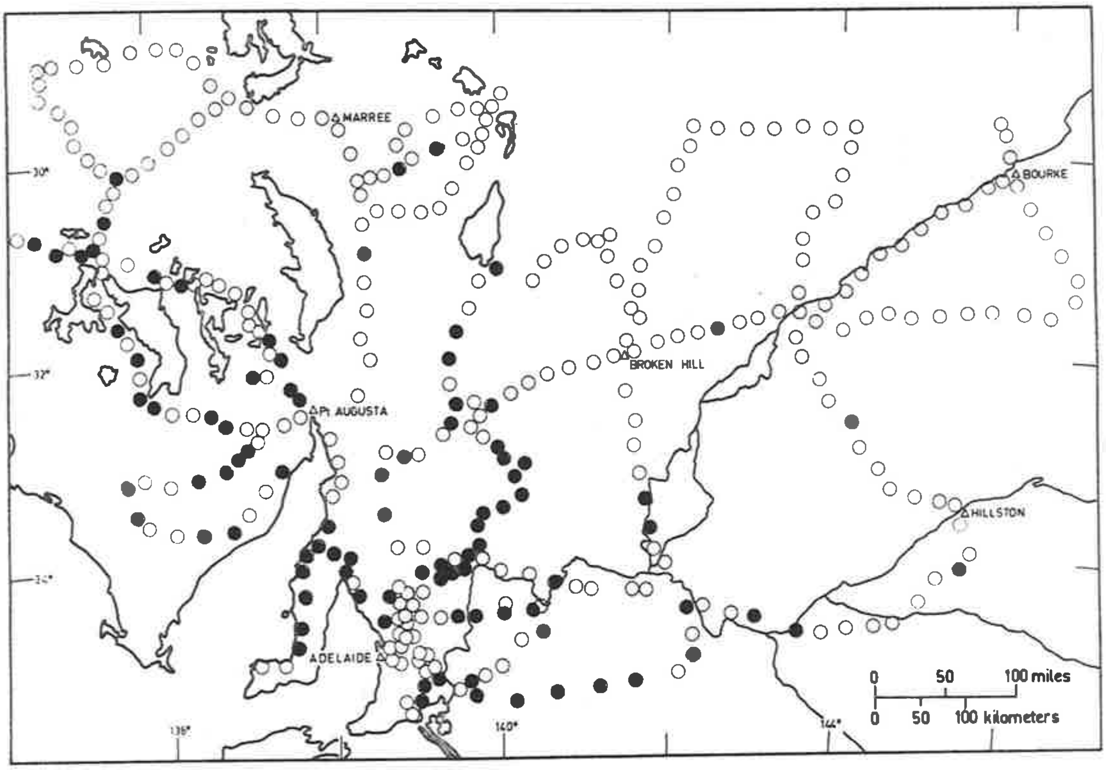
Parmelia amphixantha



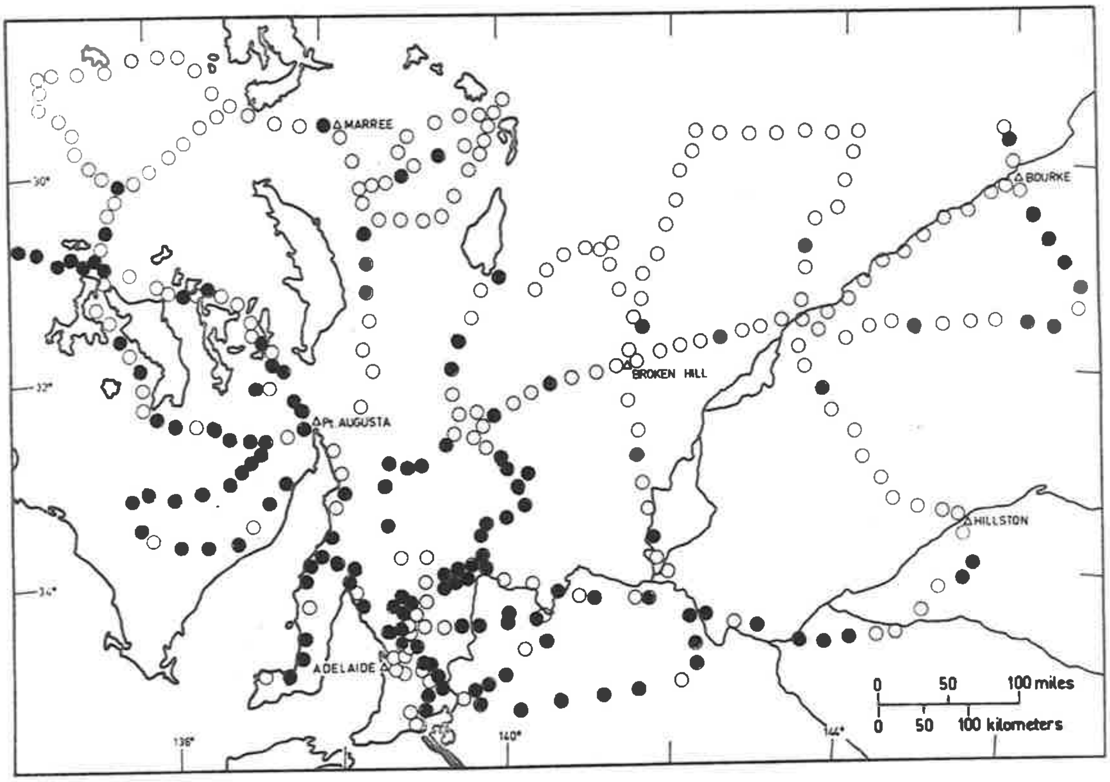
Lecidea planata



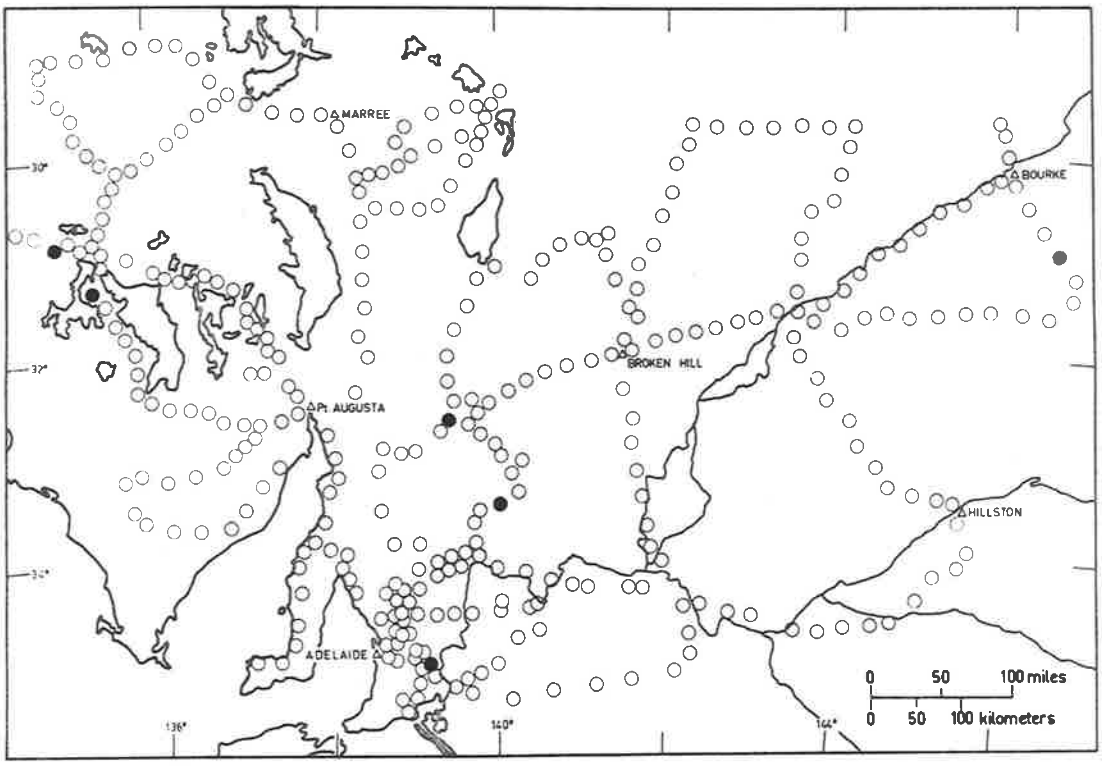
Lecidea psammophila



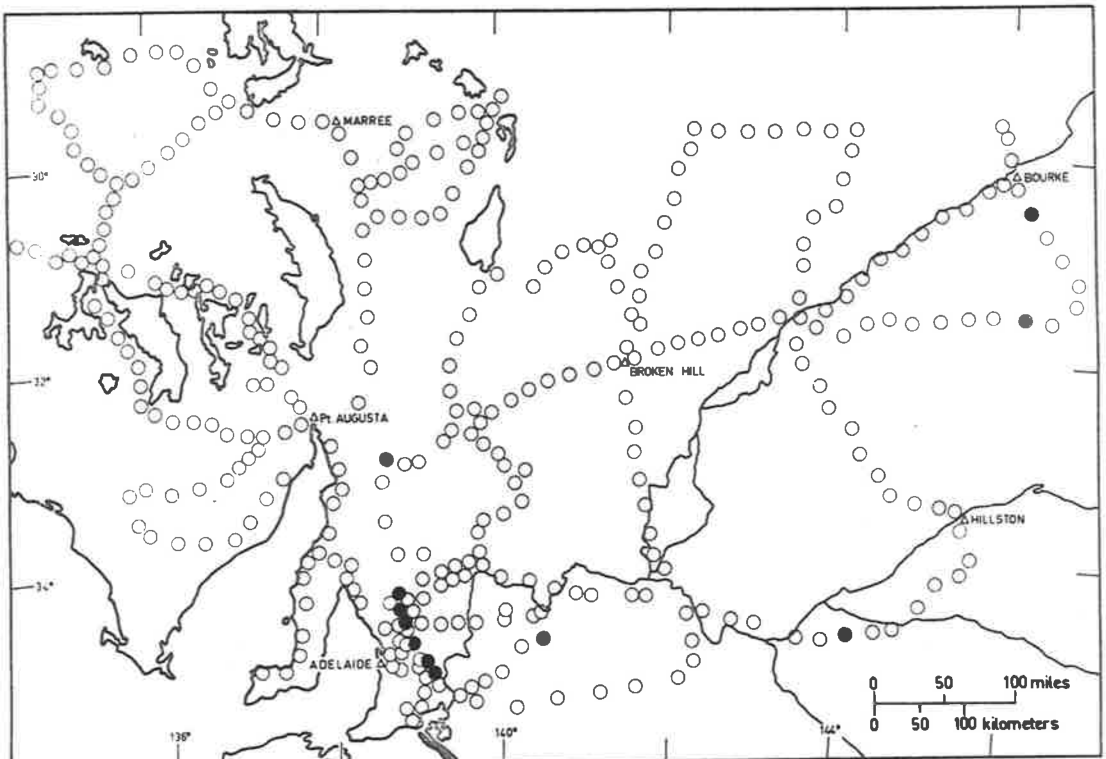
Lecidea crystallifera



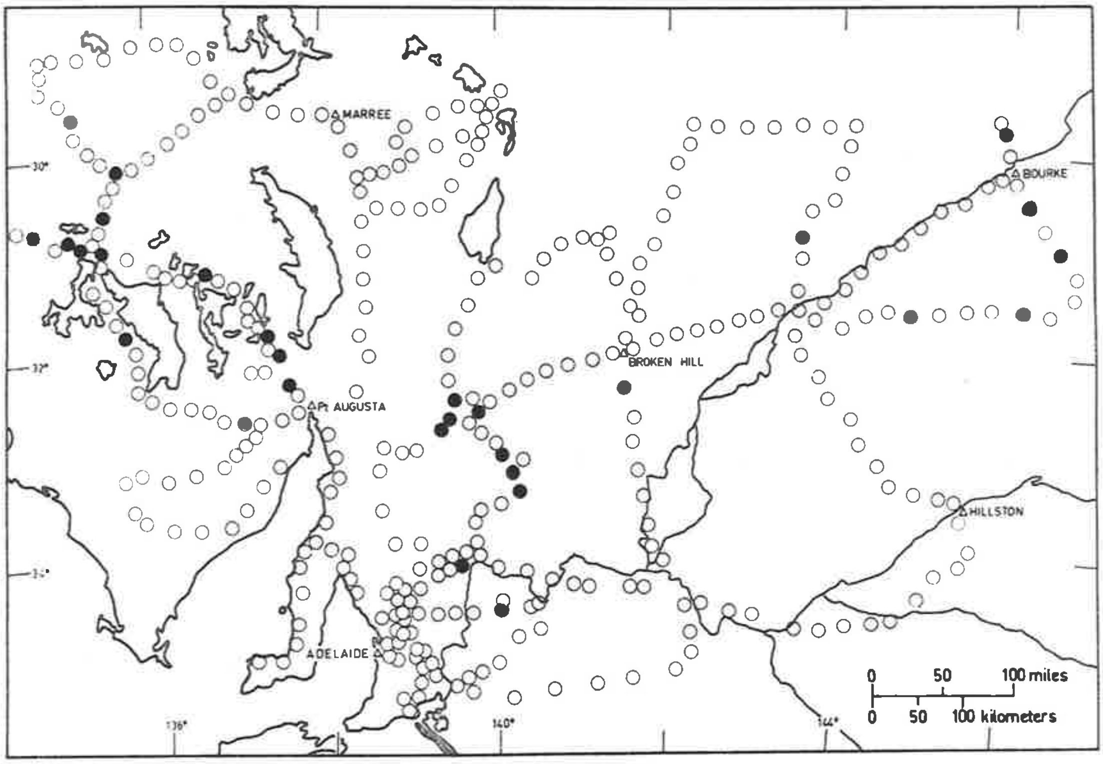
Lecidea decipiens



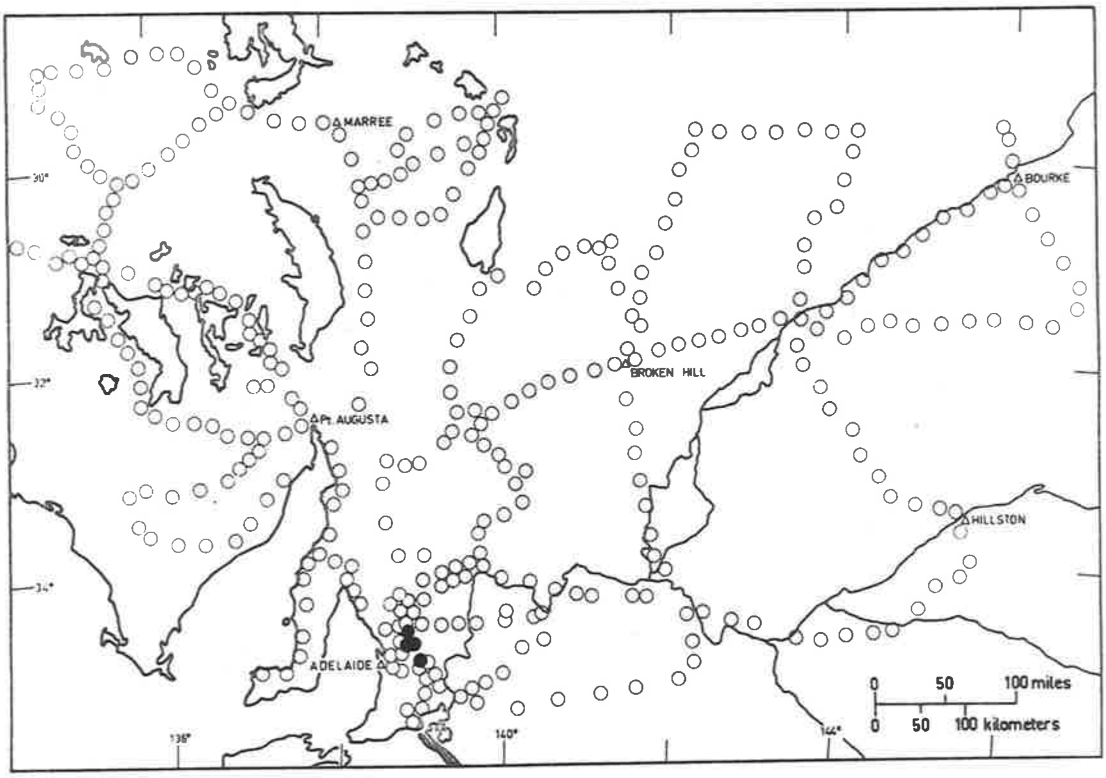
Lecanora atra



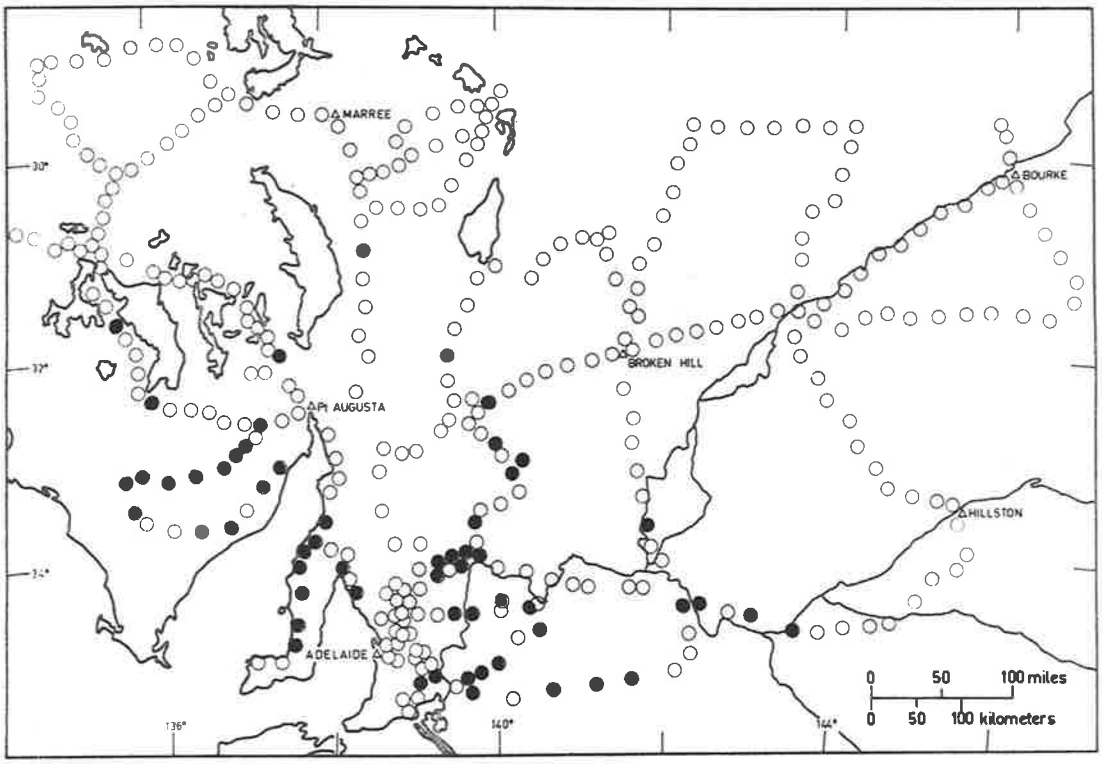
Lecidea coarctata



Heppia polyspora



Heterodea mülleri



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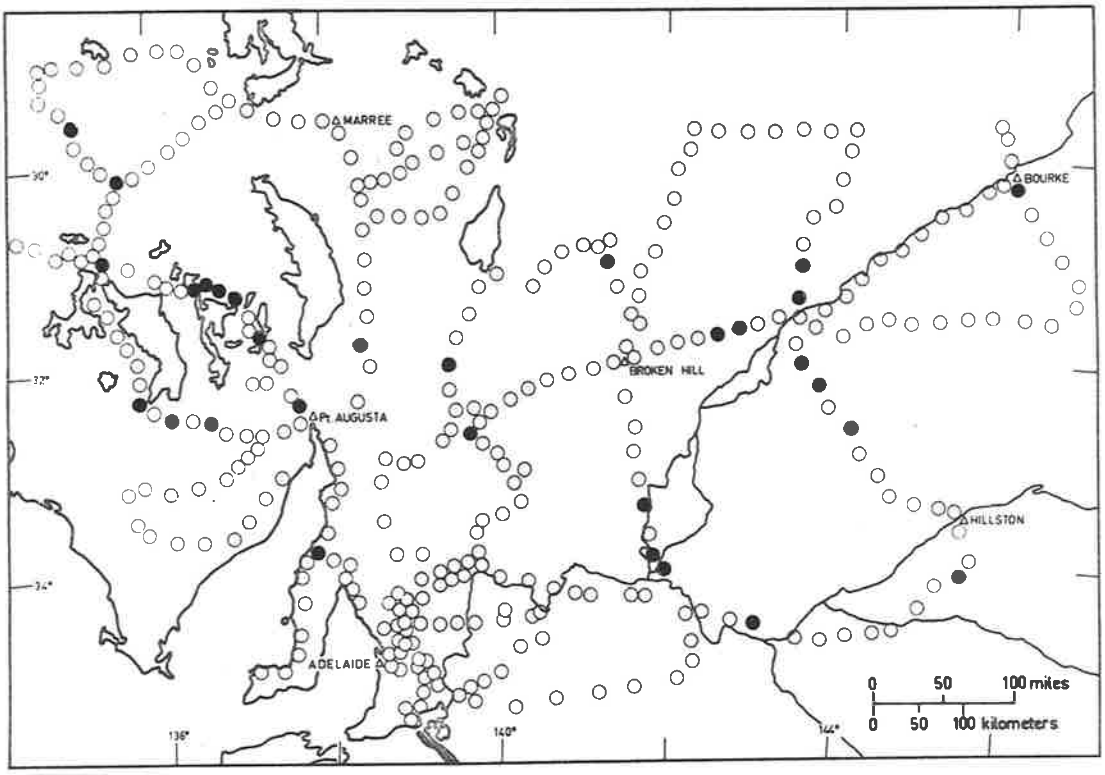
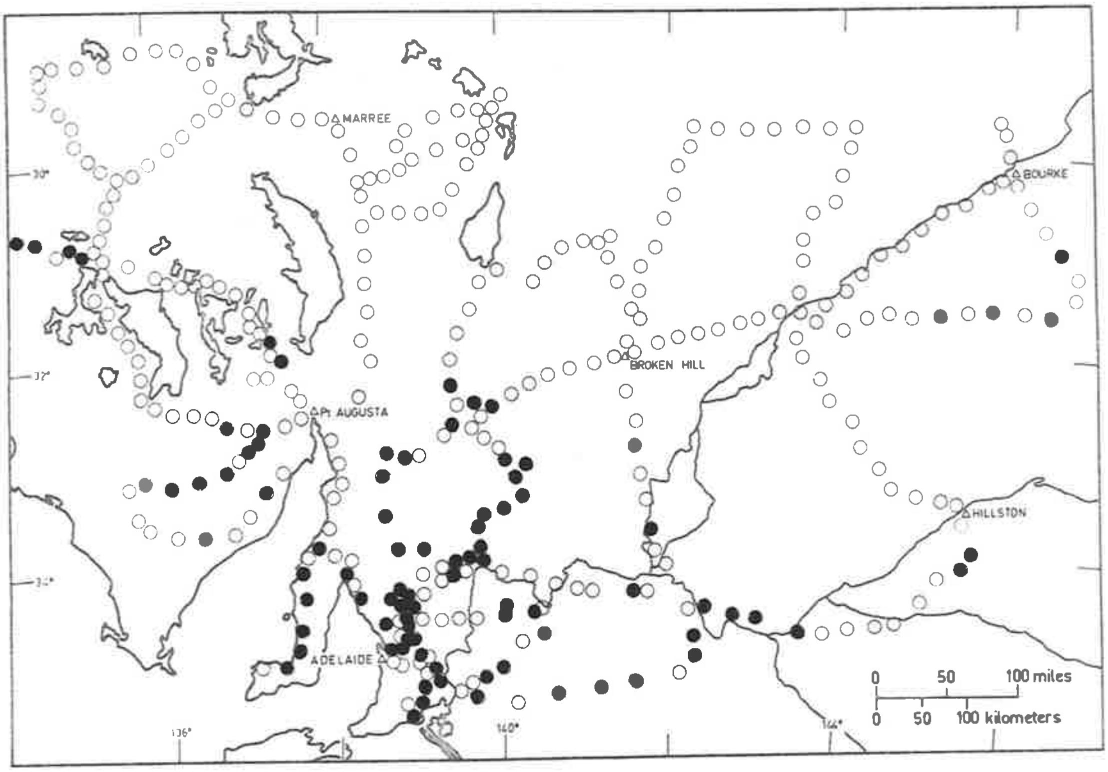
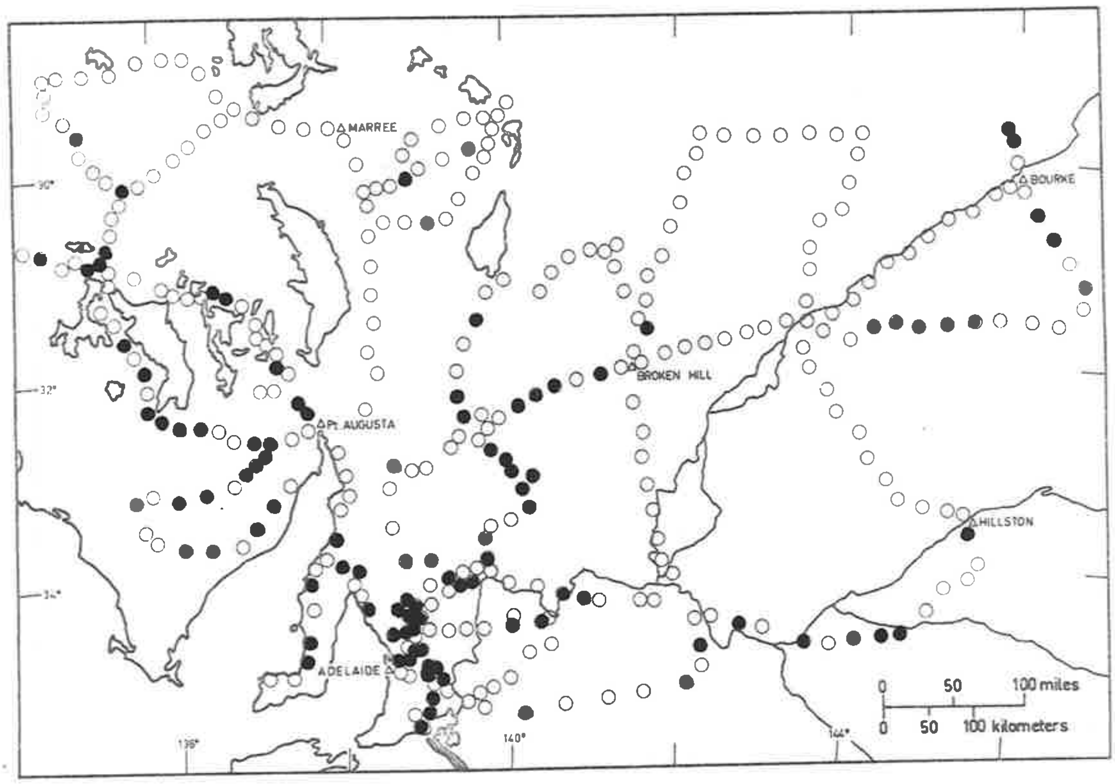


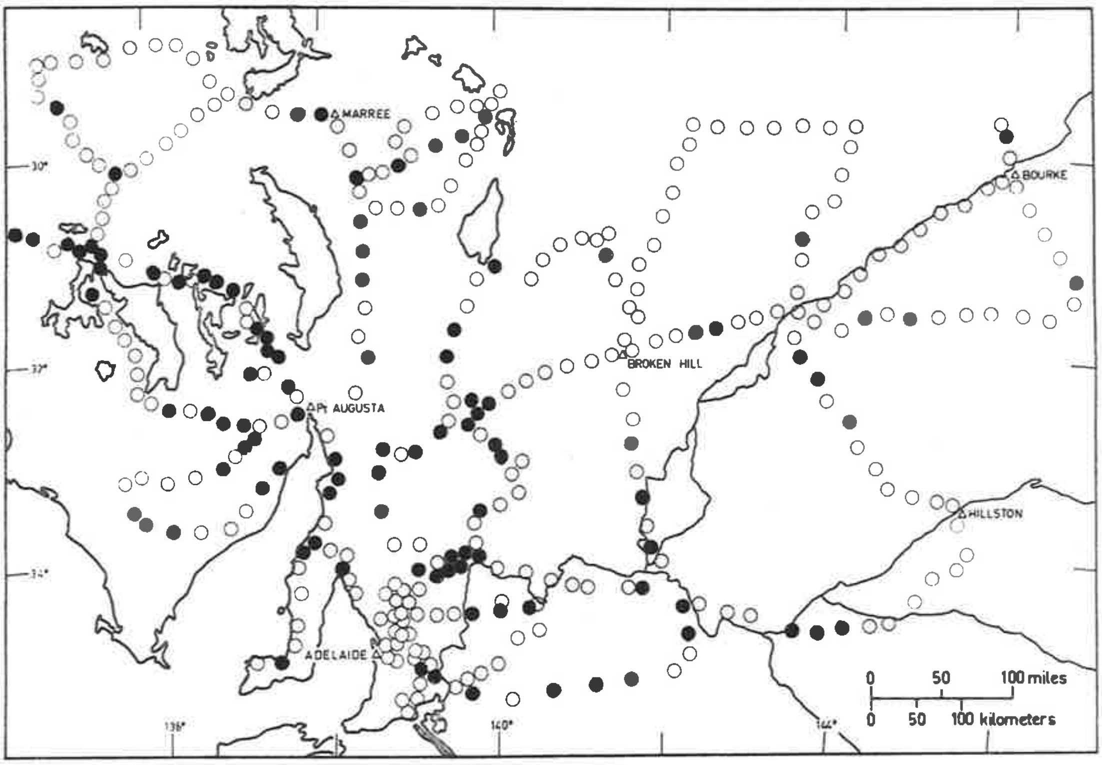
Heppia lutosa



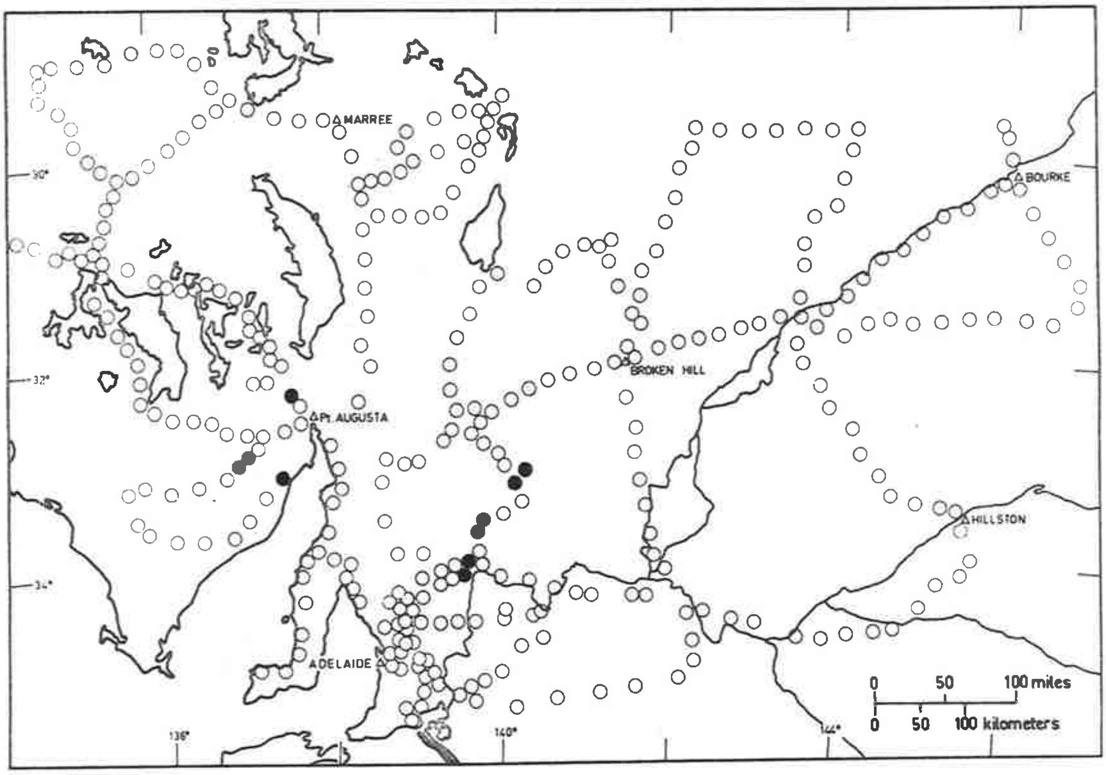
Diploschistes scruposus



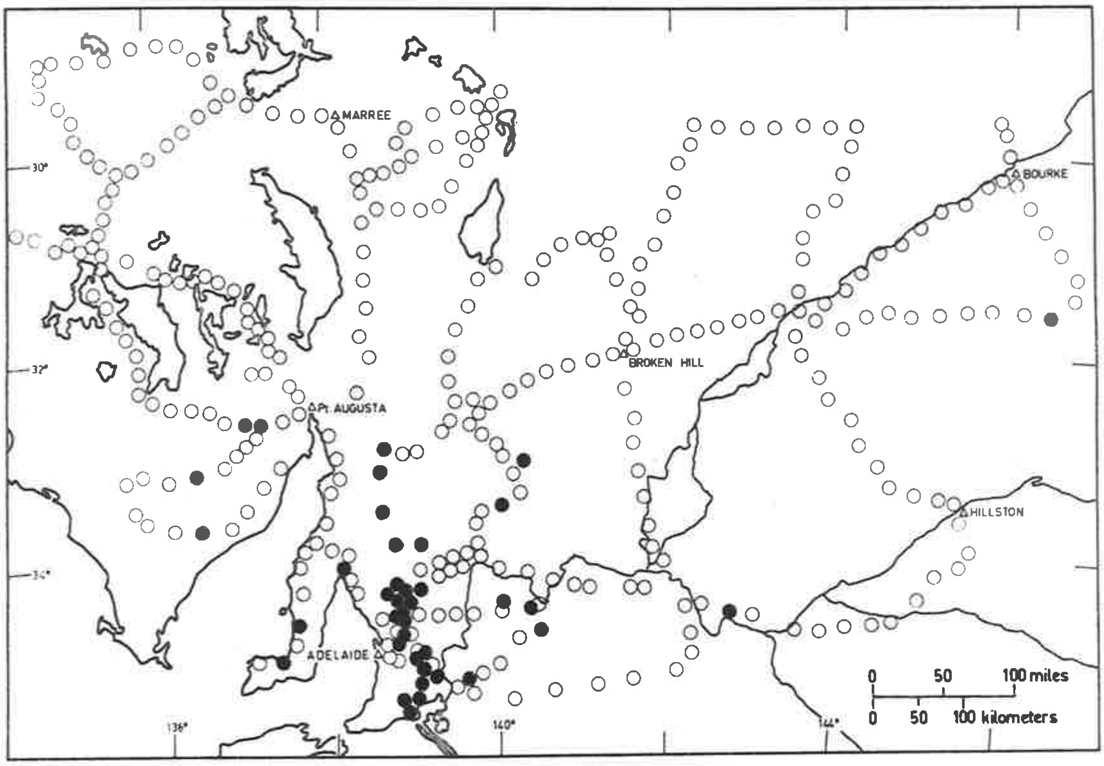
Endocarpon pusillum



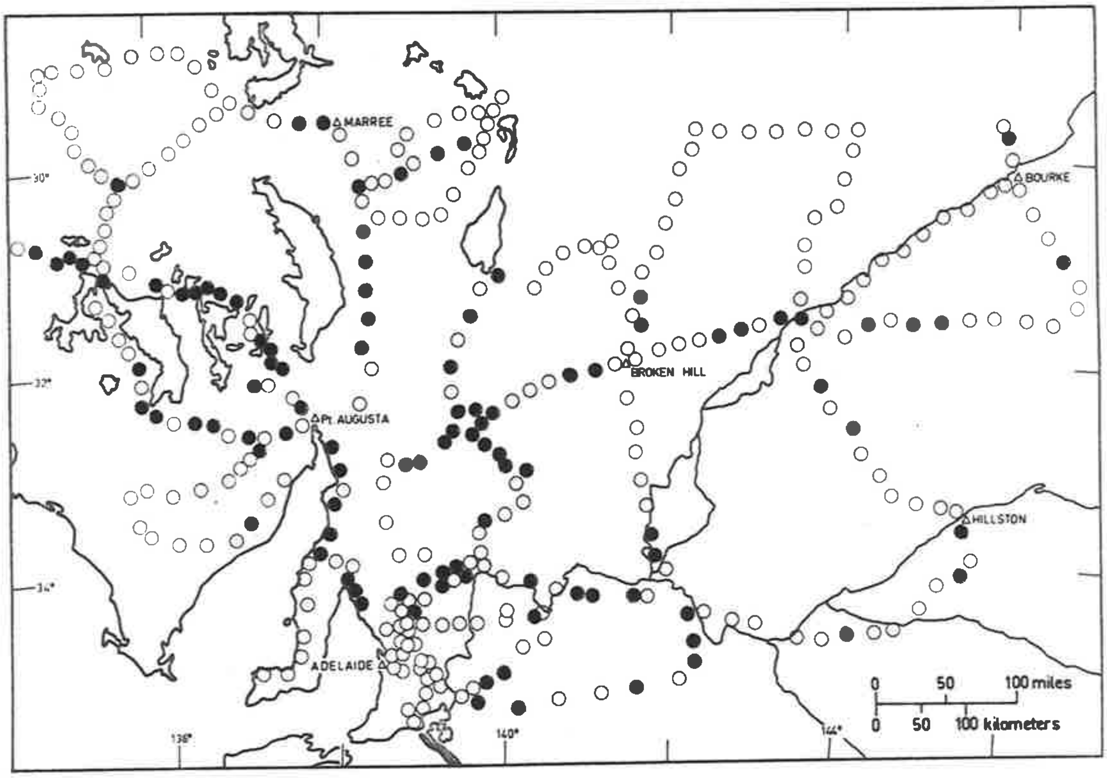
Dermatocarpon lachneum



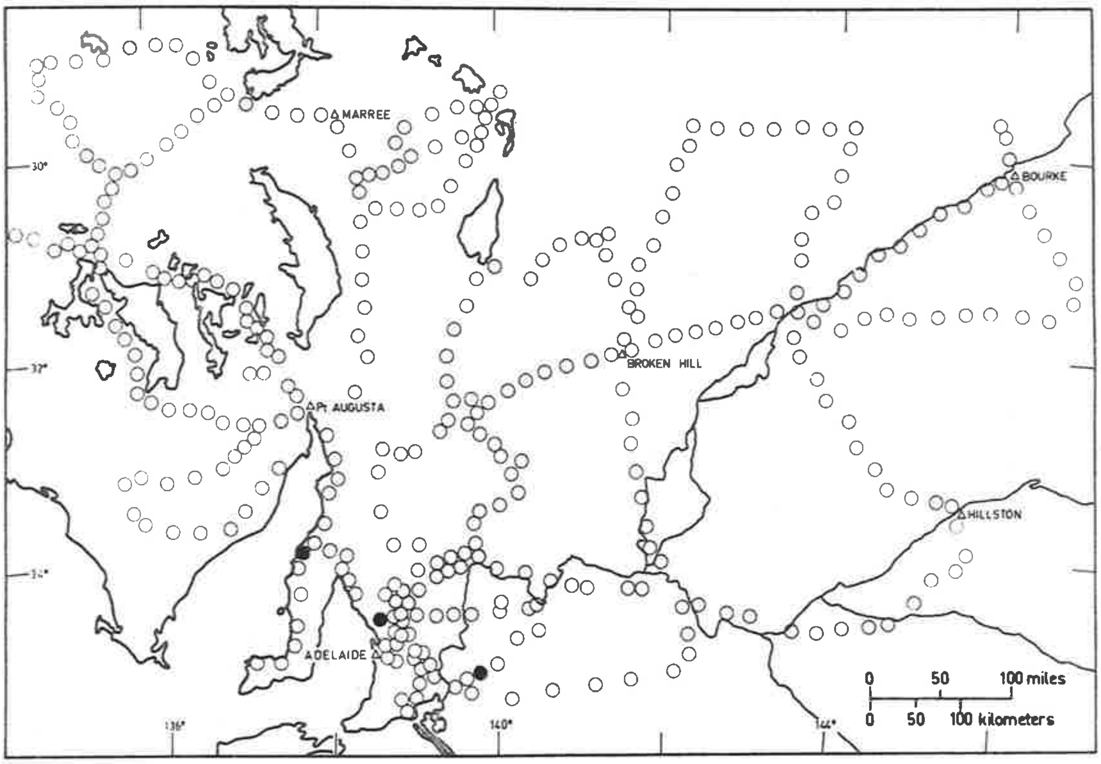
Diploschistes ocellatus



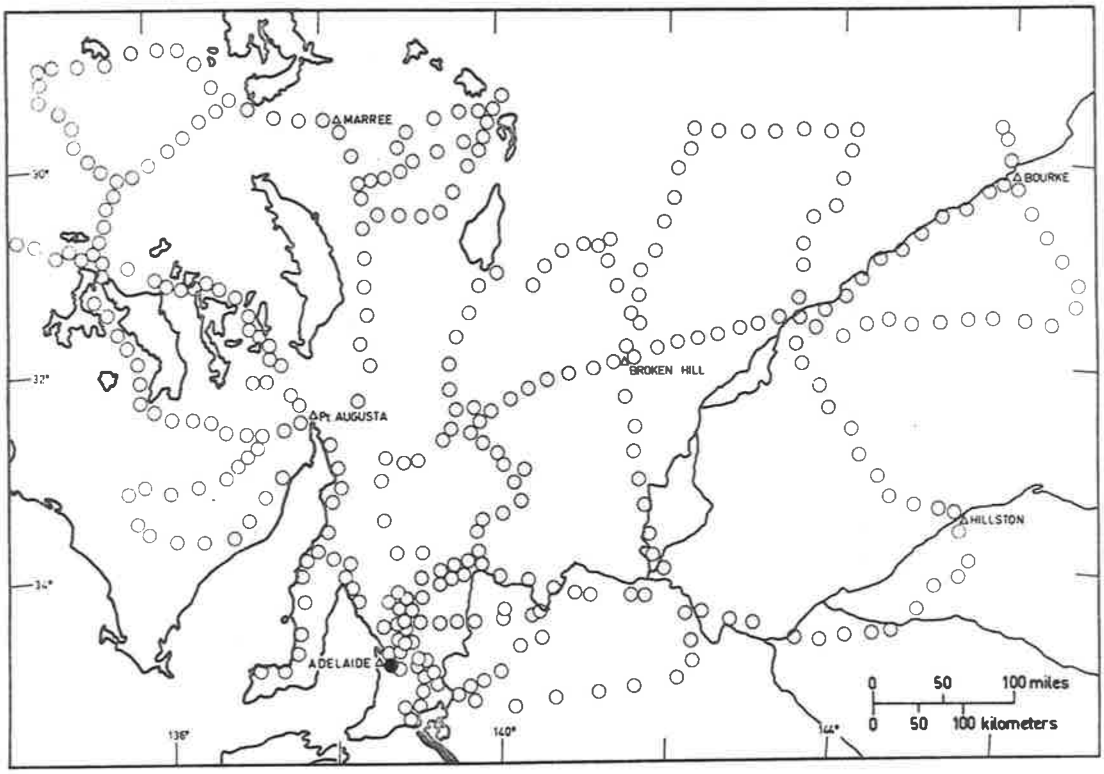
Cladonia squamules



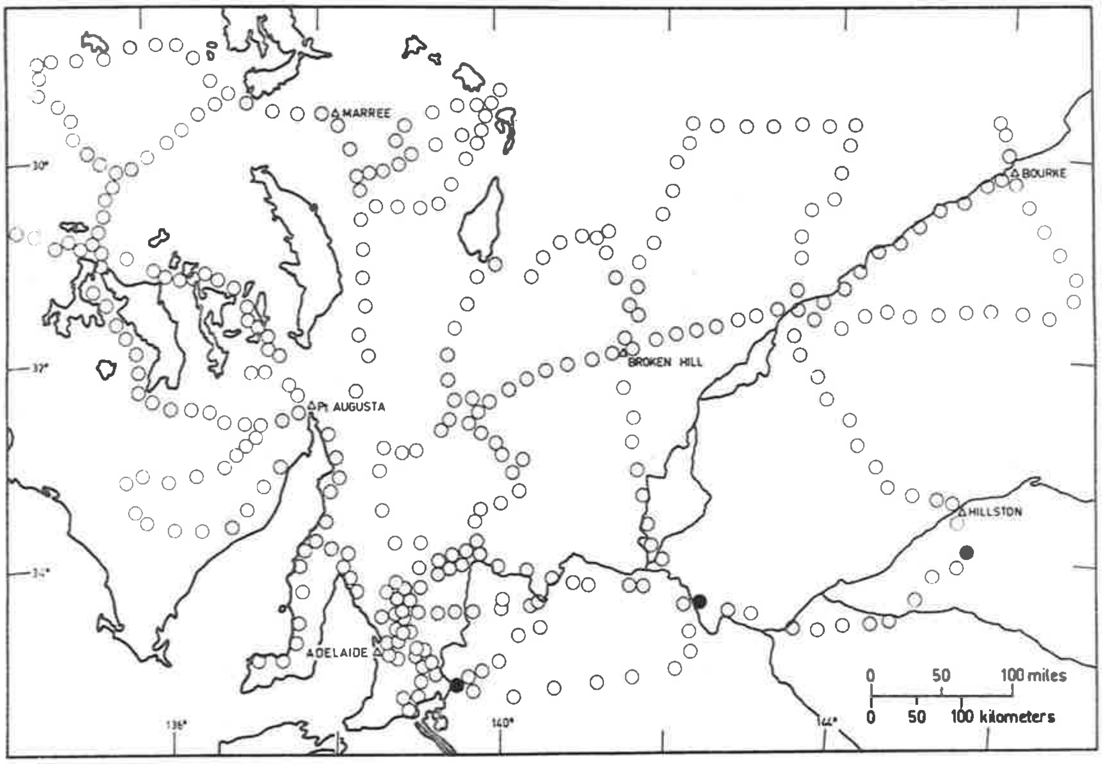
Collema coccophorus



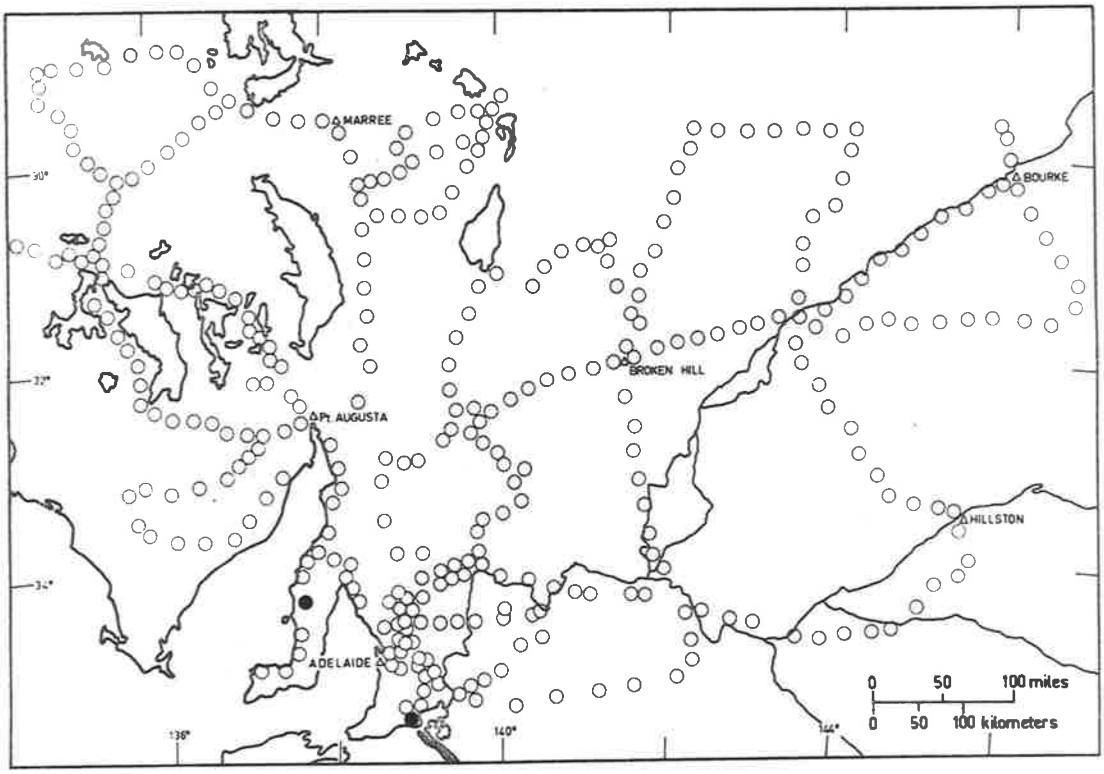
Cladonia verticillata



Cladonia sp.



Cladonia foliacea



Cladonia subsquamosa

(4) Frequency in relation to calcium

The relationship between frequency and determined calcium is shown in Fig. 6.3. Two species, *Dermatocarpon lachneum* and *Collema coccophorus*, occurred across the entire range of calcium concentration. Most species were absent from the higher class which, because of the logarithmic class interval, represents half the total range.

(5) Frequency in relation to sodium

The relationship between frequency and determined sodium is shown in Fig. 6.4. The shape of the histograms in Fig. 6.4 suggests that sodium concentration does not play an important role in determining species distribution within the range of concentrations encountered. Most species are broadly spread across a large part of the range, but some have more limited ranges, especially *Diploschistes ocellatus, Caloplaca subpyracella, Cladia aggregata, Aspicilia calcarea* mod. *fruticosa* and *Buellia epigaea.*

(6) Frequency in relation to soil surface type.

The frequency of the more common species on each soil type is presented graphically in Fig. 6.5. No soil lichen can occur on areas completely paved with rocks, but occur on all other soil surface types. Maximum frequency for all species occurs on either crusted loam or hard setting surfaces. *Collema coccophorus* and *Endocarpon pusillum* both occur on all surface types that support any soil lichens. *Aspicilia calcarea* mod. *fruticosa, Diploschistes ocellatus* and *Parmelia molliuscula* occur only on crusted loams, and *Heterodea mülleri* occurs only on hard setting surfaces. All other species occurred on more than one soil surface type, resulting in 7 of the total of 42 species occurring on clay surfaces, 30 on hard setting surfaces, 39 on crusted loams, 6 on amorphous surfaces and 18 on sands.

(7) Frequency in relation to mean daily maximum temperature for January

The frequency of the more common species in each temperature class is presented in Fig. 6.6. The species are ordered in this figure first by mode of the frequency histogram, then by tolerance of high temperatures. No species has a maximum frequency in the highest maximum temperature class. Only one species, *Heppia lutosa,* falls in the second highest class, all others are in the two lower groups.

(8) Frequency of lichen-crust formation in relation to environmental variation

The histograms in Fig. 6.7 summarize the relationships between frequency of crust formation and mean annual rainfall, soil extract pH, soil extract calcium and sodium concentrations, the nature of the soil surface and mean daily maximum temperature for January. It was calculated that 45% of sites examined with a winter rainfall maximum, and 13% of sites with a summer rainfall maximum, were crusted.

5. THE RELATIONSHIP BETWEEN ORDINATIONS AND SPECIES-GROUP MEMBERSHIP

In this section the environmental factors which are related to the distribution of species - groups, are determined by comparing the environmental ordinations of species with species-group membership.

In Table 6.2 the species are ordered by the rainfall corresponding with their modal frequency, and also the community group to which the species belongs. It is apparent that species in group A all have their highest frequencies in high rainfall areas, species of group B in somewhat lower rainfall areas, and species of groups C and D at still lower rainfall levels. Mean annual rainfall must therefore be considered a factor related to the distribution of the species involved.

When species are ordered on the basis of the ratio:

$$\frac{\text{frequency in winter rainfall areas}}{\text{frequency in summer rainfall areas}}$$

TABLE 6.2

The relationship between the ordination of species on the basis of frequency mode for rainfall, and the assigned species-groups. Species with modal frequencies in high rainfall areas are at the top of the list.

Species	Species-group A	B	C	D
Heterodea mülleri	+			
Parmelia conspersa	+			
Siphula coriacea	+			
Cladonia squamules	+			
Lecidea planata		+		
Cladia aggregata	+			
Lecidea coarctata		+		
Diploschistes scruposus	+			
Parmelia amphixantha		+		
Lecidea psammophila		+		
Parmelia pulla	+			
Endocarpon pusillum				+
Lecidea crystallifera			+	
Lecanora atra		+		
Buellia subcoronata		+		
Fulgensia bracteata			+	
Lecidea decipiens				+
Buellia epigaea			+	
Toninia caeruleonigricans			+	
Acarospora smaragdula			+	
Aspicilia calcarea				+
Parmelia molliuscula			+	
Parmelia australiensis			+	
Chondropsis semiviridis			+	
Aspicilia calcarea mod. *fruticosa*			+	
Diploschistes ocellatus			+	
Dermatocarpon lachneum				+
Collema coccophorus				+
Synalissa sp.				+
Caloplaca subpyracella				+
Heppia polyspora				+
Heppia lutosa				+

TABLE 6.3

The relationship between the ordination of species based on the ratio $\frac{\text{frequency in winter rainfall areas}}{\text{frequency in summer rainfall areas}}$ and assigned species groups. The bar across the table separates species which occur in summer rainfall areas (above the bar) from those that do not (below the bar).

Species	Species-group A	B	C	D
Buellia subcoronata		+		
Lecidea planata		+		
Lecidea psammophila		+		
Heppia polyspora				+
Heppia lutosa				+
Lecidea coarctata		+		
Lecanora atra		+		
Caloplaca subpyracella				+
Parmelia amphixantha		+		
Dermatocarpon lachneum				+
Collema coccophorus				+
Endocarpon pusillum				+
Synalissa sp.				+
Lecidea decipiens				+
Aspicilia calcarea				+
Diploschistes scruposus	+			
Toninia caeruleonigricans			+	
Cladonia squamules	+			
Lecidea crystallifera			+	
—	—	—	—	—
Aspicilia calcarea mod. *fruticosa*			+	
Acarospora smaragdula			+	
Buellia epigaea			+	
Chondropsis semiviridis			+	
Cladia aggregata	+			
Diploschistes ocellatus			+	
Fulgensia bracteata			+	
Heterodea mulleri	+			
Parmelia australiensis			+	
Parmelia conspersa	+			
Parmelia molliuscula			+	
Parmelia pulla	+			
Siphula coriacea	+			

TABLE 6.4

The relationship between the ordination of species on the basis of frequency mode for soil-extract pH, and the assigned species groups. Species with modal frequencies on acid (low pH) soils are at the top of the list.

Species	Species-group A	Species-group B	Species-group C	Species-group D
Buellia subcoronata		+		
Cladia aggregata	+			
Heterodea müllerì	+			
Lecidea coarctata		+		
Lecidea psammophila		+		
Parmelia amphixantha		+		
Parmelia pulla	+			
Lecanora atra		+		
Siphula coriacea	+			
Lecidea planata		+		
Parmelia conspersa	+			
Cladonia squamules	+			
Endocarpon pusillum	+			+
Diploschistes scruposus	+			
Lecidea decipiens				+
Heppia polyspora				+
Buellia epigaea			+	
Parmelia molliuscula			+	
Caloplaca subpyracella				+
Synalissa sp.				+
Acarospora smaragdula			+	
Diploschistes ocellatus			+	
Parmelia australiensis			+	
Chondropsis semiviridis			+	
Heppia lutosa				+
Aspicilia calcarea				
Dermatocarpon lachneum				+
Collema coccophorus				+
Lecidea crystallifera			+	
Fulgensia bracteata			+	
Toninia caeruleonigricans			+	
Aspicilia calcarea mod. *fruticosa*			+	

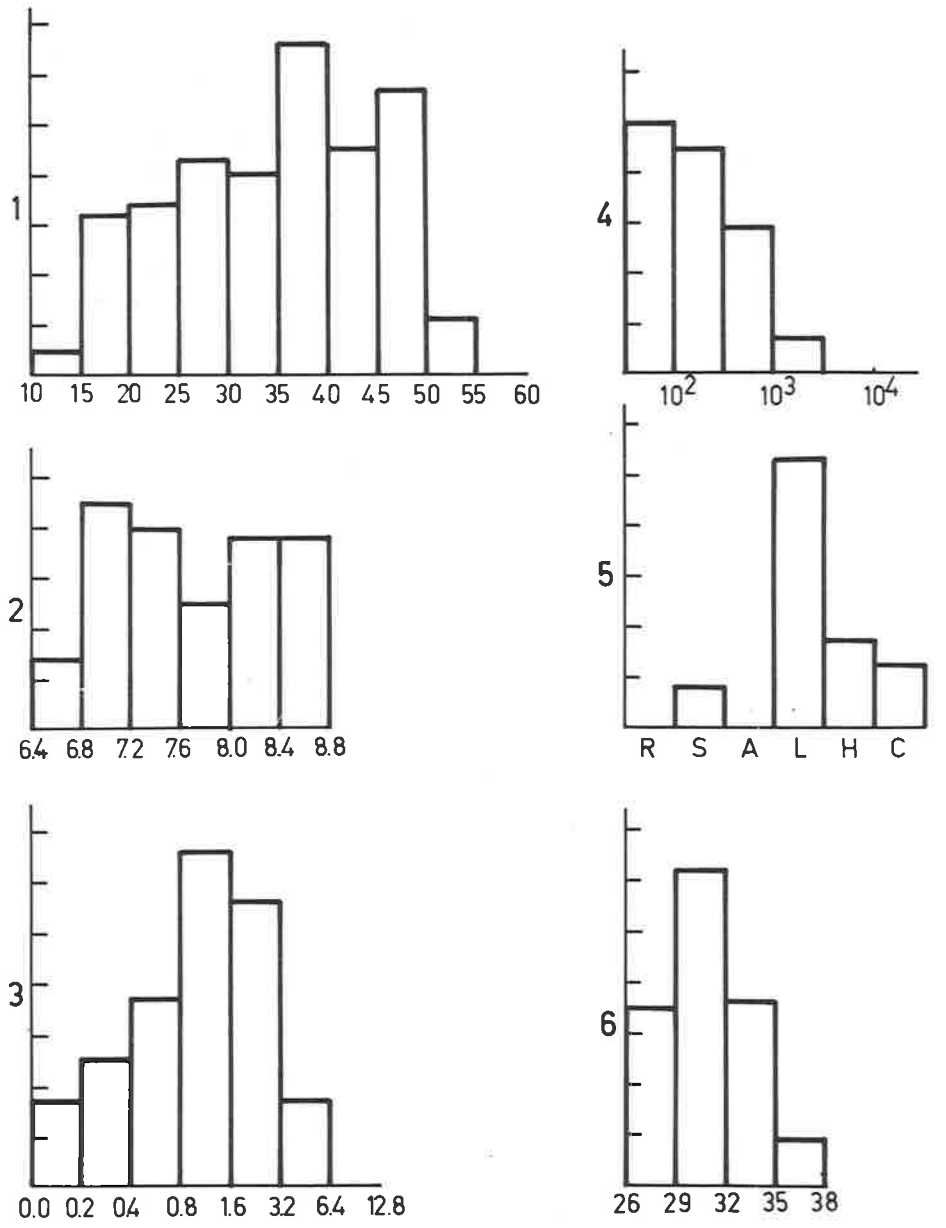

1
10 15 20 25 30 35 40 45 50 55 60
2
6.4 6.8 7.2 7.6 8.0 8.4 8.8
3
0.0 0.2 0.4 0.8 1.6 3.2 6.4 12.8
4
10^2 10^3 10^4
5
R S A L H C
6
26 29 32 35 38

TABLE 6.5

The relationship between the ordination of species on the basis of frequency mode for soil-extract calcium concentration and the assigned species-groups. Species with modal frequencies on soils with low calcium concentration are at the top of the list.

Species	Species-group A	B	C	D
Lecidea planata		+		
Siphula coriacea	+			
Heterodea müllerі	+			
Lecidea psammophila		+		
Buellia subcoronata		+		
Lecanora atra		+		
Cladia aggregata	+			
Lecidea coarctata		+		
Heppia lutosa				+
Heppia polyspora				+
Parmelia conspersa	+			
Caloplaca subpyracella				+
Aspicilia calcarea				+
Endocarpon pusillum	+			+
Acarospora smaragdula			+	
Aspicilia calcarea mod. *fruticosa*			+	
Buellia epigaea			+	
Chondropsis semiviridis			+	
Parmelia australiensis			+	
Cladonia squamules	+			
Parmelia amphixantha		+		
Parmelia pulla	+			
Synalissa sp.				+
Toninia caeruleonigricans			+	
Fulgensia bracteata			+	
Parmelia molliuscula			+	
Diploschistes ocellatus			+	
Diploschistes scruposus	+			
Lecidea crystallifera			+	
Lecidea decipiens				+
Dermatocarpon lachneum				+
Collema coccophorus				+

TABLE 6.6

The relationship between the ordination of species on the basis of frequency mode for soil-extract sodium concentration and the assigned species-groups. Species with modal frequencies on soil with low sodium concentrations are at the top of the list.

Species	Species-group A	B	C	D
Diploschistes scruposus	+			
Buellia subcoronata		+		
Parmelia amphixantha		+		
Heppia polyspora				+
Chondropsis semiviridis			+	
Caloplaca subpyracella				+
Cladia aggregata	+			
Aspicilia calcarea mod. *fruticosa*			+	
Buellia epigaea			+	
Diploschistes ocellatus			+	
Acarospora smaragdula			+	
Toninia caeruleonigricans			+	
Cladonia squamules	+			
Synalissa sp.				+
Endocarpon pusillum	+			+
Aspicilia calcarea				+
Lecidea decipiens				+
Lecidea crystallifera			+	
Fulgensia bracteata			+	
Parmelia australiensis			+	
Parmelia molliuscula			+	
Lecidea planata		+		
Lecanora atra		+		
Lecidea coarctata		+		
Siphula coriacea	+			
Parmelia pulla	+			
Dermatocarpon lachneum				+
Parmelia conspersa	+			
Lecidea psammophila		+		
Heterodea mülleri	+			
Heppia lutosa				+
Collema coccophorus				+

TABLE 6.7

The relationship between the ordination of species on the ratio $\frac{\text{frequency on hard surface soils}}{\text{frequency on crusted loams}}$ and the assigned species-groups. Species which were more common on hard soil surfaces are at the top of the list.

Species	Species-group A	B	C	D
Cladia aggregata	+			
Cladonia squamules	+			
Diploschistes scruposus	+			
Endocarpon pusillum				+
Heterodea mülleri	+			
Lecidea coarctata		+		
Lecidea planata		+		
Lecidea psammophila		+		
Parmelia amphixantha		+		
Parmelia conspersa	+			
Parmelia pulla	+			
Siphula coriacea	+			
Acarospora smaragdula			+	+
Aspicilia calcarea				
Aspicilia calcarea mod. *fruticosa*			+	
Buellia epigaea			+	
Buellia subcoronata		+		
Caloplaca subpyracella				+
Chondropsis semiviridis			+	
Collema coccophorus				+
Dermatocarpon lachneum				+
Diploschistes ocellatus			+	
Fulgensia bracteata			+	
Heppia lutosa				+
Heppia polyspora				+
Lecanora atra		+		
Lecidea crystallifera			+	
Lecidea decipiens				+
Parmelia australiensis			+	
Parmelia molliuscula			+	
Synalissa sp.				+
Toninia caeruleonigricans			+	

TABLE 6.8

The relationship between the ordination of species on the basis of frequency mode for mean maximum temperature for January and the assigned species-groups. The species with model frequencies in low temperature areas are at the top of the list.

Species	Species-group A	B	C	D
Heterodea mülleri	+			
Siphula coriacea	+			
Cladia aggregata	+			
Cladonia squamules	+			
Parmelia conspersa	+			
Parmelia pulla	+			
Lecidea psammophila		+		
Lecidea planata		+		
Parmelia amphixantha		+		
Lecidea coarctata		+		
Diploschistes scruposus	+			
Endocarpon pusillum				+
Lecanora atra		+		
Buellia subcoronata		+		
Buellia epigaea			+	
Toninia caeruleonigricans			+	
Acarospora smaragdula			+	
Parmelia molliuscula			+	
Diploschistes ocellatus			+	
Aspicilia calcarea mod. *fruticosa*			+	
Chondropsis semiviridis			+	
Parmelia australiensis			+	
Fulgensia bracteata			+	
Aspicilia calcarea				+
Lecidea crystallifera				+
Lecidea decipiens				+
Synalissa sp.				+
Collema coccophorus				+
Dermatocarpon lachneum				+
Caloplaca subpyracella				+
Heppia polyspora				+
Heppia lutosa				+

it is apparent that groups B and D occur in summer rainfall areas, whereas those species in groups A and C either do not occur, or occur only rarely in areas with summer rainfall (Fig. 6.3). Seasonal distribution of rainfall is thus demonstrated to be closely related to species distribution.

If the species are ordered on the basis of modal frequency in relation to pH of the soil extract (Table 6.4) it is apparent that species in groups A and B tend to occur on acid-neutral or slightly alkaline soils, whereas species of groups C and D tend to occur on strongly alkaline soils. The same effect, although not as sharply defined, is apparent if calcium concentration of the soil extract is considered (Table 6.5). This indicates that while both pH and calcium content of the soil extract are related to distribution patterns, pH is more closely related to distribution than is calcium concentration.

When the species are ordered by frequency mode in relation to soil extract sodium concentration, no relation with species-grouping can be detected (Table 6.6). This implies that species in all groups react in a similar way to sodium concentration.

Since all species have their highest frequencies on either crusted loams or on hard setting soils, it is possible to group the species into two classes; those with maximum frequency on hard setting soils, and those with maximum frequency on crusted loams. It is apparent from Table 6.7 that species of group A are all more common on hard setting soils, and that species of group C are all more common on crusted loamy soils. Excepting *Endocarpon pusillum* (which could alternatively be placed in the group A), group D species are more common on crusted loamy soils. Four members of group B are more common on hard soils, and two members more common on loamy soils.

This indicates that the nature of the soil surface is more strongly related to factors influencing the distribution of species-groups A and C than to those factors influencing groups B and D.

Ordering of species by frequency mode in relation to normal January maximum temperatures shows a close relationship between temperature at which modal frequency is found and species-group (Table 6.8). Essentially group A is most common in the lowest temperature class, groups B, C and D occur in an ascending order of temperature classes. The placing of *Buellia epigaea* is ambiguous, so it is included in the low temperature preference, but at the end of the series with low temperature modes. The species of group A are, with the exception of *Diploschistes scruposus*, limited to the lower temperature classes, and those of group B are relatively more common in the three lower classes. Generally species of group C are confined to the two central temperature classes, whereas species in group D occur in each class, except *Heppia polyspora* and *H. lutosa*, which occur in all but the lowest temperature class. This is the most clear cut relationship between species-grouping and environmental ordination found, indicating either a strong causative influence or close correlation with such an influence on the distribution of species.

6. DISCUSSION.

(1) Factors controlling the distribution of lichen species.

The environmental variables discussed ordered the species of the species-groups in three different ways. Mean annual rainfall and mean maximum temperature for January both arrayed the four separate species-groups quite distinctly, in the order A, B, C, D. This order proceeded from wet to dry frequency modes for rainfall and from cool to hot frequency modes for temperature. Within the study area it was true that the wettest areas were coolest, and that the driest areas were the hottest. In the light of this relationship it is not unexpected that both rainfall and mean maximum January temperature appeared to affect the species frequency in a like manner.

In terms of seasonal rainfall, there were only two detectable groupings. Species-groups A and C were linked together in this ordination, both occurring in areas with a marked predominance of winter rainfall. Similarly species-groups B and D were found to occur in areas with winter rainfall and also areas with predominantly summer rainfall.

A similar grouping of species reflecting the order resulting from the rainfall and temperature ordinations result from consideration of the three influential soil factors (surface type, pH, and calcium content). Species in groups A and B tended to have modal frequencies on soils which were relatively acid with low calcium concentration and hard surfaces. Species in groups C and D tended to have modal frequencies on soils which were relatively alkaline, with high calcium concentration and crusted surfaces.

Thus, while mean annual rainfall or mean maximum temperature for January could explain the formation of the species-groups, the seasonal distribution of rainfall, and soil characteristics could also be used to explain those groups.

The situation is not, however, as simple as it appears from the discussion above. Soil type is largely controlled by climate. Acid, hard setting soils with low calcium content are mostly restricted to wetter areas: alkaline and loamy soils with high calcium content are more or less restricted to dry areas. Hence, it is expected that soil factors will produce ordinations reflecting those produced by mean annual rainfall.

Similarly the remaining factor, seasonal distribution of rainfall, is not independent of mean annual rainfall because the highest rainfall reached in the summer rainfall area was not nearly as high as that reached in the winter rainfall area. The exclusion of species in species group A from areas with summer rainfall predominance could be a reflection of the relatively low rainfall in that area. Only one species in group A commonly occurred in areas with rainfall as low as the wettest area with summer rainfall. For the lower rainfall areas, however, there are areas of similar mean annual rainfall in both summer and winter rainfall zones.

Thus, the absence of species of group C from summer rainfall areas must be the result of the seasonal distribution of rainfall, or of a variable related to it, but not related to soil type.

Therefore, on a broad scale there is no necessity to invoke factors other than climate to explain the distribution of soil surface lichens. It appears that mean annual rainfall, mean maximum temperature and the seasonal distribution of rainfall are the major parameters required to explain the distribution patterns discovered.

When mapped (Fig. 5.22) it was apparent that species of group A occur in the cool, wet winter rainfall area near Adelaide. Species of group B occur mostly in the rather warmer, somewhat drier summer rainfall area in central New South Wales. group C species occur in the dry, warm winter rainfall areas of South Australia. Species of group D occur in dry, warm summer or winter rainfall areas.

The factors differentiating species-groups C and D are more clearly indicated than those differentiating species-groups A and B. To determine which of the variables does in fact control distribution of any species would require detailed experimental studies.

Some species showed a remarkable tolerance to the extremes of environment encountered in this study. Material referred to the species *Endocarpon pusillum* occurred on all soil surface types that supported any lichen growth across the complete pH and sodium range, from the highest to lowest rainfall and January temperature classes, and in all but the highest calcium concentration range. Other species with wide tolerances included *Cladonia* sp. squamules, *Collema coccophorus, Diploschistes scruposus, Lecidea crystallifera, Lecidea decipiens* and *Dermatocarpon hepaticum.*

Some species in group C, notably *Diploschistes ocellatus*, *Aspicilia calcarea* mod. *fruticosa* and *Buellia epigaea* have singularly restricted ranges in relation to all the variables examined.

A comparison of special interest is that between the tolerance ranges of *Aspicilia calcarea* and *A. calcarea* mod. *fruticosa*. The fruticose modification always occurred in a restricted range within the wider range of the crustose form. The fruticose modification occurs only in the drier (15-30cm) rainfall areas compared with a range from 15cm to 45cm for the crustose form, only in winter rainfall areas (crustose form in both summer and winter rainfall), in the pH range 7.2-8.9 (crustose form pH 6.8-8.9), in the calcium concentration range 0.41-0.80 m.mole/gm soil (crustose form 0.0-3.2m mole/gm soil), in a sodium concentration range 0.10-0.31 m mole/gm (crustose form 0.03-3.17 m mole/gm) and in a restricted January normal maximum temperature range central to that occupied by the crustose form. Because both forms can occur in close proximity to one another, micro-environmental factors are probably involved in determining fruticose or crustose development even within the narrow range of soil and climatic variables suited to the fruticose modification.

(2) Factors controlling the distribution of lichen crusts

Since a lichen crust is the result of development of populations of the lichen species, it was expected that the factors influencing the distribution of the crust would be those influencing individual species.

It was apparent from the data that crusts develop over a very wide range of rainfall and pH conditions. Crust formation did, however, show a marked relationship to soil calcium and sodium concentration (most common in the mid and low ranges respectively). Crusts were developed predominantly on loamy soils, although they did occur on soils with hard-setting, clay and sandy surfaces.

The data relevant to seasonal distribution of rainfall indicated that crusts tended not to occur in areas with summer rainfall. However, a considerable development of crust in central New South Wales suggested that the general absence of crusts from areas with summer rainfall was related to the relatively low rainfall common in those areas. The absence of crusts from areas with high mean maximum temperatures for January may be explained in a similar manner.

Distribution of lichen crusts was thus apparently controlled by mean annual rainfall and by the related factors of calcium and sodium concentrations and the nature of the soil surface.

CHAPTER VII

THE AUTECOLOGY OF *CHONDROPSIS SEMIVIRIDIS*

In the preceding chapter a number of factors believed to control lichen distribution were enumerated. It was recognized, however, that the factors actually controlling the distribution of any given species could only be determined by experimental studies. Experimental assessment of the roles of the factors apparently controlling the distribution of a single species is reported in this chapter.

1. CHOICE OF SPECIES AND FIELDS OF STUDY

It was decided that the species chosen for study ought to have a restricted distribution largely embraced by the study area, so that inferences about factors affecting its distribution could be made. There was practical advantage in use of a foliose or fruticose lichen, as crustose and squamulose lichens are difficult to work with in physiological studies, because of their close attachment to the substrate.

Chondropsis semiviridis met the requirements listed above and had the added advantage that its taxonomic status was beyond dispute, as chemical strains or species were not known to occur in the genus. The existence of areas in which

C. semiviridis literally could be picked up by the handful ensured a sufficient supply of material.

C. semiviridis is unusual in a number of ways. The thallus is hygrochasic: when wet it lies flat on the soil with its green upper surface showing and its yellow surface apressed to the soil. When dry it rolls up into a ball, with its lower surface outermost (Plate 2,3), and the upper cortex becomes almost opaque, masking the green of the algal layer. The thallus is almost perfectly dichotomous, with an angle of about 90° between branches. Reproduction must be almost entirely vegetative by fragmentation of thalli, as soredia and isidia are not formed, and fertile specimens are very rare. Spores were not described until Filson (1967) augmented the original species description. Thallus fragments are presumably scattered by the wind; large thalli probably rarely move very far because of their habit of curling around sticks and litter on the soil surface, so anchoring themselves in the manner described by Weber (1967b).

Information in Chapter VI suggested that mean annual rainfall, seasonal distribution of rainfall, and possibly maximum temperatures were the factors limiting distribution of *C. semiviridis*. Since *C. semiviridis* was not attached to soil the likelihood of control of its distribution by soil type was rejected. Frequency of

PLATE 2

Chondropsis semiviridis when dry, showing the thallus rolled into a ball. The scale is callibrated in half millimetres.

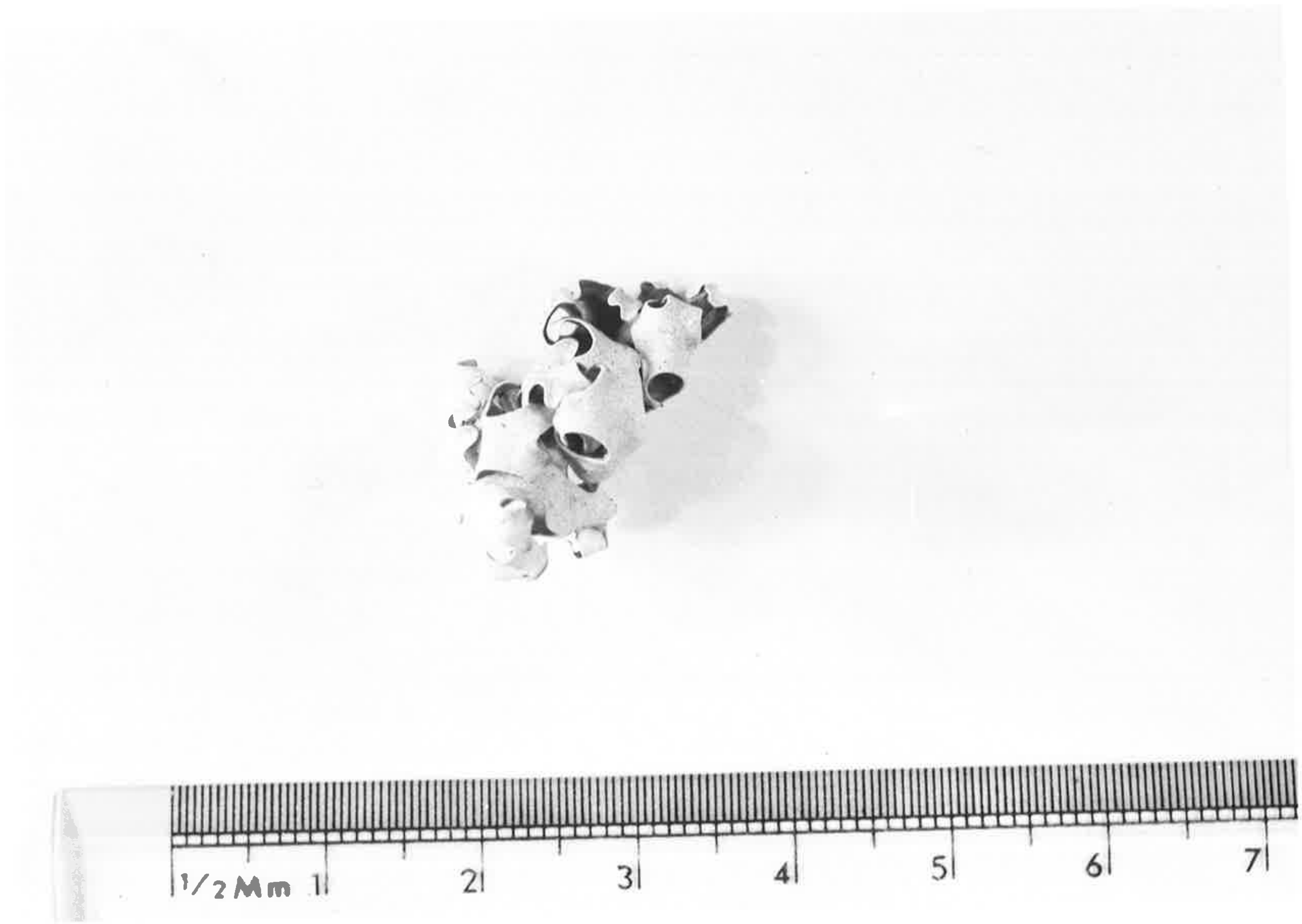
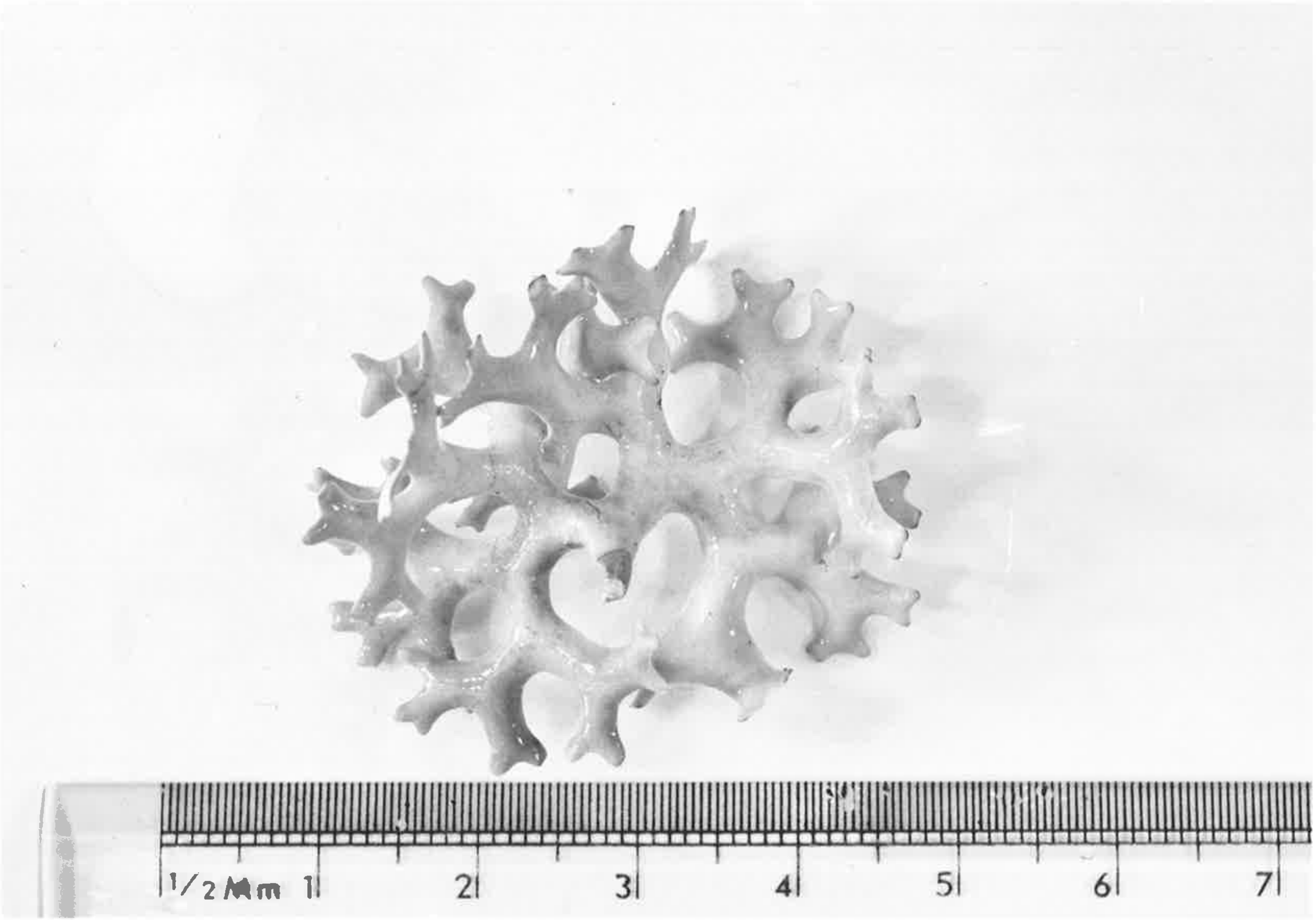

1/2 Mm 1
2
3
4
5
6
7

PLATE 3.

The same thallus of *Chondropsis semiviridis* shown in Plate 2, but after wetting. To the same scale as Plate 2.


1/2 Mm 1
2
3
4
5
6
7

C. semiviridis in relation to these three climatic factors was extracted and presented in Figure 7.1, which indicates that *C. semiviridis* tends to occur in areas which are both cool and dry. It is completely absent from wet or very hot areas, and does not occur in areas with summer rainfall, although there were areas with summer rainfall apparently suited to the species in terms of temperature regime and mean annual rainfall.

Although Lange (1953) had suggested that drought was not a factor controlling lichen distribution in Europe, Reid (1960a,b) showed zonation of lichens in relation to water supply and demonstrated that considerable physiological stress could follow the ending of a drought. Reid also showed that upon wetting of a lichen thallus respiration rose rapidly to very high levels but photosynthesis did not, hence depleting food reserves. It has been shown that when wet, lichens are much more susceptible to heat damage than when dry (Lange 1966). Thus there appeared to be a physiological basis for control of distribution by the factors selected for investigation.

The autecological study, therefore, resolved into three more or less independent parts:

(1) a preliminary study to check the distribution of the species from available herbarium records, and to document variation within the species;

(2) a study on the effect of drought on viability of the species, including studies of metabolic activity in the air-dry condition to allow estimation of use of food reserves during drought;

(3) a study of the effect of heat stress on the viability of the species, and of the temperatures likely to be encountered by the thallus in nature.

(2) SPECIES DISTRIBUTION AND THALLUS VARIATION

(1) Collection of information

The primary source of information on the distribution of *C. semiviridis* had to be the author's own collections, as these provided information about where *C. semiviridis* was, or was not, found; other herbaria contain only records of presence of the species. The government herbaria of South Australia, Victoria, New South Wales and Queensland supplied lists of locations for collections they held, as did the herbarium of the University of Western Australia. Mr. G.C. Bratt (West Moonah, Tasmania) and Dr. D.N. McVean (Australian National University, Canberra) provided information about collections in their private herbaria.

The locations from which all known Australian collections were taken are listed in Appendix 6. The distribution of these locations is shown in Fig. 7.2.

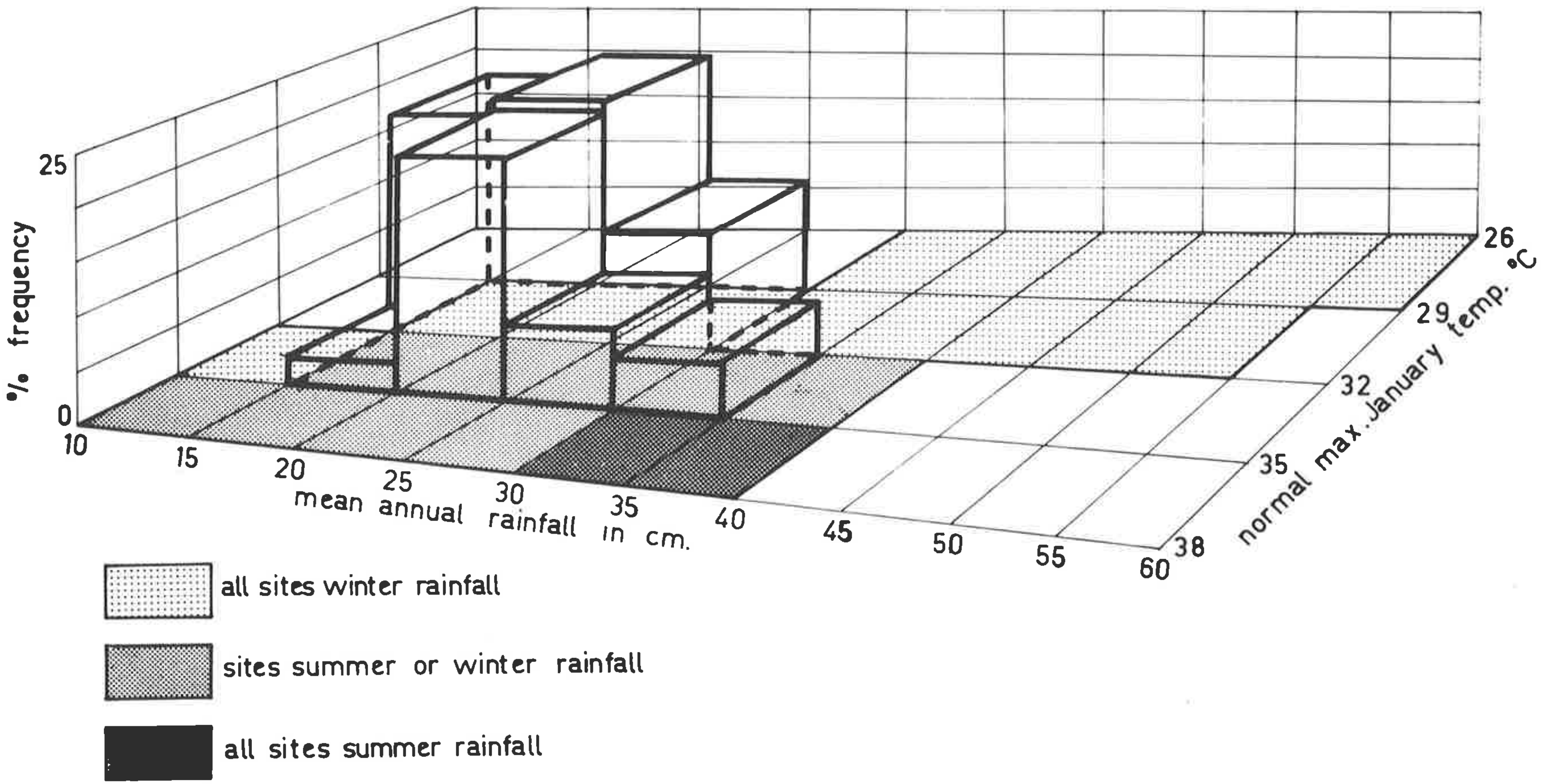
Collections have also been made in New Zealand (Martin, 1966): the author has seen material from the alps of the South Island. Robert Brown reported a collection from Table Mountain, Van Diemens Land (now Mt. Wellington, near Hobart, Tasmania) but careful searches have not found any on that mountain since then; this has been regarded as a confused location in the past (Bibby, 1955), but in light of collections on the Snowy Mountains and New Zealand Alps it may not have been so. It is possible that fire may have recently destroyed any colonies once there.

For a number of sites sufficient material had been collected to allow statistical study of lobe width. For seven such sites, the width of the lobe immediately preceding the final dichotomy was measured on a number of specimens, and means and standard deviations for lobe width calculated for each of these locations. Environmental correlations were sought for lobe width variation.

Study of variation of lobe width showed considerable variation in width between sites (Table 7.1), width apparently being closely related to mean annual rainfall (Fig. 7.3). During the study a number of thalli with well developed apothecia were found. It was also noted that epiphytic growth of *Parmelia* spp. occurred on some older thalli.

FIGURE 7.1.

The relationship between the frequency of *Chondropsis semiviridis*, mean annual rainfall, and normal maximum temperature for January.



% frequency
25
0
10
15
20
25
30
35
40
45
50
55
60
mean annual rainfall in cm.
26
29
32
35
38
normal max. January temp. °C
all sites winter rainfall
sites summer or winter rainfall
all sites summer rainfall

FIGURE 7.2

The locations from which *Chondropsis semiviridis* has been collected for herbarium records, in relation to the 15cm and 35cm rainfall isohyets, and the northern limit of the area with a seasonal maximum rainfall in winter.

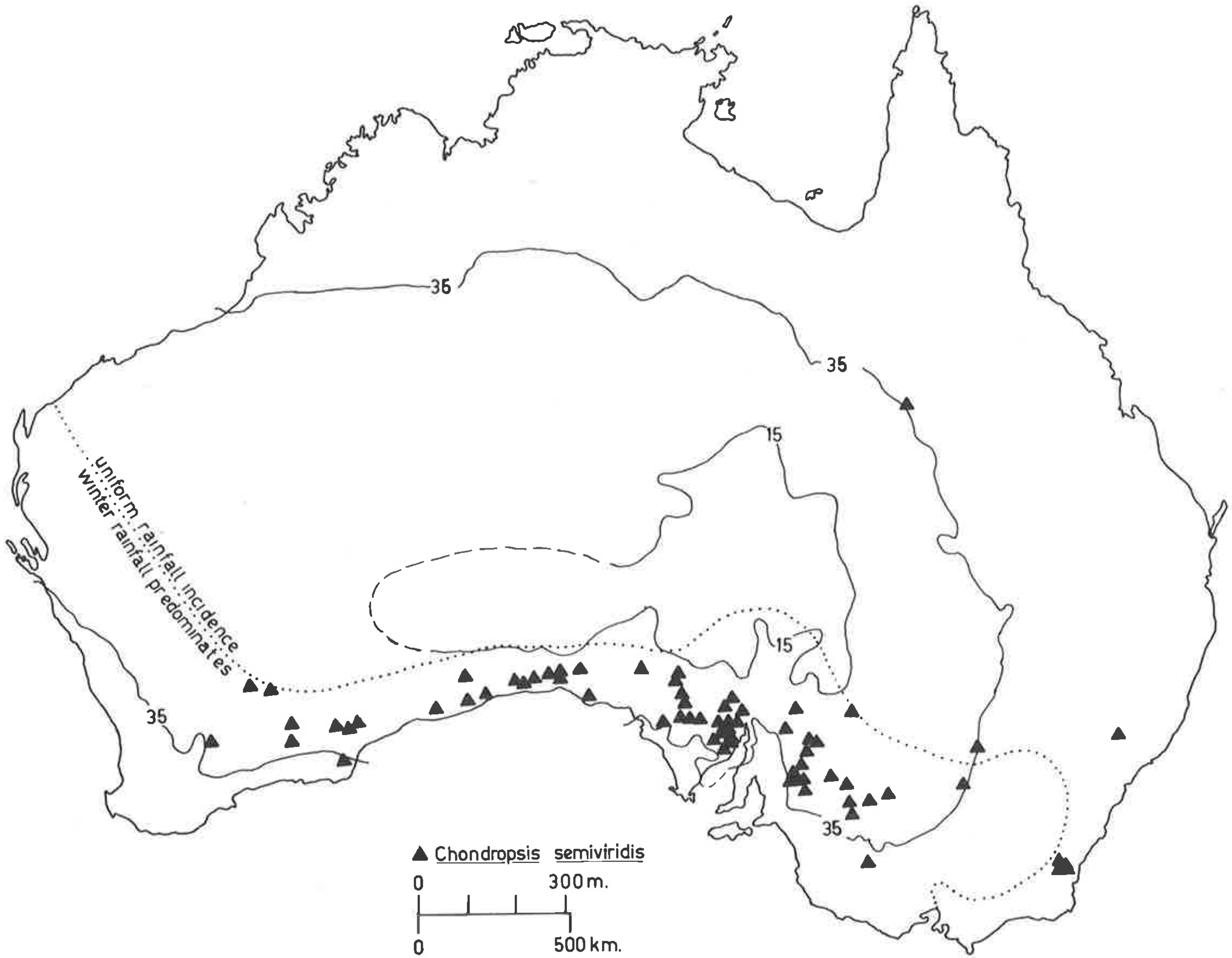

35
35
15
15
35
35
uniform rainfall incidence
winter rainfall predominates
Chondropsis semiviridis
0
300 m.
0
500 km.

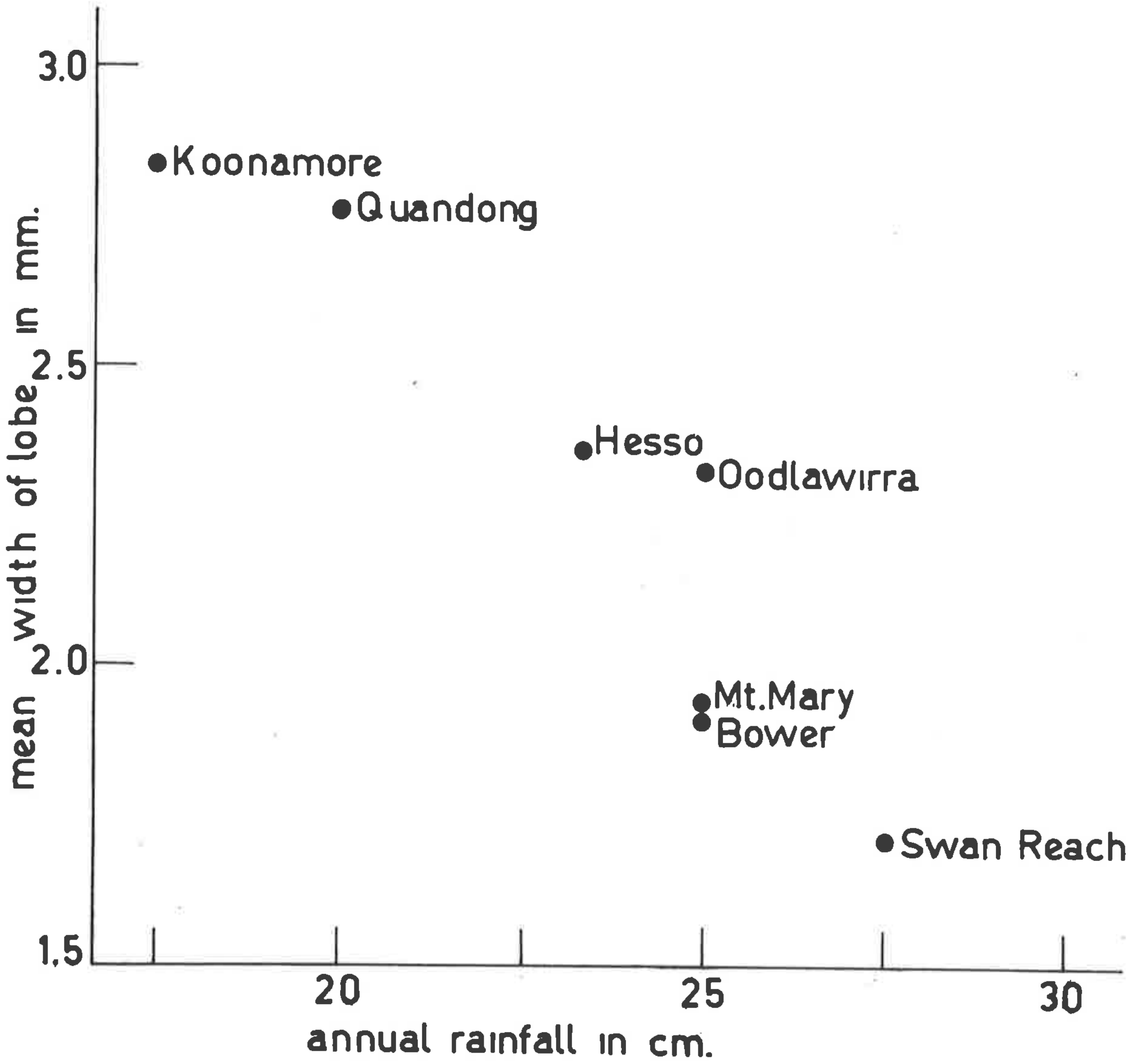
TABLE 7.1

The mean width of the penultimate lobe of *C. semiviridis* at various sites.

Site	Number of thalli used	Number of measurements	Mean Width	σ
Swan Reach	15	100	1.71mm	.28
Bower	16	100	1.91mm	.46
Mount Mary	8	79	1.94mm	.34
Oodlawirra	13	101	2.33mm	.38
Hesso	16	101	2.36mm	.34
Quondong	13	75	2.76mm	.41
Koonamore	14	100	2.84mm	.45

FIGURE 7.3

The relationship between mean width of lobe of *Chondropsis semiviridis* from the named locations and the mean annual rainfall at those locations.



3.0
2.5
2.0
1.5
mean width of lobe in mm.
Koonamore
Quandong
Hesso
Oodlawirra
Mt.Mary
Bower
Swan Reach
20
25
30
annual rainfall in cm.

(2) The distribution pattern

The pattern of distribution within the study area was not materially affected by the extra information collected, but the distribution was extended across the Nullarbor Plain into Western Australia. Nearly all locations for the collections lie between the 15cm and 35cm rainfall isohyets, in areas with a pronounced winter rainfall season. Erratic occurrences have been reported from Scone in northern New South Wales, and from the Müller River in Queensland. The species also occurred on the sub-alpine highlands near Cooma in southern New South Wales, where its development was profuse on shallow soils in a rain-shadow area with a rainfall below 50cm per annum.

3. EFFECT OF DROUGHT

To study the effect of drought on *C. semiviridis*, it was decided that gas-exchange was the most suitable parameter to measure the damage done by drought, and to assess probable viability of the thalli. The use of gas-exchange as an indicator of viability was proposed by Lange (1953) and had been found to correlate closely with percent survival of lichen algae.

Reid (1960a,b) showed that studies of longer duration than those of Lange (1953) were necessary if after-effects of stress were to be observed. It was possible that damage done by drought could be of such a nature that it did not immediately show in gas-exchange studies, but had an irreversible effect leading to premature death.

In nature *C. semiviridis* spends most of its life in an air-dry state. It was not immediately apparent, therefore, under what conditions it might reasonably be expected to exist without suffering greater damage to its physiology, than that suffered while air dry. Since time did not permit studies to determine these conditions, physiological studies on the effect of drought were necessarily short-term.

Three aspects of drought-related stress were studied:

(1) the effect of wetting on photosynthesis and respiration of previously droughted thalli;

(2) the effect of prolonged drought on the respiration rate to which wetted thalli stabilize;

(3) the rate of respiration of thalli when air dry.

(1) Methods

(a) Effect of wetting

Using only terminal dichotomies of thalli the effect of temperature on respiratory and photosynthetic rates of lobes saturated with water was measured in Warburg manometers. A thiourea-in-diethanolamine carbon dioxide buffer was used for photosynthetic studies (Umbreit, Burris and Stauffer 1964). The relation between temperature and gas-exchange is shown in Figure 7.4. Using the graphs in Figure 7.4 it was decided that 25°C was an appropriate temperature to study gas exchange, as no adverse effect of temperature was apparent after an exposure of several hours at that temperature, and the metabolic rate was high.

All short term studies were made using an oxygen electrode, and long term studies using Warburg manometers. To study the effect of wetting, fragments of thalli were introduced into the reaction chamber of an oxygen electrode full of water at 25°C, and the rate of oxygen consumption in the dark, or evolution in the light, recorded. After not more than 30 minutes the thalli were removed, oven dried and weighed so that rates of oxygen exchange/gm dry weight could be calculated. The study of respiration was extended to 48 hours using Warburg manometers.

(b) Effect of prolonged drought

To study the effect of prolonged drought, collections were made over a three year period, and stored dry in brown paper bags. For preliminary respiratory studies terminal lobes were wetted and allowed to stand wet for 12 hours whilst transient wetting effects passed. Oxygen uptake was measured in Warburg manometers. To assess the change in stress following wetting (Reid 1960a,b) as drought period lengthened, dry terminal lobes were placed in an oxygen electrode reaction cell filled with water; the time taken to reach compensation point, and to replace the oxygen used in the initial respiratory burst, was noted.

(c) Measurement of respiration rates in air-dry thalli

In order to determine the demand on metabolic reserves of the lichen caused by long periods in air-dry conditions it was decided to measure respiration of air-dry thalli. Thalli were placed in a desiccator over a saturated solution of sodium chloride in water at 25°C, (Relative Humidity = 75%) or over a saturated solution of ammonium nitrate in water at 25°C (Relative Humidity = 60%) (Wexler and Hasegawa 1954) for seven days, by which time equilibrium was reached between atmospheric vapour pressure and the water content of the thalli.

The thalli were then transferred to Warburg manometers in which solutions of sodium hydroxide of a concentration calculated to maintain the relative humidity at 75% or 60% (Robinson and Stokes 1959) had been introduced to the centre well instead of the usual potassium hydroxide. Extra large wicks of filter paper were used to ensure absorption of the carbon dioxide evolved. The respiratory rates of thalli in equilibrium with air of known humidities were then calculated.

(2) Results

The initial burst of oxygen uptake apparently reached a peak after about 3 minutes, and then slowly fell to about half the peak value in 40 minutes. This level was then maintained for 48 hours (Fig. 7.5). Oxygen evolution gradually rose to a stable value within 30 minutes, and then maintained that value. In this study compensation point was reached in 8 minutes, and restoration of oxygen to its original concentration in the reaction chamber took about 16 minutes.

Even the longest droughted material available (38 months) showed some respiratory activity. It is apparent from Figure 7.6 that the respiratory half-life for droughted *C. semiviridis* is about 9 months, respiration rate falling from about 50µl O_2/gm/hr for fresh material to about 24µl O_2/gm/hr at 8 months, to about 12µl O_2/gm/hr at 18 months and to a little above 8µl O_2/gm/hr at 24 months.

The effect of prolonged drought on the time taken to reach compensation point and restoration point is shown in Figure 7.7. Material subject to a 36 week drought reached compensation point, but failed to show production of oxygen in excess of usage. Material after a 64 week drought showed no photosynthetic ability. Oxygen consumption proceeded at a uniform rate regardless of light conditions. It is, however, possible that material stored in the light may have shown some photosynthetic activity, as the chlorophyll may have decayed more rapidly in the dark than in the light.

The rate of oxygen uptake of air-dry thalli was extremely low, averaging 0.37µl O_2/gm/hr at 60% Relative Humidity and 0.39µl O_2/gm/hr at 75% Relative Humidity. This was about 1% of the rate when saturated with water at the same temperature (25°C).

4 EFFECT OF HIGH TEMPERATURE

(1) Methods

Variation in gas-exchange physiology was used as an indicator of viability after exposure to heat. Following the method of Lange (1953), heat resistance was measured by calculating rates of gas exchange after treatment as a percentage of the rate before treatment.

Terminal lobes of *C. semiviridis* were incubated at a range of temperature from 25°C to 105°C on filter papers in closed petri dishes for 30 minutes. There were two treatments with equal replication: water saturated thalli and air-dry thalli. On removal from the oven, all material was thoroughly wetted, allowed to stand for several hours, then gas exchange rates measured using an oxygen electrode.

(2) Results

The effect of heat on gas-exchange is illustrated in Figure 7.8. When wet thalli were used it was apparent that exposure to temperatures in excess of 30°C for 30 minutes impaired both oxygen uptake and oxygen evolution. Gas exchange was completely stopped by exposure for 30 minutes to a temperature of 55°C. On the other hand, dry thalli were much more resistant. Oxygen evolution proved more sensitive than oxygen uptake to dry heat; oxygen evolution was reduced by exposure to temperatures in excess of 65°C, and ceased by 85°C, whereas oxygen consumption was not affected at temperatures below 75°C, and not stopped by a treatment less severe than 105°C.

5 TEMPERATURE STRESS ACTUALLY ENCOUNTERED IN THE FIELD

(1) Methods

As part of a programme to document the climatic environment on the Koonamore Vegetation Reserve, 250 miles north of Adelaide, and on the northern boundary of the distribution of *C. semiviridis*, an air and soil temperature recording apparatus was installed in December 1967. Temperature sensors were PHILLIPS

E 241 AP, IK5 thermistors, which were linked to a BOTH type R12 galvanometric recorder. The whole system was powered by a 3M 510-12 gas heated thermo-electric generator.

Thermistors were installed at 10cm and 0.5cm depths in the soil, and at 5cm, 25cm and 1m heights in the air. The thermistors in air were housed in small double roofed, vented aluminium shields. The whole system was designed to run for a month unattended.

(2) Results

Because of technical difficulties, notably the failure of electrical insulation under the stress of arid climatic conditions, no reliable temperature recordings were obtained until February 1969. At this stage pressure of other work and mechanical failure in the recorder limited the amount of data which could be collected. Complete and accurate records were obtained for the months of February, March, April and December 1969.

Using the record for the month February 12 - March 11 1969, an indication of heat stress could be obtained. Figure 7.9 shows the daily march of temperature at 0.5cm depth in the soil, and at 25cm in the air.

During that month the highest soil temperature measured at 0.5cm depth was 65°C, which was recorded twice for short periods (see Figure 7.9). Table 7.2 shows the average number of consecutive hours per day with temperatures in excess of the range of values indicated.

TABLE 7.2

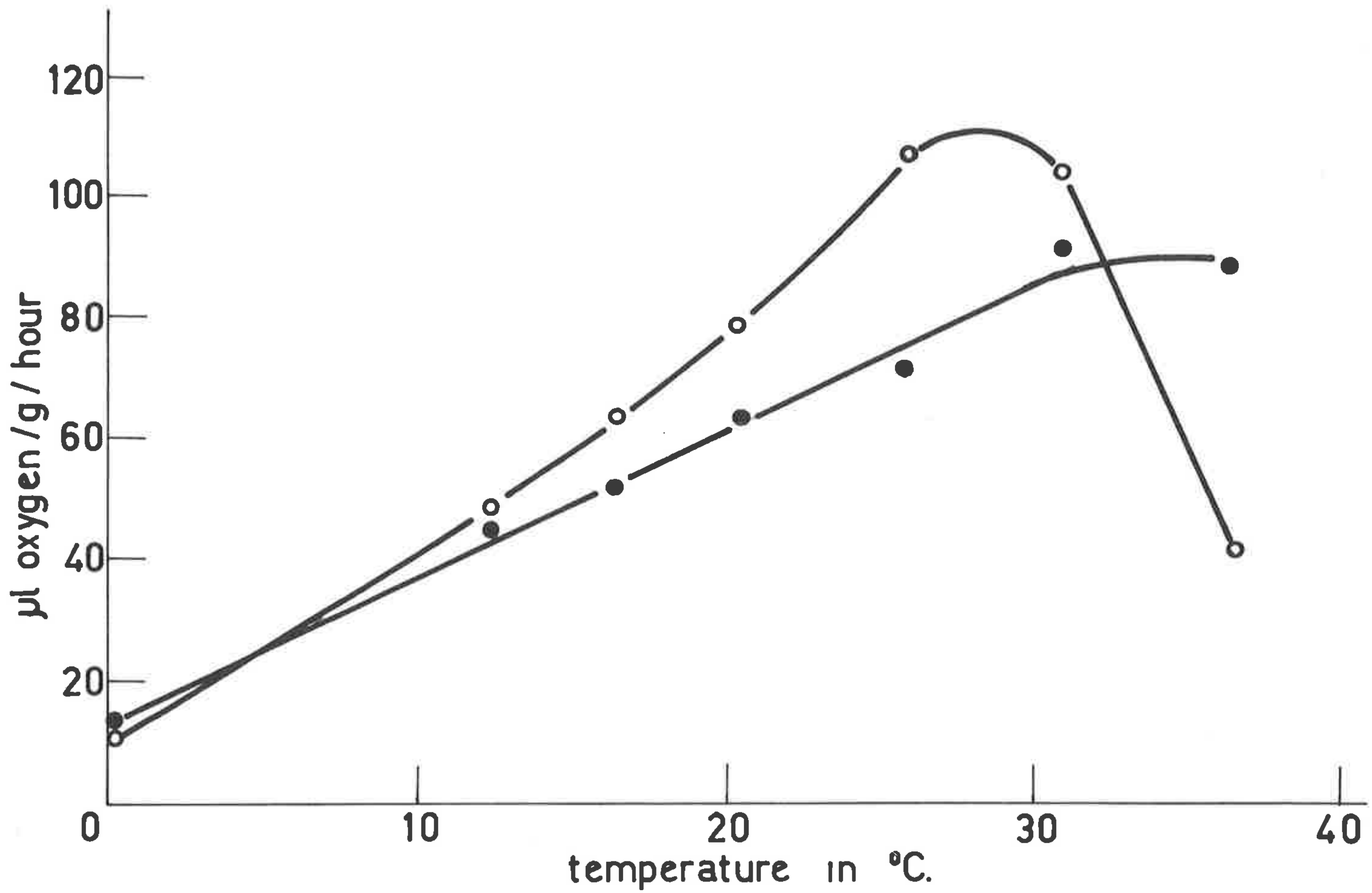
Mean number of hours per day above the indicated temperatures during one month (February 12th - March 11th, 1969).

	Air temperature (at 25cm)		
	35°C	40°C	45°C
Hours	10.1	6.9	1.4
	Soil temperature (at 0.5cm)		
	40°C	50°C	60°C
Hours	4.9	1.9	0.3

On one occasion soil temperature at 0.5cm depth was in excess of 60°C for a period of five consecutive hours; on the same day air temperature was in excess of 45°C for six consecutive hours.

FIGURE 7.4

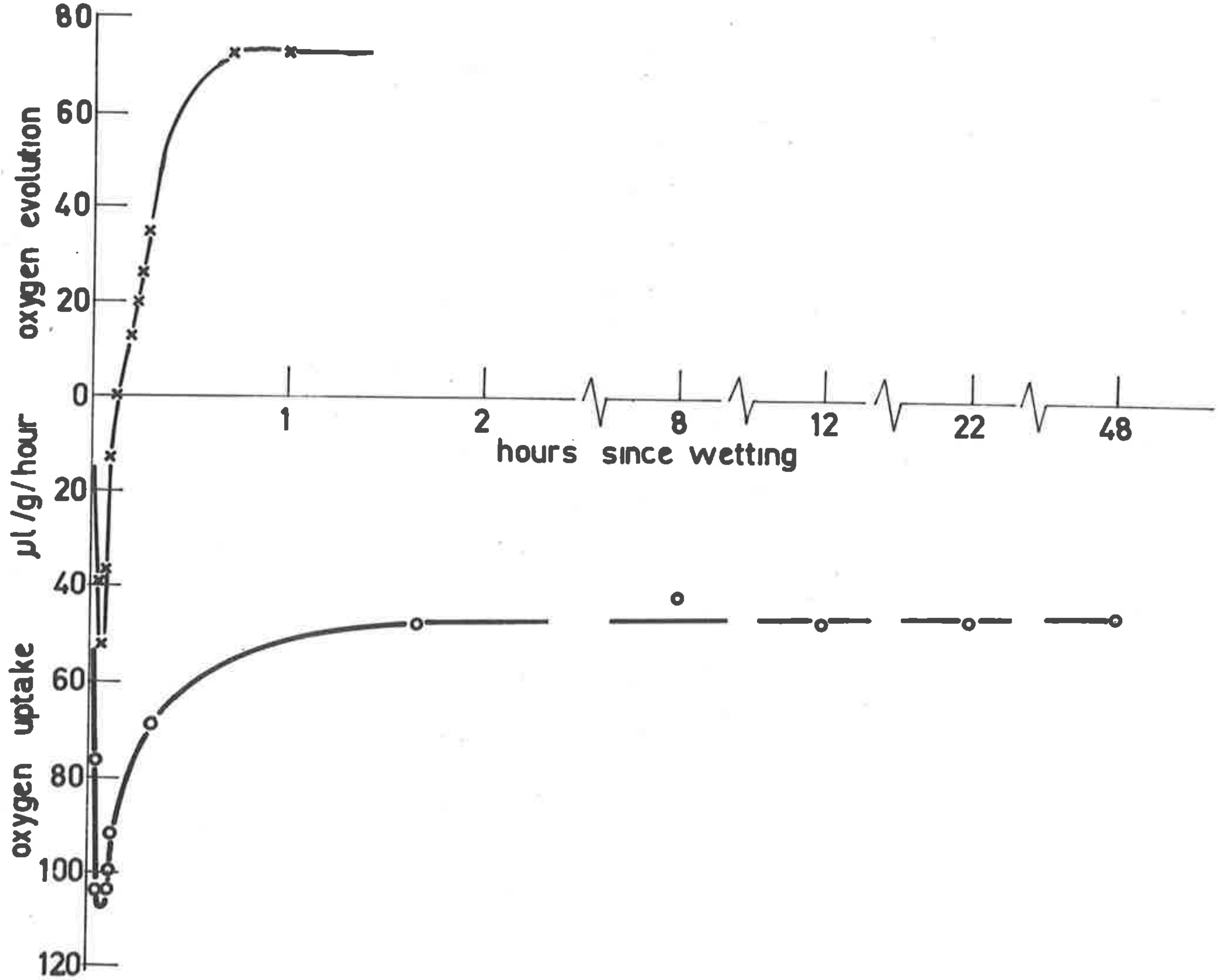
The relationship between gas-exchange of *Chondropsis semiviridis* and temperature. Open circles represent oxygen evolution in the light, filled circles represent oxygen uptake in the dark.



120
100
80
60
40
20
0
10
20
30
40
µl oxygen / g / hour
temperature in °C.

FIGURE 7.5

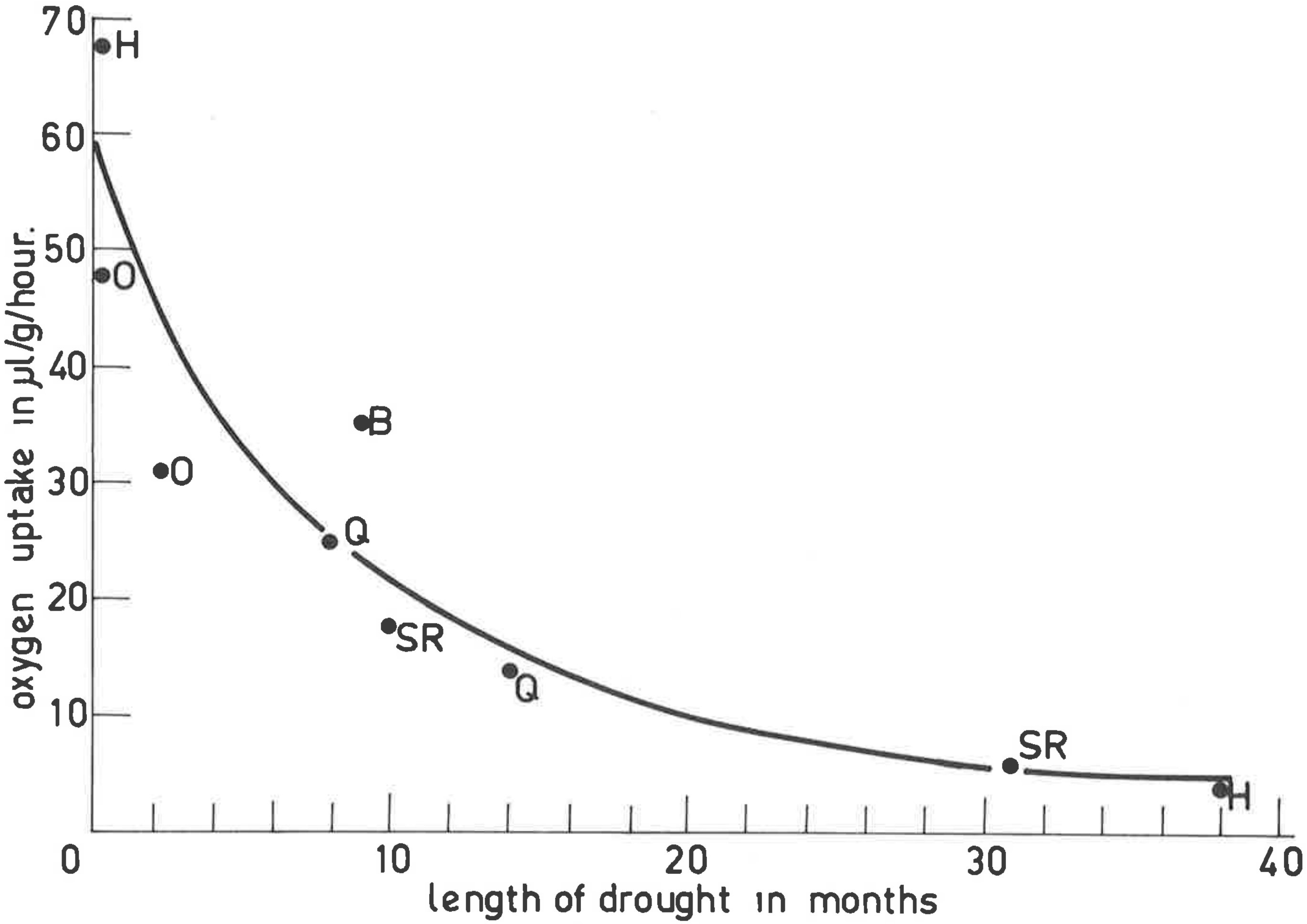
The change in rate of oxygen exchange by *Chondropsis semiviridis* after dry thalli were immersed in water. Crosses represent oxygen exchange in the light, circles represent oxygen exchange in the dark.



oxygen evolution
µl /g/ hour
oxygen uptake
80
60
40
20
0
20
40
60
80
100
120
1
2
8
12
22
48
hours since wetting

FIGURE 7.6

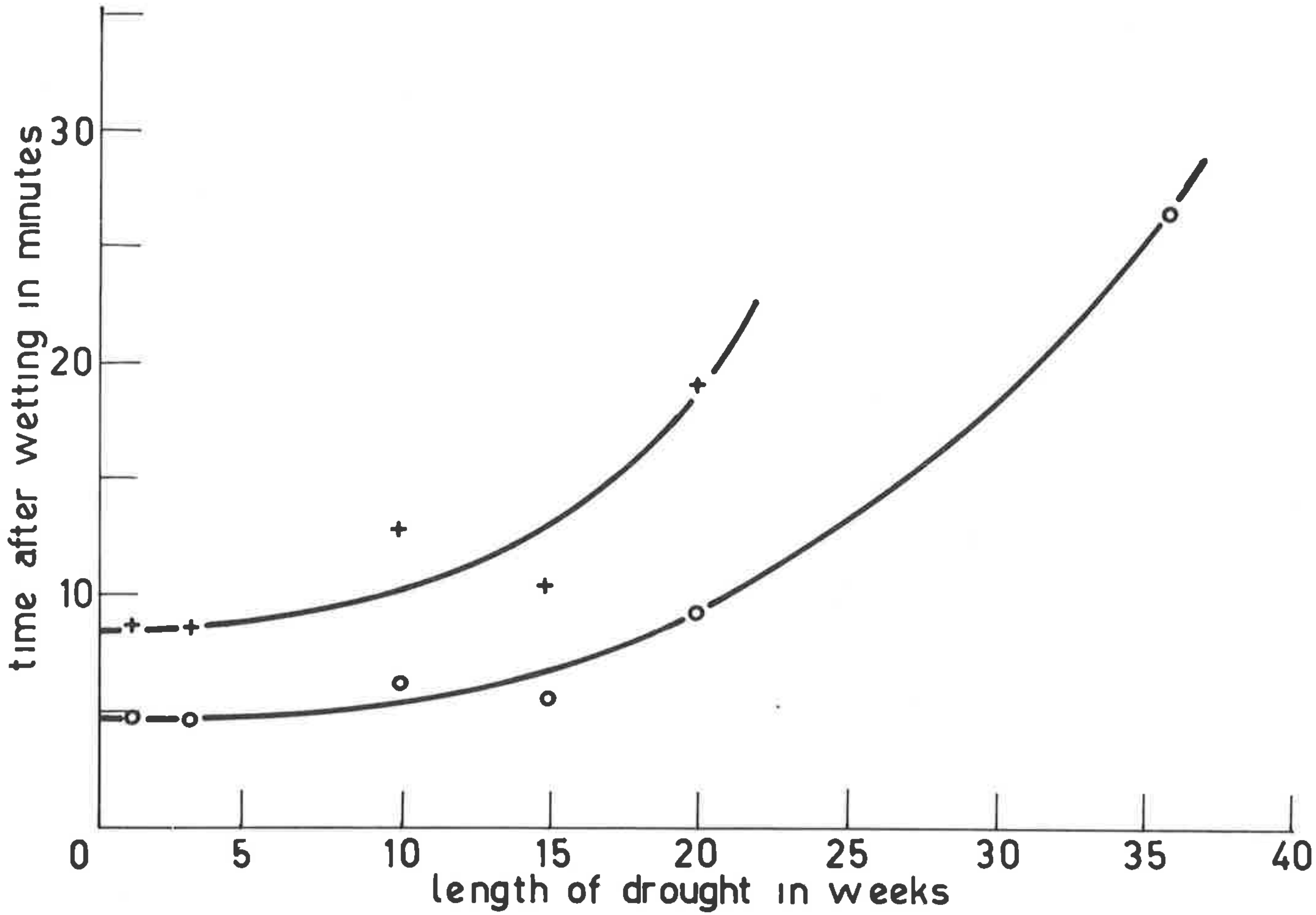
The rate of oxygen uptake by *Chondropsis semiviridis* thalli subject to varying lengths of drought, then wet for several hours before measurements were made. The letters indicate the location from which the experimental material was collected: H, Hesso; O, Oodlawirra; Q, Quondong; B, Bower; and SR, Swan Reach.



oxygen uptake in µl/g/hour.
70
60
50
40
30
20
10
H
O
O
B
Q
SR
Q
SR
H
0
10
20
30
40
length of drought in months

FIGURE 7.7

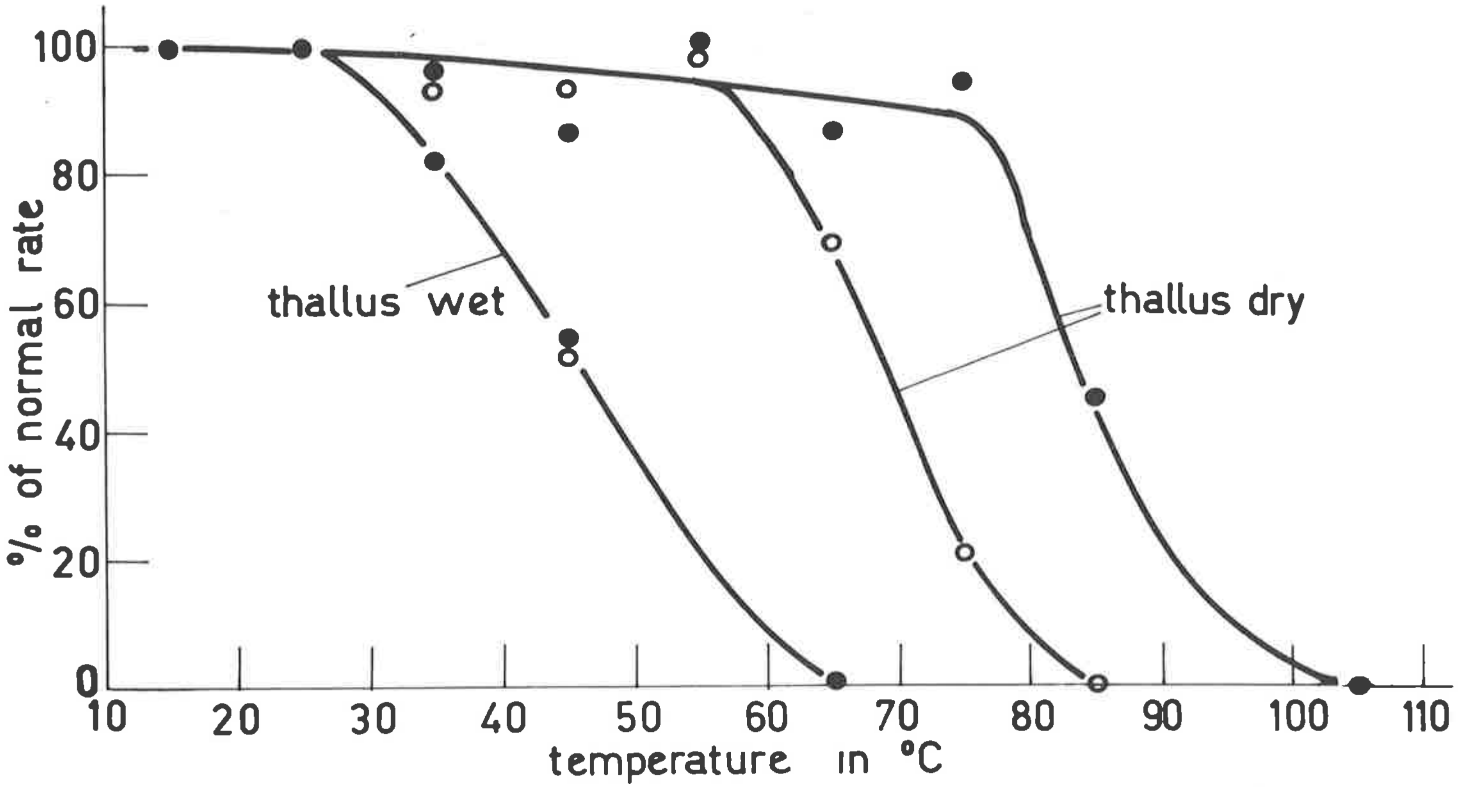
The relationship between time taken for *Chondropsis semiviridis* thalli to reach compensating rates of gas exchange, and to replace oxygen in the medium used in the initial burst of respiration, after various lengths of drought. Open circles indicate the former. Material subject to 64 weeks did not reach compensation point. Crosses indicate time taken to replace the oxygen initially consumed: material subject to 36 weeks drought did not replace the oxygen used initially.



time after wetting in minutes
30
20
10
0
5
10
15
20
25
30
35
40
length of drought in weeks

FIGURE 7.8

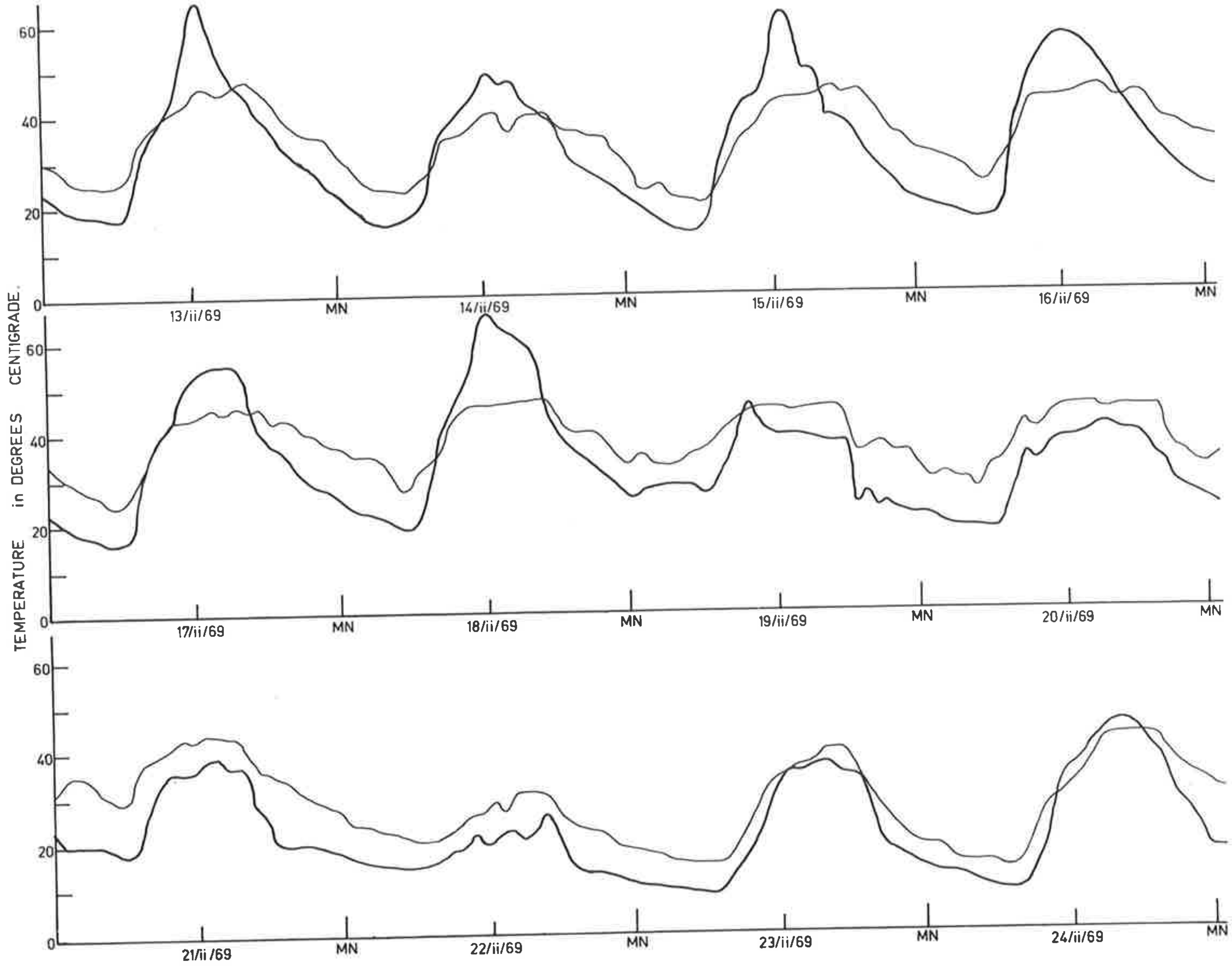
The effect of heat on the gas exchange of wet and dry *Chondropsis semiviridis* thalli. Open circles represent the rate of oxygen evolution in the light; filled circles represent the rate of oxygen consumption in the dark.



100
80
60
40
20
0
% of normal rate
10
20
30
40
50
60
70
80
90
100
110
temperature in °C
thallus wet
thallus dry

FIGURE 7.9

The diurnal variation in temperatures at Koonamore Vegetation Reserve between 13th and 24th of February, 1969. The thicker line represents temperature at 0.5cm depth in the soil, the finer line represents temperature at 25cm in the air.



TEMPERATURE in DEGREES CENTIGRADE.
0
20
40
60
13/ii/69
MN
14/ii/69
MN
15/ii/69
MN
16/ii/69
MN
17/ii/69
MN
18/ii/69
MN
19/ii/69
MN
20/ii/69
MN
21/ii/69
MN
22/ii/69
MN
23/ii/69
MN
24/ii/69
MN

6. IMPLICATIONS OF AUTECOLOGICAL STUDIES

It was apparent that the initial surge of respiratory activity lasted only a few minutes, compared with several days in lichens studied by Reid (1960b). *C. semiviridis* when wet for only a few minutes in full sun would therefore be capable of augmenting its food reserves, whereas those species studied by Reid would have seriously depleted their's. It appeared that *C. semiviridis* was adapted to making use of light showers and heavy morning dews.

This is conformable with the findings of Lange, Schulze and Koch (1970), who, in a study in the Negev showed that *R. maciformis* absorbed sufficient moisture overnight from dew and the air to permit a three hour burst of photosynthesis at dawn. To do this *R. maciformis* must recover from the effect of wetting as rapidly as *C. semiviridis*. The measurements they made showed that in the Negev (much drier than any Australian desert) *R. maciformis* could, with a morning dew, fix an average of 0.54mg CO_2/gm dry weight per day. Thus it appears that the response of *C. semiviridis* to wetting is similar to that shown by the other arid lichen studied in detail, but different from the response of humid zone materials.

The ability of the species to survive drought was considerable. Short term experiments indicated that after a drought period of 20 weeks oxygen evolution could rapidly recover to the stage where it exceeded oxygen uptake, and so the thallus was presumably capable of continued growth. This period of 20 weeks is longer than any drought period the lichen is likely to meet in Australia. However, the respiration during five dry days would metabolize the amount of photosynthetic product produced by the same thallus when saturated with water, and in full sun for one hour. This is calculated on the basis of an average relative humidity at Koonamore Vegetation Reserve of about 60%, (Osborn, Wood and Paltridge 1935), and assuming a temperature of 25°C and a respiratory rate when dry less than 1% of the wet rate. Lange, Schulze and Koch (1970) showed that photosynthesis in desert lichens ought to occur relatively commonly after dawn, either in response to absorption of moisture from the air, or by wetting from dew. Since *C. semiviridis* takes many hours to unroll at 100% relative humidity, and will not unroll at all in 75% relative humidity, absorption of water vapour from air at night probably does not permit photosynthesis to occur at high levels although it would stimulate respiration. It is likely that in nature only liquid water (dew or rain) allows *C. semiviridis* to unroll and expose its photosynthetic surfaces to full light.

Therefore, *C. semiviridis* must be restricted in distribution to areas within which the thallus intercepts rain or is wet by dew for at least 73 hours per annum in sun light (The amount of time calculated as necessary for replacement of metabolic reserves used in a year by air-dry thalli). Respiratory increase due to absorption of water vapour at night without corresponding photosynthesis, would increase the necessary wet daytime hours required for the lichen to survive. Accepting the estimate of a 3 hour photosynthetic burst in response to dew, and allowing for the same photosynthetic period in response to rainfall *C. semiviridis* could not survive in an area with less than 25 days with either dew or rain per annum. Since in southern Australia mean number of rain days per annum and mean annual rainfall are closely related, it is not surprising that the dry limit of distribution of *C. semiviridis* coincides with a rainfall isohyet.

Thalli of *C. semiviridis* are very sensitive to heat when wet. At a temperature of 45°C, an air temperature not uncommon in the study area, the thallus, if wet, has its photosynthetic ability reduced to half in thirty minutes. When dry the thallus is much more heat resistant, showing no damage after 30 minutes at 55°C, and little damage at 65°C. The latter temperature is the highest recorded at a depth of 0.5cm in the soil during the summer of 1968-9 at the Koonamore Vegetation Reserve, near the northern limit of *C. semiviridis*. Sensitivity to heat while wet thus explains the absence of *C. semiviridis* from those areas with a pronounced summer rainfall maximum.

The southern limit may be explained if it is assumed that *C. semiviridis* requires relatively high light intensities to photosynthesize. The data of Staflelt (1939) suggest that this is so for many lichens. Such intensities probably do not occur on the soil surface in the rather denser vegetation of higher rainfall areas but only in sparsely vegetated regions. This results in thalli on the soil in high rainfall areas being exposed simultaneously to high respiration rates and low photosynthetic rates, especially during the winter.

If it is assumed that the physiology of the alpine material from Cooma is the same as that from arid lands, there is no simple explanation for the distribution of the species. It is possible that the alpine vegetation is too sparse to reduce the light intensity, suspected to prevent *C. semiviridis* growing in other wet areas, to a level preventing its growth. The low temperature and humidity in winter may also serve to minimize the effect of low light intensities on the metabolic reserves of the thalli.

In summary, it can be said that the hypotheses concerning factors affecting the distribution of *C. semiviridis* have been largely validated. It has been shown that the interaction of rainfall and temperature would prevent if from surviving in many areas with a predominantly summer rainfall, and that the infrequent rains associated with low rainfall areas would prevent it from surviving there. While there is no evidence that over-supply of water *per se* restricts its distribution, it is suggested that competition for light from higher plants while the thallus is metabolically active usually prevents *C. semiviridis* from growing in areas with rainfall in excess of 35cm per annum.

CHAPTER VIII*

LICHEN POPULATIONS ON SOIL CRUSTS AROUND SHEEP WATERING PLACES

During the broad scale sampling of lichen populations it became apparent that historical factors were important in determining the species constituting a soil surface lichen crust.

The expansion of wheat farming in the years 1880-1884 and subsequent retreat of the farmers from arid areas (Meinig 1963) left large areas once covered with shrub steppe bare and all their surface soil eroded. Poor, disclimax grasslands came into being on these areas. Subsequent grazing has apparently prevented regeneration of shrubs on many of these areas: it appears also to have restricted lichen growth. In other areas which had not been ploughed, adjacent paddocks have very different lichen floras; the only plausible explanation for which appears to lie in varying histories of stocking. It was decided, therefore, to study the effect of stocking on the soil surface lichens.

The effect of stocking on arid lands in Australia has been studied by a number of workers, including Osborn, Wood and Paltridge (1932), Beadle (1948), Jessup (1951), and Barker and

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* This chapter contains the substance of a paper entitled "Lichen populations on arid soil crusts around sheep watering places in South Australia" accepted for publication in *Oikos*.

Lange (1969). All these studies indicated that considerable deterioration in the vegetation had been caused by stocking.

A fundamental ecological unit of the sheep-vegetation system appears to be the piosphere (Lange 1969). The piosphere concept holds that a special ecological situation comes into operation when a watering place for stock is established in otherwise waterless rangeland, and stock which must drink are depastured there. This causes a gradient in stocking pressure which attenuates with radial distance from the watering place (Lange 1969), and which is reflected by changes in the vegetation (Osborn, Wood and Paltridge 1932, Barker and Lange 1969).

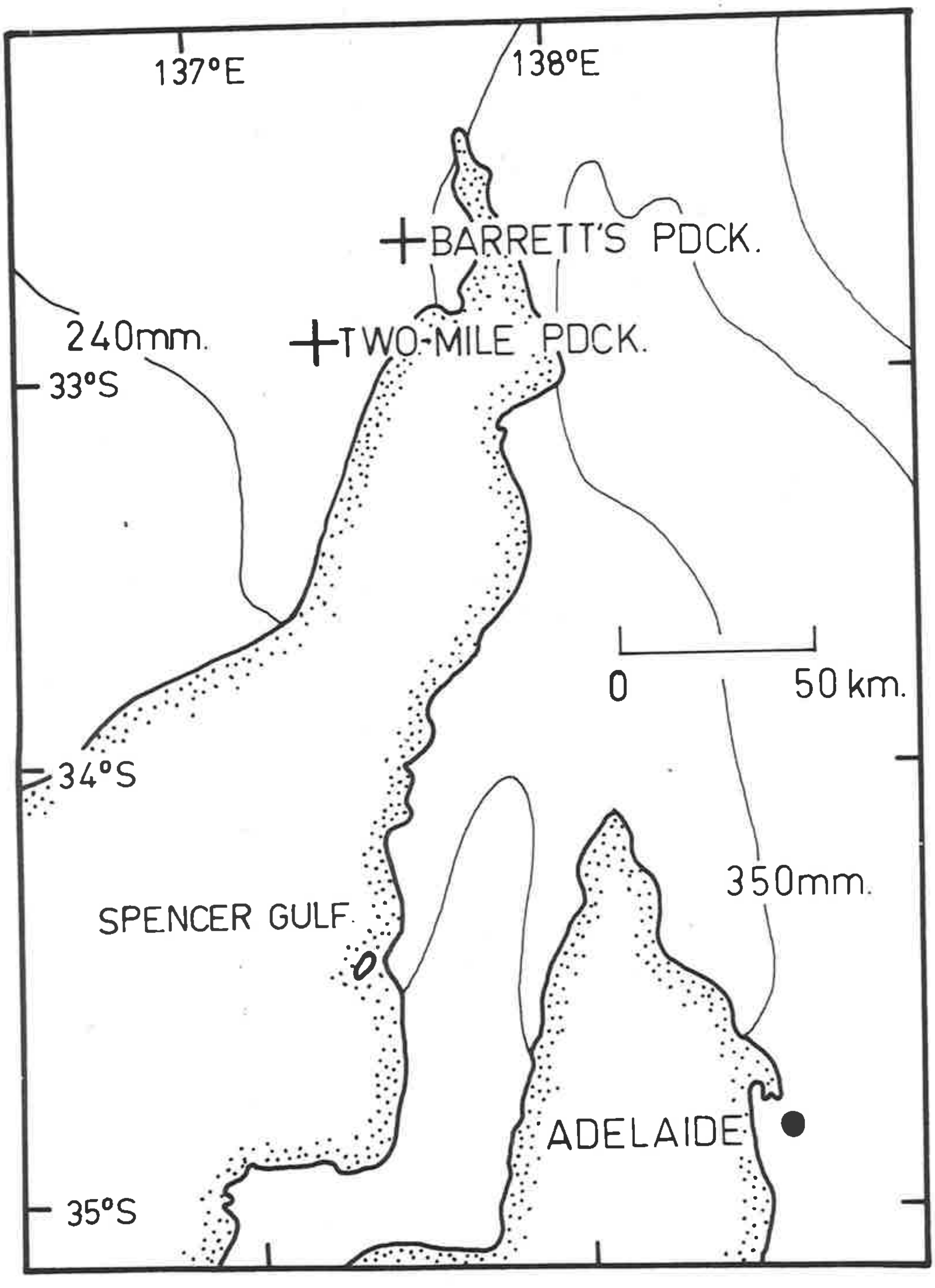
Because study of the piosphere was apparently such a sensitive method of detecting changes in plant populations resulting from stocking pressure, it was decided to use the piosphere concept in this study of the effect of stocking pressure on soil surface lichen populations.

1. STUDY AREAS

Analyses of piosphere situations were undertaken at two locations in South Australia, one in Two-mile paddock on Middleback Station, the other in Barrett's paddock on Tregelana Station (Figure 8.1). A "station" in Australian usage is a large area (usually in excess of 100Km^2) of arid land used for grazing.

FIGURE 8.1

The location of study sites at Two-mile and Barrett's paddocks in relation to the 240mm and 350mm rainfall isohyets.


137°E
138°E
BARRETT'S PDCK.
240mm.
TWO-MILE PDCK.
33°S
0
50 km.
34°S
350mm.
SPENCER GULF
ADELAIDE
35°S

Two-mile paddock, with an area of 20Km^2, has two sheep watering places about 5Km apart. One of these, Two-mile dam, was chosen as the focus for an initial study and attention directed to adjoining country served by this watering place, covered with *Kochia sedifolia* F.v.M. shrubs interspersed with small groves of *Acacia sowdenii* Maiden trees. The soils are mainly solonized brown calcareous earths. Sheep have watered at the dam for 70 years, and change in vegetation close to the dam is quite noticeable.

Barrett's paddock, with an area of 15Km^2, has only one watering place for sheep; a trough supplied with water through a pipeline. The trough is situated near the centre of the western boundary of the paddock, about 150m from the fence. There is a slight downslope from west to east. The vegetation is complex, with dense groves of *Casuarina cristata* Miq. and *Acacia sowdenii* over a shrub stratum mostly of *Kochia sedifolia* or *Atriplex vesicaria* Heward. The soils are solonized brown calcareous earths. The eastern part of the paddock is subject to inundation after heavy rains. The watering place has been in use for 30 years.

2. METHODS

(1) Sampling

Samples were laid out on radial traverses designed to bring out pattern centred on the watering point. At sample sites, a transect 20m long was laid out and the presence was noted of all lichen species in each of ten 15cm x 20cm quadrats placed 2m apart.

In Two-mile paddock, 10 traverses at intervals of 10° were placed with transects at ranges of 18, 45, 90, 135, 180, 225, 315, 405, 495, 585, 675 and 760 metres from the dam.

At Barrett's paddock a permanent radial grid existed, with 32 traverses at intervals of $11\frac{1}{4}$° forming a complete circle for sampling. The positions of samples on this grid were staggered on alternate traverses; samples along one series of traverses were at ranges of 10, 23, 70, 135, 225, 360, 630, 990 and 1170 metres, and on the alternate traverses at ranges of 10, 45, 90, 180, 270, 450, 810 and 1170 metres from the watering place.

(2) Data treatment

Frequency of each species at each range from the watering place was calculated as the percentage of quadrats at that range with the given species occurring in it.

In order to demonstrate changed species composition around the watering place, species incidence data derived by pooling the data from the ten small quadrats in each transect were subject to Influence Analysis (Lange 1968).

3. RESULTS

(1) Two-mile paddock

Twenty taxa of lichen occurred in the 120 transects, at least one species occurring in each. The taxa, and their frequencies at each range from the dam, are listed in Table 8.1.

Many significant interspecific associations, all positive, occurred at *chi* levels on one degree of freedom > 3.3 ($p < 0.001$).

The underlying patterns in this mass of interactions were revealed first by grouping those species associated at the highest attained levels of significance, then by lowering the significance level and admitting further associated species into consideration. This process resulted in the recognition of nodes in the populations. The development of these nodes is shown in Figure 8.2.

Two separate nodes existed at the highest levels of significance. They remained independent and gained further species as significance levels were lowered, until the level at which $chi > 3.5_{1df.}$ was reached. At that significance level the two nodes fused so that 10 of the 20 species were linked into a single node, node III.

TABLE 8.1

Percentage Frequency of lichen species at Two-mile paddock at each range from the watering place. 100 quadrats were examined at each range.

Species	No.	Range from water in metres											
		18	45	90	135	180	225	315	405	495	585	675	760
Acarospora smaragdula (Wahlenb.) Th.F.	1	0	2	0	0	0	1	1	3	7	4	5	9
Aspicilia calcarea Mudd. (crustose)	2	4	0	5	13	31	18	38	46	54	56	59	47
Aspicilia calcarea Mudd. (fruticose)	3	0	0	0	0	0	0	3	2	1	7	6	9
Caloplaca ? subpyracella (Nyl.) Zahlbr.	5	0	0	0	1	1	1	0	1	2	2	2	0
Cladonia foliacea Schaer.	7	0	0	0	0	0	0	0	6	2	9	13	4
Collema ? coccophorus Tuck.	8	25	42	57	47	67	62	56	59	51	52	55	62
Dermatocarpon lachneum (Ach.) A.L. Sm.	9	0	1	3	1	2	2	10	11	5	16	15	17
Diploschistes ocellatus (D.C.) Norm.	10	0	0	0	0	0	0	1	1	1	3	2	3
Diploschistes scruposus (Schreb.) Norm.	11	0	0	0	0	0	1	6	11	5	4	10	9
Endocarpon pusillum Hedw.	12	5	2	1	4	11	11	26	29	24	35	43	33
Fulgensia bracteata (Hoffm.) Räs.	13	0	0	1	0	1	2	25	15	33	41	24	27
Heppia lutosa Ach.	14	1	3	3	10	12	6	20	15	28	23	27	26
Heppia ? polyspora Tuck.	15	0	0	0	0	4	7	2	7	7	12	11	11
Lecidea coarctata (J.E. Sm.) Nyl.	17	0	0	0	0	1	0	0	0	0	0	4	1
Lecidea crystallifera Tayl.	18	0	1	0	0	1	2	8	9	9	11	24	11
Lecidea decipiens (Ehrh.) Ach.	19	2	0	1	2	8	11	36	35	53	54	59	56
Parmelia amphixantha Müll. Arg.	20	0	0	0	0	0	0	3	1	2	0	1	0
Parmelia molliuscula Ach.	22	0	0	0	0	0	0	0	0	0	0	1	1
Parmelia pulla (Neck.) Ach.	23	0	0	0	0	0	0	0	1	1	0	1	0
Toninia caeruleonigricans (Lightf.) Th. Fr.	24	1	3	7	4	8	3	19	22	32	29	20	22

The implications of these interactions were brought out by examining the field distribution of the interacting species, after the approach of Lange (1968). Maps could be constructed to illustrate the expression of any node. In terms of node I, each of the 120 transects in Two-mile paddock took one of the values from zero to six according to the number of nodal species contained. On a map showing the distribution of transects classified in these terms, isotels (lines enclosing areas of the same outcome) could be constructed. This was done for each of the nodes I, II and III (Figure 8.3a,b).

(2) Barrett's paddock

Twenty-four taxa of lichen occurred in 146 of the 175 transects. These taxa and their frequencies are listed in Table 8.2.

As at Two-mile paddock, many significant interspecific interactions, all positive, occurred. These were grouped into nodes, the development of which is shown in Figure 8.4.

Three independent nodes existed at the highest levels of significance. These three gained species as the significance level was lowered, but remained independent at the lowest *chi* level ($chi > 3.3_{1df.}$) considered. The terminal nodes (nodes IV, V and VI) contained respectively ten, six and three species, a total of 19 species out of the 24 recorded

TABLE 8.2

Frequency of lichen species and number of quadrats studied at Barrett's paddock for each range from the watering place

Species	No.	Range from water in metres														
		10	23	45	70	90	135	180	225	270	360	450	630	810	990	1170
Acarospora smaragdula (Wahlenb.) Th. Fr.	1	0	0	0	0	0	0	3	1	2	0	4	2	7	2	1
Aspicilia calcarea Mudd. (crustose)	2	0	0	1	2	5	7	16	25	23	18	17	28	17	40	37
Aspicilia calcarea Mudd. (fruticose)	3	0	0	0	0	1	0	1	0	1	1	5	6	1	6	1
Buellia epigaea Tuck.	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Caloplaca ? subpyracella (Nyl.) Zahlbr.	5	0	0	0	0	0	0	1	0	0	1	1	1	1	2	1
Chondropsis semiviridis (Nyl.) Nyl.	6	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
Cladonia foliacea Schaer.	7	0	0	0	0	0	1	0	0	4	2	2	2	1	3	6
Collema ? coccophorus Tuck.	8	0	16	27	31	32	44	45	60	50	51	51	50	62	65	58
Dermatocarpon lachneum (Ach.) A.L. Sm.	9	0	0	1	0	0	2	2	6	2	7	3	7	2	13	8
Diploschistes ocellatus (D.C.) Norm.	10	0	0	0	0	0	0	0	1	0	3	2	4	3	3	2
Diploschistes scruposus (Schreb.) Norm	11	0	0	0	0	0	1	3	1	2	1	4	2	1	2	4
Endocarpon pusillum Hedw.	12	0	0	2	3	1	5	7	16	9	12	10	13	13	30	28
Fulgensia bracteata (Hoffm.) Räs.	13	0	0	0	0	0	1	5	5	1	4	7	12	6	12	10
Heppia lutosa Ach.	14	0	5	8	9	13	17	19	32	24	27	26	31	27	39	38
Heppia polyspora Tuck.	15	0	0	1	1	1	6	3	3	2	2	5	8	4	14	10
Lecanora atra (Huds.) Ach.	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lecidea coarctata (J.E. Sm.) Nyl.	17	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1
Lecidea crystallifera Tayl.	18	0	0	0	0	0	1	3	3	2	1	4	4	3	9	9
Lecidea decipiens (Ehrh.) Ach.	19	0	0	0	0	1	8	17	22	16	11	21	31	20	40	31
Parmelia amphixantha Müll. Arg.	20	0	0	0	0	0	0	1	0	0	0	0	0	7	1	9
Parmelia australiensis Cromb.	21	0	0	1	1	4	0	0	0	0	0	0	0	0	1	2
Parmelia molliuscula Ach.	22	0	0	0	0	0	0	2	1	0	0	0	0	0	1	2
Parmelia pulla (Neck.) Ach.	23	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Toninia caeruleonigricans (Lightf.) Th.Fr.	24	0	0	0	0	1	2	7	10	4	2	7	16	4	22	9
Number of quadrats examined		150	160	130	160	150	130	110	110	100	90	100	90	90	90	170

for the site. Meaningful isotel maps (Figures 8.5, 8.6) could be constructed for nodes IV and V. Node VI species were too infrequent for meaningful mapping.

4. DISCUSSION

(1) Two-mile paddock

The frequency data left no doubt that the watering place was the focus of an influence which reduced the frequency of each soil crust lichen species. Different species were affected to different degrees and according to different relationships, as was apparent from the nature of the curves in Figure 8.7. *Collema coccophorus* was relatively insensitive to the influence causing the pattern, its frequency not falling until very close to the watering place. Other less sensitive species included *Aspicilia calcarea* (crustose), *Endocarpon pusillum*, *Heppia lutosa*, *Lecidea decipiens* and *Toninia caeruleonigricans*. Because the watering place was the centre of pattern for both stocking and drainage, these effects could not be ascribed solely to stocking pressure, but could have been the product of a topographic variable.

Influence analysis also showed the watering place to be the centre of an influence, because nodal species were mostly absent near the watering place (Figure 8.3a,b).

FIGURE 8.2

Development of nodal structure derived from data collected in Two-mile paddock as *chi* (significance) levels of association are reduced. Numbers refer to species names listed in Table 8.1.

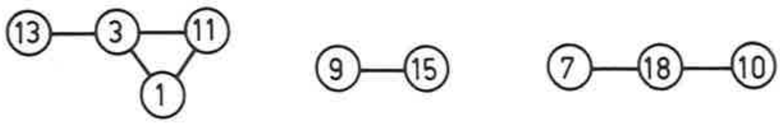
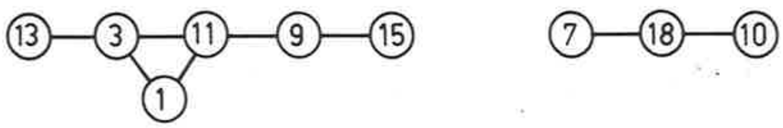
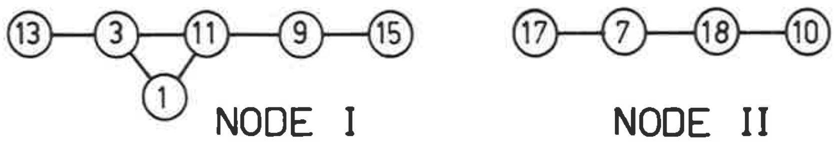
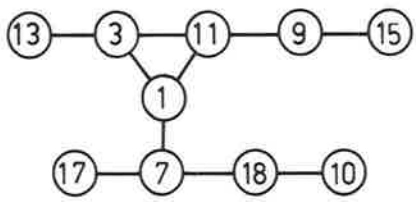
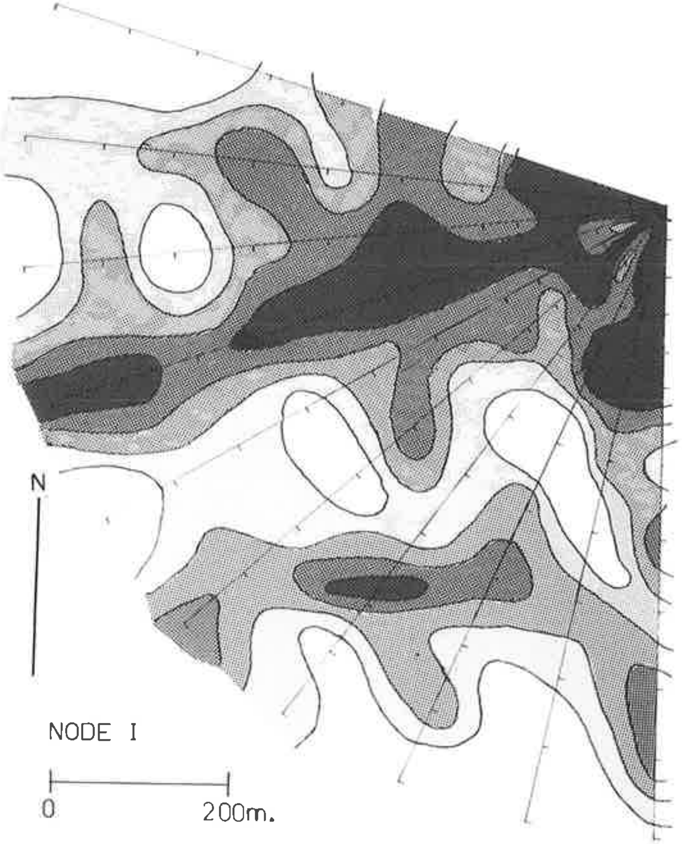
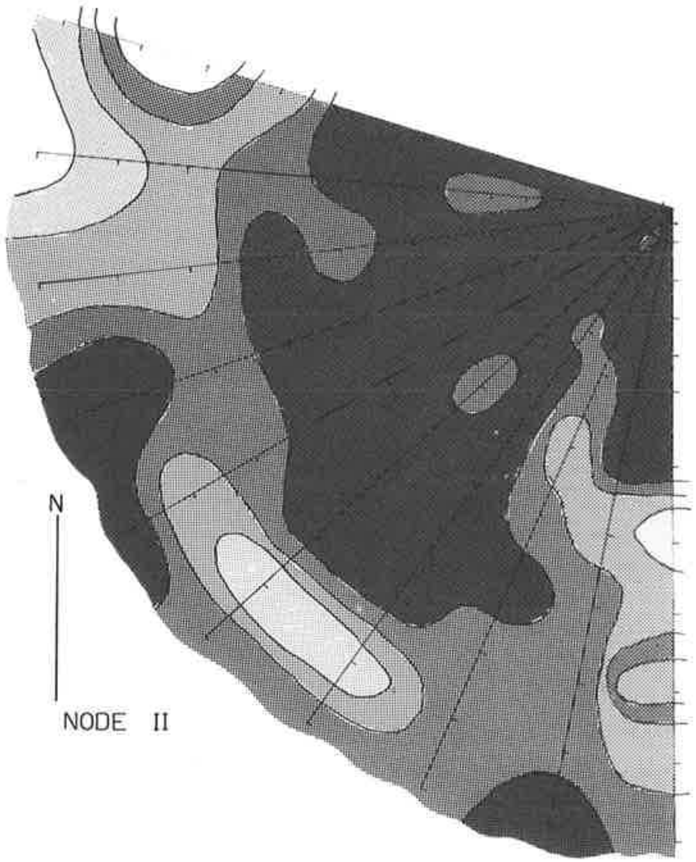
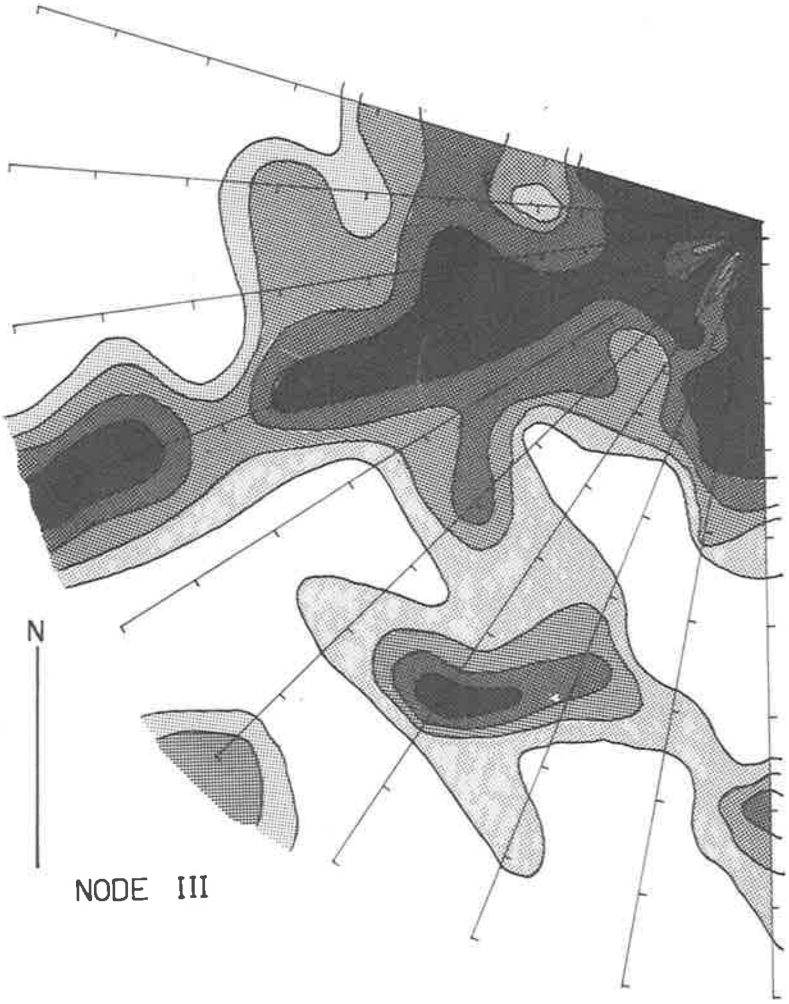
chi	NODAL STRUCTURE
⩾ 4.0	
⩾ 3.9	
⩾ 3.8	
⩾ 3.7	 NODE I NODE II
⩾ 3.5	 NODE III

FIGURE 8.3.

Isotel maps for nodes I, II and III in Two-mile paddock. The intensity of shading portrays the number of nodal species present, from the darkest shading representing areas with no nodal species present to white, indicating four or more nodal species.


N
NODE I
0
200m.


N
NODE II



NODE III

FIGURE 8.4

Development of nodal structure derived from data collected at Barrett's paddock as *chi* (significance) levels of association are reduced. Numbers refer to species names listed in Table 8.2.

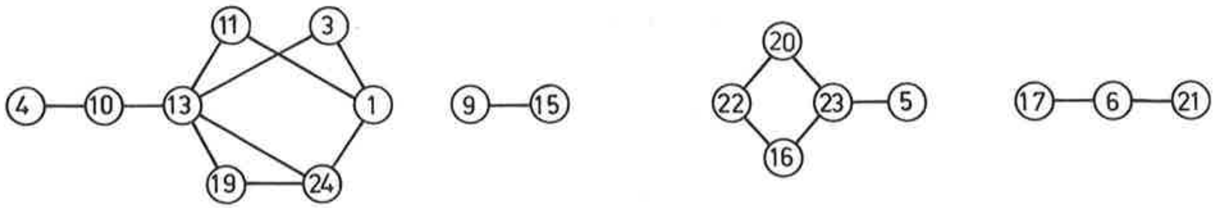
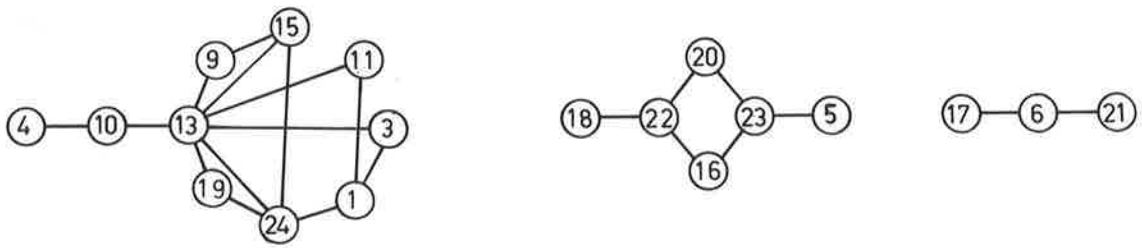
chi	NODAL STRUCTURE
⩾5.0	
⩾4.5	
⩾4.0	
⩾ 3.5	
⩾ 3.3	

FIGURE 8.5

Isotel maps for node IV in Barrett's paddock. Intensity of shading has the same meaning as in Figure 3.

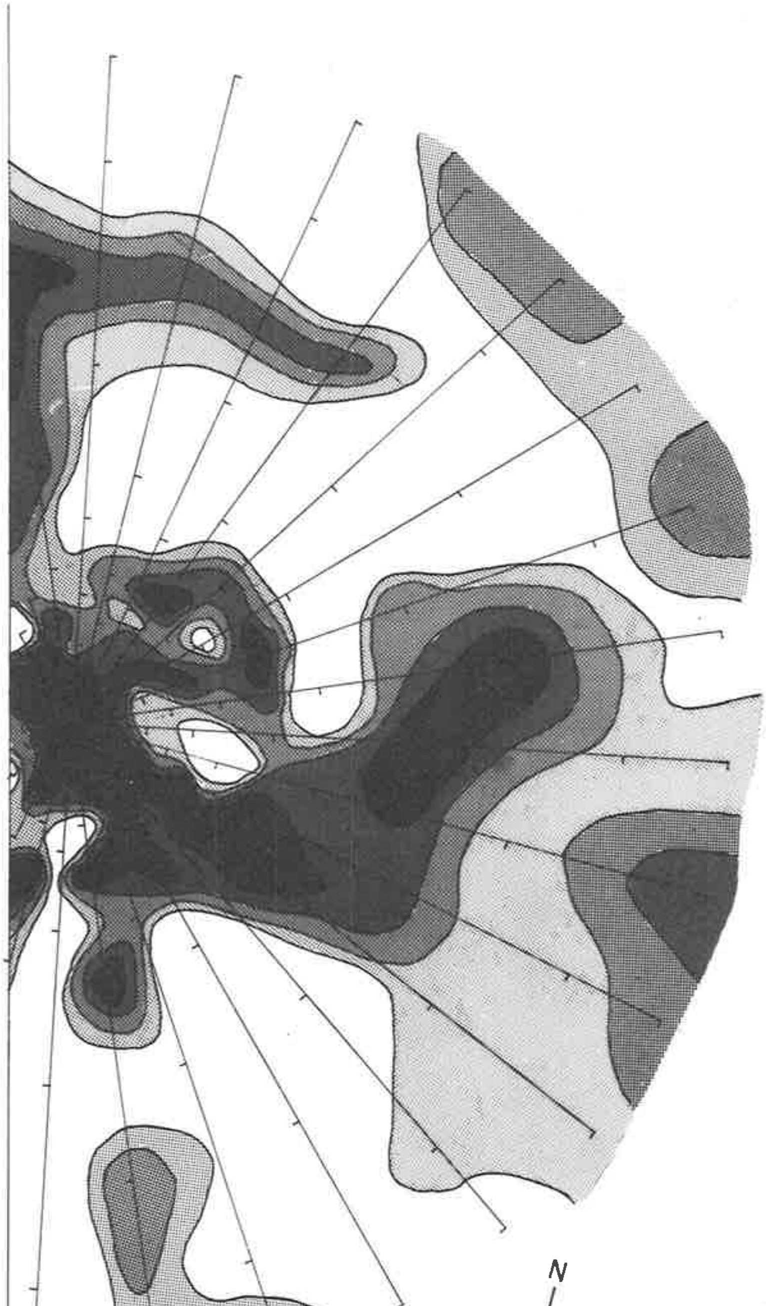

N
0
200m.

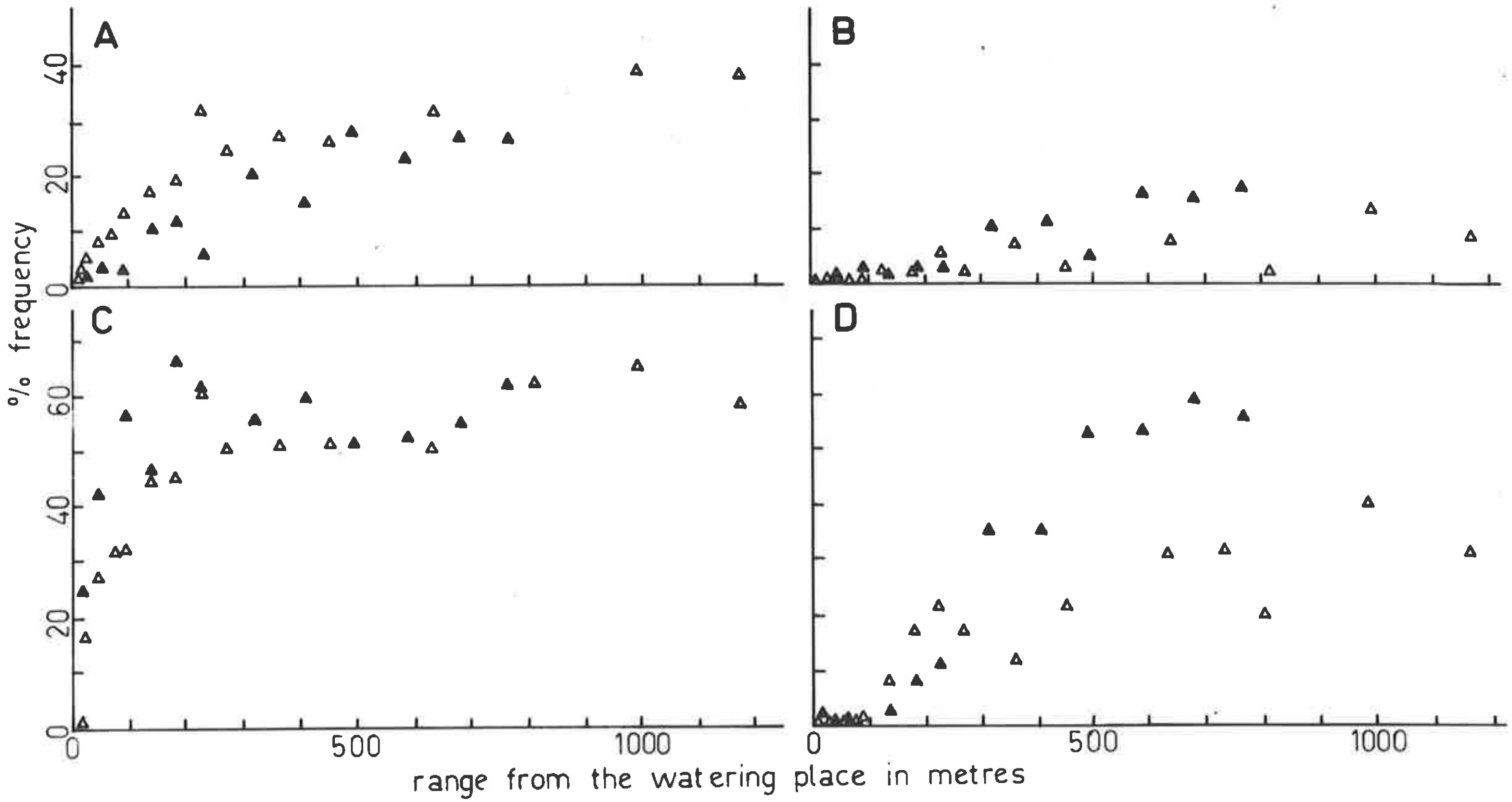
FIGURE 8.6

Isotel map for node V in Barrett's paddock. Intensity of shading has the same meaning as in Figure 3.


N
0
200m.

FIGURE 8.7

Relationship between % frequency and distance from the watering place for
(a) *Heppia lutosa*,
(b) *Dermatocarpon lachneum*,
(c) *Collema coccophorus*, and
(d) *Lecidea decipiens*.
Solid triangles indicate frequency at Two-mile paddock, open triangle at Barrett's paddock.


A
B
C
D
% frequency
0
20
40
0
20
40
60
0
500
1000
0
500
1000
range from the watering place in metres

It was interesting that nodes I and II, while independent of each other (and with isotels differently disposed), both reflected an influence centred on the watering place.

A feature of nodes I and III (Figure 8.3a,b) was a long tongue of low ratings along one traverse which ran along a drainage line into the dam. This observation would support an hypothesis that the low ratings were associated with topography.

In other piosphere studies all isotels of interactions between plant species were essentially concentric on the watering place, and it seemed reasonable to expect that all isotels of any significant interactions in piosphere lichen crust populations would be similar. This was not the case. At distance from the watering place general concentricity disappeared and the pattern became a mosaic, making the drawing of isotels somewhat arbitrary, even though the pattern is real. The mosaic pattern showed no correlation with obvious environmental variables.

(2) Barrett's paddock

The layout of species frequency value around the watering place in Barrett's paddock was very similar to that around Two-mile dam (Figure 8.7). At Barrett's paddock there was no reasonable doubt that the influence causing the low frequency values near the watering place was stocking pressure, as the watering place was supplied by a pipeline, and was hence sited independently of topography.

Examination of the isotel maps for nodes IV and V (Figures 8.5 and 8.6) showed the watering place to be the centre of an area of low ratings. This left no reasonable doubt that stocking pressure was an influence causing the low ratings. It was clear from Figure 8.5 that there were two tongues of low ratings running more or less east-west across the study area. One was north of the watering place, and the other was an extension of the low value zone around the watering place. The more northerly tongue was found to correspond with a watercourse, hence it appeared that watercourse conditions had an effect similar in consequence to intense stocking. From aerial photographs it was apparent that the tongue extending from the watering place was coincident with an extraordinary density of sheep tracks apparently skirting *Casuarina* thickets. This observation appeared to account for the distorted concentricity of isotels about the watering place.

The species of node V, while showing a pattern of isotels (Figure 8.6) similar to that of node IV, (Figure 8.5) did not show a tongue of low values along the watercourse. Node V species were apparently susceptible to stocking pressures, but were not influenced by the topographic factors effecting the species of node IV.

(3) Community structure

Data presented suggested that under intense stocking pressure a lichen flora dominated by *Collema coccophorus* was likely to result. Other species that remain under such conditions included *Aspicilia calcarea* and *Heppia lutosa* at both sites. Foliose species appeared to be more sensitive to stocking pressure than did the crustose species.

It was noteworthy that no species of lichen showed development of populations in watercourses, or in response to stocking. Thus the overall soil crust lichen vegetation differed from the higher plant flora which, in the piosphere, had elements which increased in frequency under the highest stocking pressures. Deterioration of higher vegetation under stocking need involve no change in plant cover, but simply change in species composition. In contrast, deterioration of lichen populations in this study implied reduction in lichen cover, and resultant soil mobility.

It is clear that node III, at Two-mile paddock, and node IV, at Barrett's paddock, behave in very similar ways in relation to stocking and topographic factors. The species composition of these nodes is also very similar (Table 8.3).

TABLE 8.3

The composition of node III at Two-Mile Paddock and that of Node IV at Barrett's paddock.

Nodal Species	Node III	Node IV.
Acarospora smaragdula	+	+
Aspicilia calcarea (fruticose)	+	+
Dermatocarpon lachneum	+	+
Diploschistes ocellatus	+	+
Diploschistes scruposus	+	+
Fulgensia bracteata	+	+
Heppia polyspora	+	+
Cladonia foliacea	+	-
Lecidea coarctata	+	-
Lecidea crystallifera	+	-
Buellia epigaea	-	+
Lecidea decipiens	-	+
Toninia caeruleonigricans	-	+

Two nodes at Barrett's paddock were absent at Two-mile paddock. It was not clear what these nodes reflected except a difference in environment between the two paddocks. Node V contained three foliose species *Parmelia amphixantha*, *P. molliuscula* and *P. pulla*, and node VI two vagant foliose species that lie free on the soil surface, *Chondropsis semiviridis* and *Parmelia australiensis*. The only foliose species occurring in a nodal group at Two-mile paddock was *Cladonia foliacea*; all other species were crustose or squamulose.

There are two factors which may explain the difference between these two sites. First, the higher rainfall at Barrett's paddock which is generally regarded as more favourable for the development of foliose lichens (Galun 1962); and second, the longer grazing history at Two-mile paddock may have caused more complete destruction of foliose forms than has yet occurred at Barrett's paddock.

CHAPTER IX

OTHER BIOTA IN THE SOIL CRUST

From the beginning of the study it was recognized that organisms other than lichens were significant in the soil crust. In particular it was believed that algae would be an important component; these were therefore studied at some length. During the study it became apparent that in some places Bryophyta formed a prominent part of the cryptogamic flora, and were therefore collected. The study was not extended to cover the soil mycoflora (other than lichenized forms), nor to bacteria, though these are important and are discussed in this section.

During the study soil samples were collected for T.G. Wood, who later made available a manuscript covering his studies on the soil microfauna. A comment on the microfauna is therefore included.

1. ALGAE

Algae have been found to be widespread in arid soils, some capable of nitrogen fixation (Singh 1961). A study of the algae in samples of soil from the study area was initiated. Culture techniques were necessary as direct examination of soil surfaces generally failed to detect any algae present. These techniques proved unduly time consuming for a subsidiary portion of the major project. This, coupled with extreme taxonomic difficulty experienced with the identification of blue-green algae, eventually led to the premature termination of the study.

(1) Method

Soil surface samples from 112 sites in South Australia and Victoria were collected in sterile McCartney bottles and returned to the laboratory. In the laboratory about 10gm of the sample were transferred under aseptic conditions to a plugged Ehrlenmeyer flask, which contained 30gm of acid washed quartz sand and 25ml of medium D (Kratz and Myers 1955), all previously autoclaved as a single unit. Control flasks were set up at the same time. The flasks were inclined at 45°, sloping the sand and culture medium to form an environmental cline from damp sand to fully aquatic. The flasks were then incubated in continuous light (3,000 lux) at 25°C for eight weeks. During this time fluid levels were maintained by the addition of sterile distilled water.

After incubation the cultures were examined under a dissecting microscope and samples selected for determination. Works by Geitler (1932), Prescott (1951) and Desikachary (1959) served as bases for determination; nomenclature generally follows Geitler (1932). The taxonomy of the

Oscillatoriaceae has been revolutionized since the study by Drouet (1968), so no generic names are given for that family.

(2) Results

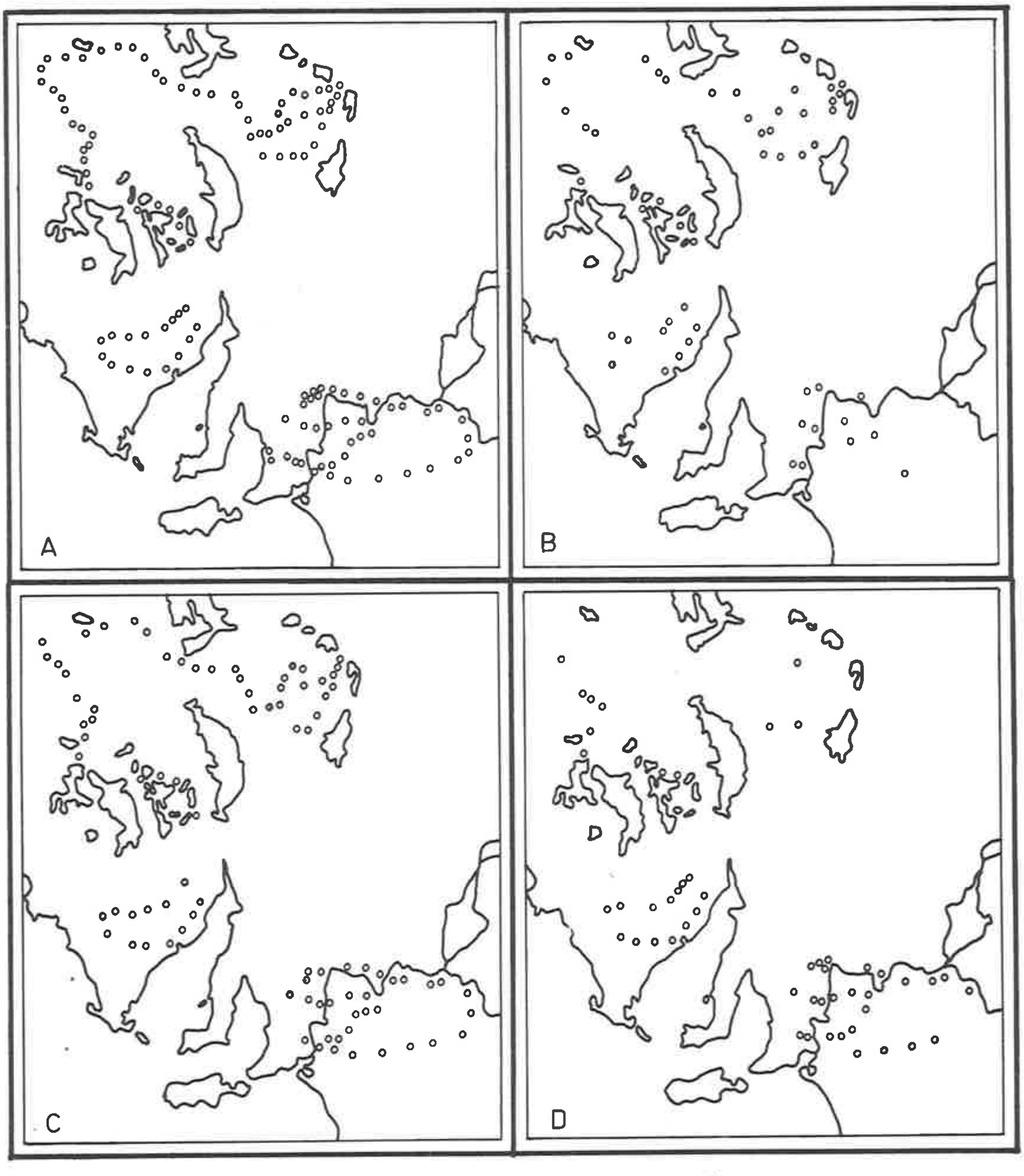
All but two of the one hundred and twelve cultures prepared produced some blue-green algal growth. A coccoid green alga was very common, as were moss protonema, both of which were more abundant in soil samples from the mallee vegetation regions. Very fine fungal hyphae commonly occurred amongst the algae and the sand grains. Filamentous green algae and diatoms were rare, and occurred only in samples from very high (50cm per annum) rainfall areas.

The cultures produced blue-green algal forms which could be ascribed to four genera known to fix nitrogen; *Anabaena* Bory, *Nostoc* Vaucher, *Scytonema* Agardh and *Tolypothrix* Kutzing. Other genera recorded were *Microchaete* Thuret, and *? Aphanocapsa* Naegeli. Filamentous Oscillatorian forms exhibiting a variety of mucilage ensheathment were also found. Whereas in older taxonomic treatments (Geitler 1932, Desikachary 1959) these forms would have been ascribed to many genera, the taxonomic revision of the family Oscillatoriaceae produced by Drouet (1968) suggests that these forms are probably only in one or two species.

FIGURE 9.1

The distribution of sampling sites for soil algae, and of reputedly nitrogen fixing algae.

- A All sites examined for soil algae
- B Sites from which *Anabaena* sp. appeared in culture
- C Sites from which *Nostoc* sp. appeared in culture
- D Sites from which *Scytonema* sp. appeared in culture


A
B
C
D

Anabaena was present in 51 samples in two distinct forms, probably two species. ? *Aphanocapsa* was found once only, as the only alga in drifting white sands in the north-east of South Australia. *Microchaete* was present 13 times in a single form, close to *M. tenera* Thuret. *Nostoc* occurred in several different forms in 85 cultures, often more than one form in the same culture. *Scytonema* occurred 51 times in a form close to *S. ocellatum* Lyngbye, but occasionally exhibiting branching patterns rather more like *Tolypothrix*. *Tolypothrix* in a form close to *T. bouteillei* (Breb. et Desm.) Lemm. occurred in only 3 cultures. Oscillatoriacean forms were found in 105 cultures. The distribution of the reputedly nitrogen-fixing genera is shown in Figure 9.1.

(3) Discussion

The soil algal flora found was similar to that found by other workers in arid areas. It was dominated by blue-green algae, especially Oscillatoriaceae, but contained numbers of potentially nitrogen fixing species. While nitrogen fixation is likely by some species, and the sheathed forms are undoubtedly able to bind sand into a coherent mass, it is not known how commonly these forms develop in nature as culture methods initiate the growth of resting cells of various forms as well as continuing growth of active, vegetative cells. Because of this it is not possible to say which of the algae found grew actively in the arid soils and which were present only as resting stages. Examination of intact lichen crust samples, however, showed that *Scytonema* and ensheathed Oscillatoriaceae were not uncommon in mallee vegetation areas. Elsewhere, macroscopic colonies of algae were not found except in lichenized form.

2. BRYOPHYTA

Mosses and liverworts were not collected systematically at any stage during the study, nevertheless the presence of these organisms in many areas was quite noticeable and some samples were collected and determined.

As a general observation, mosses were more common on the soil in the sub-arid areas, especially on sandy mallee soils, where *Barbula torquata* Tayl. was particularly prominent. Other mallee soil species included *Tortula muralis* Hedw. and *Aloina sullivaniana* (CM) Broth. On drier, truly arid soils *Barbula torquata* was present as small cushions, along with minute scattered individuals of *Aloina sullivaniana*. The cushions of

Barbula torquata were almost black when dry, but on the slightest shower of rain their leaves unfurled and turned bright green in a few seconds. Other mosses collected from the arid and semi-arid areas studied, and others from the same locality lodged in the State Herbarium of South Australia included *Barbula pilifera* CM and HPE, *Bryum billardieri* Schwaegr., *B. pachytheca* CM, *B. argenteum* Hedw., *Desmatodon convolutus* (Brid.) Gront., *Funaria hygrometrica* Hedw., *Sigaspermum repens* (Hook.) Lindb., *Grimmia laevigata* (Brid.) Brid., *G. pulvinata* (Hedw.) Sm., *Tortella calycina* (Schwaegr.) Dix., *Tortula princeps* De Not., *Triquetrella pappillata* (H.f. & W.) Broth., and *Weissia controversa* Hedw..

Liverworts were not as prominent as mosses on the arid and semi-arid soils. *Riccia limbata* Bisch. was probably the most common species, and was notable for its habit of contracting the centre of the thallus when drying, so withdrawing into a small crevice in the dust, disappearing but for a tracery of lobe margins visible from above. Other Hepatic species from arid soils housed in the State Herbarium of South Australia included *Riccia crinata* Tayl., *R. lamellosa* Raddi, *R. macrospora* ST. and an undetermined species of *Plagiochasma*.

3. FUNGI

Algal cultures usually showed a considerable development of fungal hyphae, mostly very fine (less than 10μ diameter), usually hyaline, and often rather irregular in thickness. This hyphal growth was sticky, binding sand grains quite strongly and forming a mat of hyphae and sand in areas not colonized by blue-green algae. This growth was very similar to that described by Bond and Harris (1964) from sandy soils in higher rainfall areas. When arid soil crusts were broken fine hyphal fragments could be seen at the edges: some very fine textured calcareous soil crusts could be gently pulled apart and the mesh of hyphae stretched across the gap between the portions of the crust. Killian and Feher (1939) and Cameron (1969) both reported that *Penicillium* and *Aspergillus* are the fungi most frequently encountered in arid soils.

4. BACTERIA

Cameron (1969) studied the bacterial populations of many types of arid soil. For some soils similar to those of much of the study area he found counts ranging from 87×10^3 to 15.3×10^5 aerobic bacteria and actinomycetes per gram, and from 0 to 8×10^5 anaerobic bacteria per gram. The most common genera found by Cameron in hot desert soils were *Bacillus*, *Pseudomonas* and *Micrococcus*. Killian and Feher (1939) isolated 98 species of bacteria in 12 genera from Saharan soils, with *Bacillus*, *Actinomyces*, *Micrococcus* and *Cellumonas* the most common genera. Correll (1967) working within the study area at Yudnapinna (near Port Augusta) found counts for aerobic bacteria capable of growth on nitrogen free media ranging from 1.04×10^4 to 1.12×10^6 per gram.

5. MICROFAUNA

Wood (1970, pers. comm.) studied the soil microfauna from 169 sites, mostly in arid and semi-arid areas. In these sites he found a mean microarthropod density of 4490/metre^2, consisting of Collembola ($2 \times 10^3/m^2$), Acari ($2.3 \times 10^3/m^2$), and Crustacea ($185/m^2$). A new species of *Folsomides* comprised 56% of the Collembola population, and was restricted to arid or semi-arid areas: it was noted that this species was absent from the small pocket of semi-arid sub-alpine land near Cooma in New South Wales in which an isolated occurrence of the sub-arid lichen *Chondropsis semiviridis* occurs. The Acari found included members of the Prostigmata, Mesostigmata, Cryptostigmata and Astigmata. An unexpected feature of the micro-arthropod fauna was the dominance of *Collembola* which were poorly sclerotised, small, and generally regarded as susceptible to desiccation.

Nematode populations were found to be low (1.76×10^4 - $3.14 \times 10^5/m^2$) compared with temperate European figures (1×10^6 - $2 \times 10^7/m^2$), with numbers consistently greater in the driest sites studied.

CHAPTER X

DISCUSSION

There have been no previous integrated ecological studies of desert lichens. This fact, more than any other, has shaped the development of this thesis: because there had been so little previous study, the scope for work was far beyond that which could be accomplished in a Ph.D. programme. After due consideration, attention was directed to two fields:

(1) the extent and floristic composition of soil-surface lichen floras in arid and semi-arid south-eastern Australia.

(2) factors influencing the distribution of the taxa involved.

It was believed that these studies would allow comment on the phytogeography of the study area, and would have implications concerning the pastoral industry based in the area.

The first of the two primary fields has been reported and discussed in chapters IV and V, and the second in chapters VI, VII and VIII.

For further discussion there remains only the phytogeographic problems, the impact of the pastoral industry on the lichen crusts, and the implications of the study for the pastoral industry.

A brief statement of achievement and suggestions for further research complete the chapter.

1. PHYTOGEOGRAPHY

Having completed a study of the lichen flora in a large part of the arid area of Australia, a unique phytogeographic opportunity arose. The lichen flora from arid areas on all other continents (except South America) had been reported on, but few attempts at phytogeographic correlation on a world scale had been made. Since Weber (1962, 1963, 1967a, 1968) had, to a large extent, rationalized the taxonomy of desert lichens, the occasion was opportune to make a phytogeographic study of the lichens from the world's arid lands, and to examine the role of lichens as phytogeographic indicators. The present study area was also large and diverse enough to allow discussion of phytogeographic matters internal to Australia.

(1) Relation to the floras of other continents

The large element of the soil surface lichen flora common to the study zone and arid areas around the world is shown in Table 10.1. Only four arid zone species found in the study area (*Buellia subcoronata*, *Lecidea crystallifera*, *Lecidea planata*, and *Parmelia australiensis*) are Australian endemics. If the material referred to as *Cladonia foliacea* does in fact belong in the genus *Heterodea*, this too would be an Australian endemic. Weber (1961) considered *Parmelia conspersa* var. *vagans*

TABLE 10.1

The distribution of some common arid zone lichen species across five continents.

	Faurel et al. Algeria	Galun, Galun & Reichert, Israel	Keller, Russia	Klement, Europe	Klement, Europe	Looman, North America	Weber, Arizona	Australia
Acarospora schleicheri			+		+	+	+	+
Aspicilia calcarea			?		+	+	+	+
Buellia epigaea		+		+		+		+
Dermatocarpon lachneum	+	+	+	+	+	+	+	+
Diploschistes scruposus		+	+				+	+
Endocarpon pusillum				+		+	+	+
Heppia lutosa	+			+		+	+	+
Lecidea decipiens	+	+	+	+	+	+	+	+
Parmelia vagans			+		+	+		*
Toninia caeruleonigricans		+	+	+	+	+		+

* *P. australiensis*

Nyl. (Syn. *P. chlorochroa* Tuck) to be an "unattached ecad of windy sites" of *P. conspersa*. It is therefore likely that *P. australiensis* could be similarly reduced.

Looman (1964b) held that the lichen floras of arid soils in North America and Asia were relics of an ancient, once more extensive flora, now separated as a result of continental drift. The number of species that Australia has in common with extra-Australian arid areas is sufficient to discount Looman's ideas; to maintain his case, Australia must have been part of the same continental block as Asia and North America. It is widely recognized, however, that Australia was part of the "Gondwana" block and North America and Asia of the "Laurasia" block (Holmes 1965). It remains, therefore, to examine other hypotheses to account for these similarities. One is convergent evolution, but this is rarely invoked to explain inter-continental disjunctions. Another explanation proposed by Looman was that lichens have extraordinary powers of dispersal. Looman rejected this explanation on the grounds that sexual reproduction (resulting in spores) was rare in arid zone lichens. This may be so, but in the present study all of the arid lichens were found bearing apothecia or perithecia at least occasionally. All the species fonnd in Australia listed in Table 10.1 were frequently found fruiting, and with spores in those fructifications. Even rare production of spores would be sufficient to allow long-range dispersal of cryptogams which are notorious for their powers of dispersal (Rogers and Meier 1936, Gregory 1961). This idea cannot be rejected as easily as Looman would have us believe.

The relatively large number of species-level intercontinental disjunctions shown by lichens (27 of the 42 taxa found in the study area also occur in North America) prompts questioning of their role, and the role of other cryptogams, in phytogeographic discussions. For organisms such as the fungi, with spores so small that they may be carried into the upper-atmosphere (Rogers and Meier 1936) it seems likely that the factors limiting their distribution are ecological rather than phytogeographic. It is not unreasonable to assume that given a long time span, the spores or many terrestrial fungi (including lichen fungi) will become spread right around the world, and will, given suitable ecological conditions, grow where they land.

The value of an organism in argument about intercontinental migration routes and biogeographic zonation is heavily dependent on the dispersal mechanism of the organism. Those organisms with minute, potentially air-borne propagules, as are bacteria, blue-green algae, fungi (including lichens), and perhaps some bryophytes and orchids, are of little value in such discussions because of their ability to spread over long distances. They may, however, be very sensitive indicators of ecological factors.

Discussing the small number of lichen endemics in arid areas, Weber (1962) wrote "It gives one the uncomfortable feeling that lichen evolution is now essentially at a standstill. If this is indeed true, then the genetic system must differ fundamentally from that of higher plants. For, as Stebbins (1952) ably points out, the environment of arid areas is a distinct stimulus to evolution". The small number of endemics does indeed suggest that lichen evolution in arid areas has nearly stopped, but that there are some endemics indicates that it has not stopped altogether. In Stebbins' (1952) discussion the reason for this slow rate of evolution can possibly be found. Stebbins traced the evolutionary stimulus of aridity to the formation of isolated communities leading to speciation which, with small fluctuations in climate, then hybridised and so on. In organisms which are probably able to disperse over a long range, isolated communities are unlikely to develop. The stimulus to speciation resulting from aridity which is so apparent in the angiosperms cannot therefore affect the lichen populations. The genetic response of the lichens is not necessarily different, but the ecological response is.

Given a long time span, then, it would be expected that those lichens now endemic to certain arid areas will, if ecological conditions are suitable, spread to the others. How long this takes will depend on the degree of specialisation of the species (i.e. the likelihood of a propagule landing in a place where it can develop), and the power of dispersal of the propagule.

A special disjunction found in the present study is that shown by *Chondropsis semiviridis* and *Parmelia amphixantha* between Australia and New Zealand. Because of the documented rain of Australian dust and spores on New Zealand (Moar 1969), it is not surprising that Australia and New Zealand have many lichen species in common. While Tasmania has 48% of its lichen flora in common with New Zealand (Martin 1965), the disjunction of arid lichens is surprising, as New Zealand has so little arid land. It appears that even species which form spores so very rarely as *C. semiviridis* are capable of long range dispersal.

The recolonization of the volcanic island Krakatoa by lichens has been slow. Although the time period involved (about 90 years) is short in geological terms, Gregory (1961) has suggested this indicates that lichens do not disperse well over long distances. The evidence presented by Moar (1969) about transport of Australian pollens, dust, and fungal spores across the Tasman sea to New Zealand (a distance of about 2000km) demonstrates what has been hypothesized about long distance transport. It appears that at least some of the fungal spores transported across the Tasman sea are viable, because they are able to cause outbreaks of rust in wheat. Long distance transport of lichen spores is, therefore, a viable hypothesis.

Since the pattern of distribution of arid soil surface lichens does not conform with the geological evidence concerning continental drift, it is likely that long-range dispersal is involved in the present distribution of arid-zone soil-surface lichens. Thus, knowledge about the drift of continents allows comment on the method of lichen dispersal. The converse, however, is not valid.

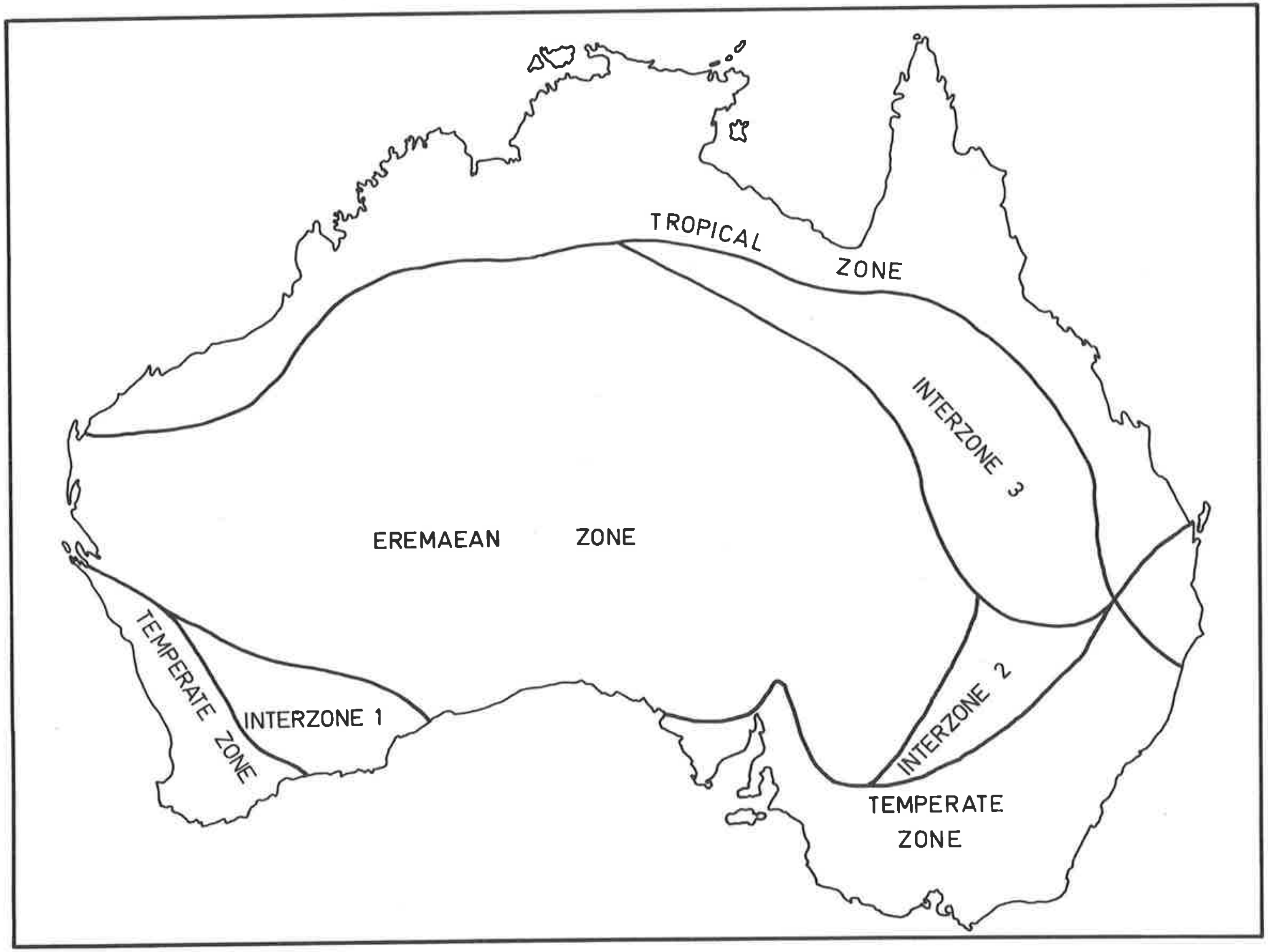
Evidence presented by Weber (1962) suggests that the similarities discussed above may prove to be even stronger than believed now. As more collecting and critical revision of arid lichen taxa proceeds, it seems likely that the number of species will be further reduced, and the percentage of inter-continental disjunctions thus increased. It is probably only in the wake of such revisions that valid biogeographic conclusions can be drawn involving any but the most striking similarities or differences.

(2) The Australian Region

The most complete phytogeographic study of the Australian region is that of Burbidge (1960), in which Australia was divided into three zones: Tropical, Temperate, and Eremaean on the basis of their phanerogamic floras. Between

FIGURE 10.1

The phytogeographic zonation of mainland Australia, after Burbidge (1960).


TROPICAL ZONE
INTERZONE 3
EREMAEAN ZONE
TEMPERATE ZONE
INTERZONE 1
INTERZONE 2
TEMPERATE ZONE

the Temperate, Tropical and Eremaean zones Burbidge defined broad interzones within which edaphic conditions caused an intermixture of the floras of the abutting regions. The present study area includes part of the Temperate and Eremaean zones, and also part of Interzone 2, as defined by Burbidge (Figure 10.1).

The distribution of lichens in the study area is compatible with Burbidge's zonation. Considering the species-groups defined in chapter V (Table 5.4) groups A and B are essentially Temperate species, and groups C and D essentially Eremaean. Interzone 2 shows relatively extensive development of group B species, but all of these (except *Buellia subcoronata*) also occur in the Temperate zone near Adelaide.

Species of group C form a band across the south of the Eremaea in South Australia, but do not extend as far north or east as species of group D. Thus, the Eremaea could be divided into two sub-zones, one fringing the Temperate zone in the south, the remainder across the north of the study area.

Species-group C contains the vagant lichens considered by Keller (1930) to be indicators of steppe vegetation, and also a species of *Diploschistes*, the genus considered by Reichert (1936, 1937) to indicate steppe vegetation. Thus, it is likely that the division of the Eremaea in South Australia into two portions on presence or absence of group C species would be equivalent to dividing it into Steppe and Desert as in North Africa and the Turko-Iranian areas.

The information presented in chapters VI and VII is proof of the sensitivity of the soil lichens to climatic variation, supporting the contention of Faurel, Ozenda and Schotter (1953), and provides a basis for the use of the soil surface lichens as climatic indicators.

2. THE IMPACT OF THE PASTORAL INDUSTRY

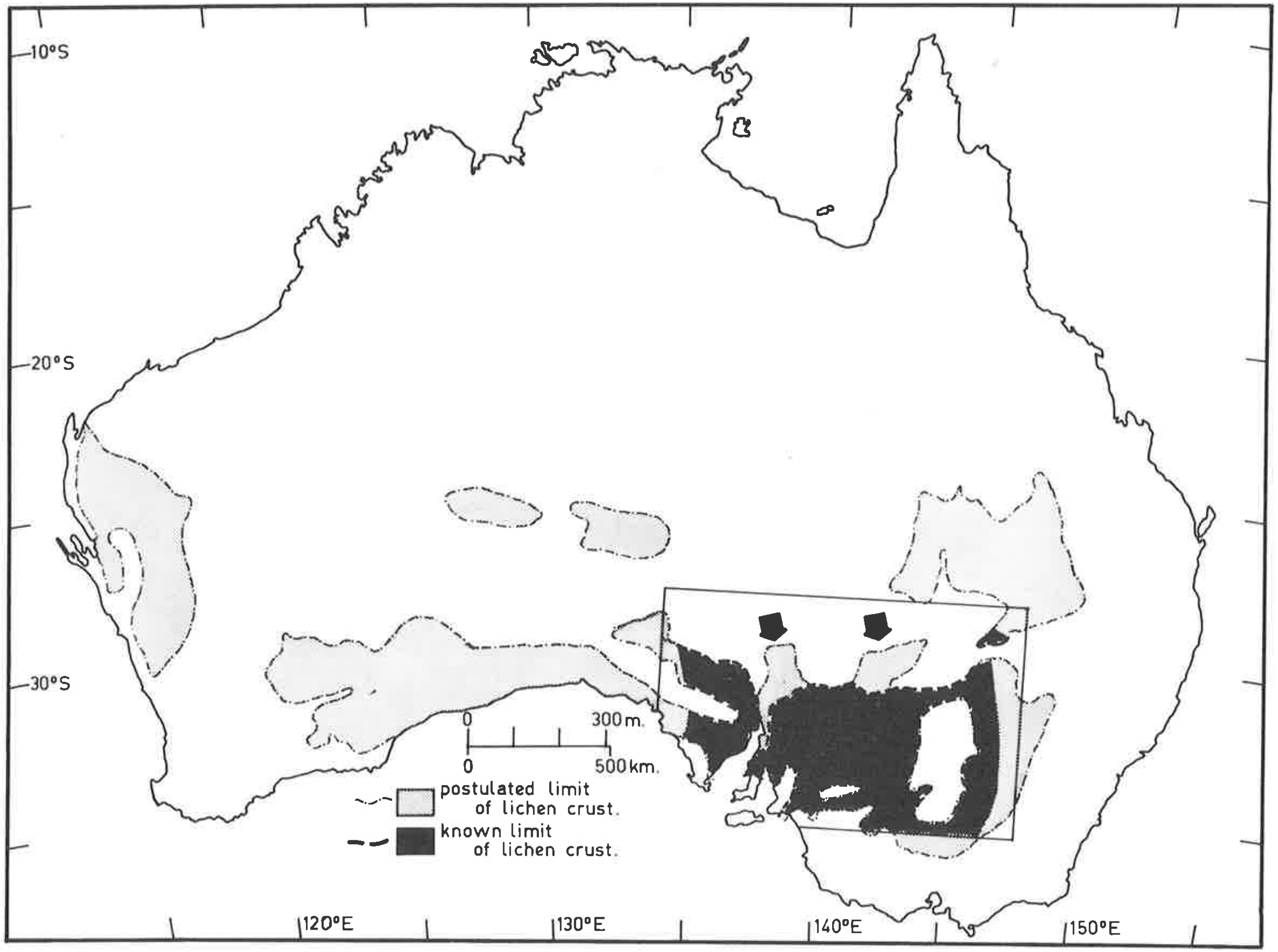
Two special fields of interest in relation to the pastoral industry have been pursued. The first was a study of the present, and inferences about the past, distribution of lichen crusts on arid soils. The second was a study of the role of the soil surface lichen crust in the nitrogen status of the soils.

(1) The probable extent and distribution of lichen crusts in South-Eastern Australia.

Data presented in chapter VI were used to construct a map showing postulated distribution of lichen crusts across southern Australia (Figure 10.2). To construct Figure 10.2 all areas with soil types known to support lichen crusts, and with suitable rainfall were demarcated. Within the study area, regions known to now support a lichen crust were demarcated from areas in which crust formation was expected, and this information also shown on Figure 10.2.

FIGURE 10.2

The postulated distribution of lichen crusts on southern Australian soils in relation to that actually found in the study area.



10°S
20°S
30°S
120°E
130°E
140°E
150°E
0
300 m.
0
500 km.
postulated limit of lichen crust.
known limit of lichen crust.

Within the study zone two extensive areas for which a lichen crust has been postulated do not support one. These are the areas centred on the Barrier Range in western New South Wales, and on the Flinders Range in South Australia (arrowed on Figure 10.2). It is probable that the rugged nature of these areas allows relatively permanent water supplies, and hence has permitted more sustained stocking than in other areas. This would explain the absence of lichen crusts from them. More intensive study in those areas may reveal the remains of lichen crusts not seen in the present study.

The predicted extension of lichen crusts across the Nullarbor Plain is supported by D.N. McVean (pers. comm.) and G.C. Bratt (pers. comm). No corroborative evidence is available for the predicted crust areas near the western coast of Western Australia, nor for the area in southern Queensland.

It is likely that the area of lichen crust will be reduced under the influence of continual stocking of the arid lands, although data from chapter VII show that stocking need not completely destroy the crust. Information in the unpublished records of the Koonamore Vegetation Reserve shows that some large areas devoid of lichens in 1926 now are covered with a lichen crust. Thus, in the absence of stock the lichen crust has regenerated on some areas from which all topsoil had been stripped. This regeneration is, however, apparently not yet complete even after a recovery period of 44 years.

(2) The crust and soil nitrogen status

The lichenized soil crust is significant in the nitrogen status of arid soils in a number of ways, including fixation of nitrogen, and preservation of the relatively high nitrogen topsoils.

The role of the crust in the nitrogen status originally stimulated this study. It can now be asserted that lichens and blue-green algae capable of fixing nitrogen are widespread in arid areas. The only nitrogen fixing lichen found was *Collema coccophorus* which had been shown to fix nitrogen by Rogers, Lange and Nicholas (1966). Other lichens with blue-green algal symbionts did occur (*Heppia lutosa, Heppia polyspora,* and *Synalissa* sp.) but the algal symbionts in these lichens were from genera not reported to fix nitrogen (*Polycoccus* and *Xanthocapsa*).

The distribution of *Collema coccophorus* is mapped at the end of Chapter IV, and its density under various stocking pressures detailed in Chapter VIII. It is significant that this species is so widespread, and that its frequency is apparently not reduced except under extremes of stocking pressure. Hence, moderate stocking probably does little to reduce the input of nitrogen into the system from this source.

Information concerning the effect of stocking intensity on the frequency or density of nitrogen fixing blue-green algae found in the area (*Anabaena*, *Nostoc*, *Scytonema* and *Tolypothrix*) was not available so no comment can be made on the effect of stocking pressure on free living algal fixation.

Correll (1967) found higher numbers of potentially nitrogen fixing bacteria inhabited the soil in *Kochia pyramidata* shrubland than in other vegetation types. Since *K. pyramidata* is commonly associated with heavily grazed areas (Jessup 1951), it is possible that stocking pressure may actually stimulate nitrogen fixation in arid soils.

Lichen crusts are widely credited with the ability to stabilize soil surfaces (Weber 1962, Cameron and Blank 1966). It was observed that areas on the Koonamore Vegetation Reserve which in 1926 were either loose sand or from which all topsoil had been stripped, are now stabilized by a continuous lichen crust with a rough, vesicular surface. Hence, lichen crusts not only preserve stable surfaces, but are capable of stabilizing eroded ones also. Such crusts protect the upper layers of the soil from wind erosion and probably from erosion due to sheet flow of water also. It is in these upper layers of the soil that nitrogen and phosphate are at their highest concentrations (Beadle and Tchan, 1955; Correll 1967). Ioannou (unpublished data) has found significant differences in nitrogen status between an area which had not been grazed and had an intact lichen crust, and an adjacent area upon which the crust had been totally destroyed, and several inches of soil apparently lost by erosion. The nitrogen status of a third area with a crust partly destroyed by stocking verged on being significantly lower ($p = 0.06$) than that of the ungrazed area. These findings are consistent with those of Shields, Mitchell and Drouett (1957) in the United States.

Hence, destruction of the lichen crust necessarily results in the loss of part of the nitrogen and phosphate capital of the area because of the inevitability of erosion, especially by wind. Particularly significant is the fact that it is the soil with the highest nutrient status which is lost, leaving behind a soil surface lower in nutrient status than that upon which the present vegetation developed.

Thus, while stocking pressure may not reduce the rate of nitrogen input into the ecosystem, it destroys the lichen crust and causes the loss of nitrogen capital, thus reducing the nitrogen status of the soil surface.

3. IMPLICATIONS OF THIS STUDY FOR THE PASTORAL INDUSTRY

The probable ecological significance of the lichen crust has been discussed in the Introduction (Chapter I) and in the preceeding sections. There is a series of events, viz:

Introduction of Stock → Destruction of Crust →
Loss of Topsoil → Change in Nutrient Status →
Change in the Vegetation.

which could have far reaching effects on the shrubby vegetation even if the stock did not directly destroy it. If the crust is destroyed and the seed bed high in nitrogen and phosphate is lost it is possible that conditions suitable for the regeneration of perennial shrubs at present forming the fodder reserves on much of southern Australia's arid lands will not be found. If this is so, when the present bushes die there will be either no bush to protect the soil surface from wind erosion, or bushes other than those now serving as fodder reserves will appear. Investigators have suggested that the incoming bushes are less palatable than those they have replaced (Beadle 1948, Jessup 1951, Correll 1967).

It is possible that in the short term, destruction of the crust is profitable to the pastoral industry, as areas without crusts appear to produce more ephemeral growth after rains than similar crusted areas nearby. While ephemeral growth is the preferred fodder for sheep in good seasons (Wilson, Leigh and Mulham 1967), in drought years it is the perennial growth which maintains stock and protects the soil from erosion. It is also likely that the growth of ephemeral vegetation after rain is slowly exhausting the nitrogen capital built up by the crust, and, as a result, the pastoral industry is mining the soil nitrogen reserves.

It is, therefore, essential for the continuity of the pastoral industry that stocking be kept to such levels that the lichen crust is not destroyed. It is likely that this delicate, and previously ignored, crust of lichens is the first part of the ecosystem to be damaged by stocking. While the crust regenerates only very slowly it is possibly the key to the regeneration of all the other vegetation strata.

4. CONCLUSIONS

The study has been successful in achieving its objectives. It has been established that:

1. Australia has, in the south-eastern part of its arid zone, a soil-surface lichen flora similar in floristic composition to that in arid areas of other continents;

2. the soil-surface lichens of the area are distributed in five species-groups, paralleling the phytogeographic zonation of the phanerogams in the area ;

3. the distribution of the lichens studied is controlled primarily by climate, but in local areas stocking intensity has had a marked effect on the species composition of the soil lichen flora;

4. stocking of domestic animals (sheep and cattle) has destroyed the lichen crust over wide areas and threatens further destruction.

5. FUTURE RESEARCH

Since it has been established that stocking is destroying the lichen crusts and that the pastoral industry is probably dependent on the presence of the lichen crust for its continuance, it is important that relevant studies proceed. Such studies ought to include a detailed one of the role of the crust in the ecosystem, and of the effect of stocking on the crust. Speculations made above regarding the effect of stocking on nitrogen fixation and nitrogen status of topsoils, and the effect of nitrogen status on vegetation succession are susceptible to study. Studies on the long term effect of the stocking of domestic animals on the ecosystem are probably the most pressing research need in the arid zone of Australia. These studies ought to be aimed at the development of guidelines for the management of the pastoral industry to ensure the continued stability and productivity of the arid lands.

There is academic value in simultaneously documenting the lichen crust in other areas at the same time as conservation oriented studies proceed, because soon there may be little evidence of lichen crusts over areas now well covered, since more and more arid land is being subject to stocking.

Two notably incomplete sections of the present study ought also be pursued. First, the autecological study of *Chondropsis semiviridis*, for which studies to determine the factors controlling its distribution along its wetter limit are needed, as are physiological studies in the field to confirm the deductions based on laboratory experiments. Second, the study on blue-green algae, if continued, would produce information on what is probably an important source of nitrogen in arid soils.

APPENDIX I

LIST OF SOUTH AUSTRALIAN LICHENS IN THE HERBARIUM OF R.W. ROGERS

This list comprises 104 species in 41 genera, arranged alphabetically. For each species its climatic zonation [arid (A), sub-arid (SA) or humid (H)] is indicated, as are its common substrates.

Acarospora cervina Mass.	A, SA	stones
A. smaragdula (Wahlenb.) Th.Fr.	A, SA	pebbles
A. schleicheri (Ach.) Mass.	A, SA, H	soil, rocks
Aspicilia calcarea (L) Mudd.	A, SA, H	soil, rocks
? *Biatorella* sp.	A, SA	soil
Blastenia sp.	H	bark
Buellia dialyta (Nyl.) Tuck.	SA, H	bark
B. epigaea (Hoffm.) Tuck.	SA	soil
B. parasema (Ach.) de Not.	A, SA, H	bark
B. spuria (Schaer.) Korb.	H	rock
B. subalbula (Nyl.) Mull. Arg.	A	rock, pebbles
B. subcoronata Mull. Arg.	SA	soil
Calcium pusillum (Ach.) Floerke	H	wood
Caloplaca aurantiaca (Lightf.) Th. Fr.	A, SA, H	wood, bark
C. cerina (Ehrt. apud Hoffm.) Th. Fr.	H	bark
C. cinnabarina (Ach.) Zahlbr.	A, SA	soil
C. ferruginea (Huds.) Th. Fr.	SA, H	bark
C. pyracea (Ach.) Th. Fr.	A	wood
C. murorum (Hoffm.) Th. Fr.	A	rock
C. subpyracella (Nyl.) Zahlbr.	A	soil

Candellaria concolor (Dicks.) Arn.	A, SA	bark
Cattillaria sp.	H	bark
Chondropsis semiviridis (Nyl.) Nyl.	A, SA	soil
Cladia aggregata (Sw.) Nyl.	H	soil
C. ferdinandi Mull. Arg.	H	soil
C. schizopora Nyl.	H	rotting wood
Cladonia fimbriata (L) Fr. (S.L.)	H	rotting wood
C. foliacea Schaer.	A, SA	soil
C. pyxidata (L) Fr.	H	soil
C. subsquamosa (Nyl.) Vain.	H	soil
C. verticillata Hoffm.) Schaer.	H	soil
Collema coccophorus Tuck.	H	soil
C. nigrescens (Huds.) D.C.	H	bark
Dermatocarpon compactum Mass.	A	pebbles
D. lachneum (Ach.) A.L. Sm.	A, SA	soil
Diploschistes actinostomus (Pers.) Zahlbr.	H	rock
D. ocellatus (D.C.) Norm.	A, SA	soil
D. scruposus (Schreb.) Norm.	A, SA, H	soil, rocks
Endocarpon pusillum Hedw.	A, SA, H	soil
Fulgensia bracteata (Hoffm.) Ras.	A, SA	soil
Heppia euploca (Ach.) Vain	A	rocks
H. lutosa (Ach.) Nyl.	A, SA	soil
H. polyspora Tuck.	A, SA	soil
Heterodea mülleri (Hampe) Nyl.	SA, H	soil
Hypogymnia lugubris Pers.	H	rocks, bark
H. aff. physodes (L) Ach.	H	rock, bark
Lecanora atra (Huds.) Ach.	A, SA, H	soil, rocks, wood
L. sphaerospora Mull. Arg.	A	pebbles
L. varia (Hoffm.) Ach.	H	bark

Lecidea coarctata (J. E. Sm.) Nyl.	A, SA, H.	soil
L. crystallifera Tayl.	A, SA	soil
L. decipiens Ach.	A, SA, H.	soil
L. glauca Tayl.	SA	soil
L. globifera Ach.	H	soil
L. planata Mull. Arg.	SA, H	soil
L. psammophila (Mull. Arg.) Zahlbr.	SA	soil
Lepra citrina Schaer.	H	wood
Lichina confinis (Mull. Arg.) C. Agg.	maritime	rocks
Maronea constans Hepp.	A, SA, H	bark
Menegazzia "caesiopruninosa" P. James M.S. name	H	bark
Ochrolechia pallescens (L) Mass.	H	bark
Pannaria rubiginosa (Thunb.) Del.	H	bark
Parmelia amphixantha Mull. Arg.	A, SA	soil
P. australiensis Cromb.	A, SA	soil
P. conspersa (Ehrh.) Ach.	A, SA, H	soil, rock
P. molliuscula Ach.	A, SA	soil
P. olivacea (L) Ach.	H	bark
P. perlata (Huds.) Ach.	H	bark
P. prolixa (Ach.) Rohl.	H	rock
P. pulla Ach.	A, SA, H	soil, bark
P. rutidota (L) Ach.	A, SA, H	bark
P. subalbicans Strtn.	A, SA, H	bark
P. subrudecta Nyl.	H	bark
P. tenuirima Hook. f. et Tayl.	H	bark
P. spp. indet.		
Peltigera aff.*canina* (L) Willd.	H	soil
Pertusaria leioplaca Lam. & D.C.	A, SA, H	bark, wood
Physcia ? aipolia (Ehrh.) Hampe	H	bark
P. albicans (Pers.) Thoms.	A, SA, H	bark
P. adscendens (E. Fr.) Oliv. em. Bitt.	H	bark

P. caesia (Hoffm.) Hampe	A, SA, H	rock
P. callosa Nyl.	A	rock
P. stellaris (L) Nyl.	A, SA, H	bark
P. syncolla Tuck.	A, SA	bark
P. tenella (Scop.) D.C. em Bitt.	H	bark
P. tribacoides Nyl.	H	bark
P. sp. indet.	H	bark
Pseudocyphellaria australiensis Magn.	H	rock
P. crocata (L) Magn.	H	rock
Ramalina fastigiata Nyl.	H	bark
R. eckloni Mont.	SA, H	bark
R. inflata Hook f. et Tayl.	A, SA, H	bark
Rhizocarpon geographicum (L) Lam et D.C.	H	rock
? *Rinodina orbata* (Ach.) Vain	A	soil
Siphula coriacea Nyl.	SA, H	soil
? *Synalissa* sp.	A, SA	soil
Teloschistes chrysopthalmus (L) Th. Fr.	A, SA, H	bark
T. sieberianus (Laur.) Hillm.	SA, H	bark
T. spinosus (Hook f et Tayl.) J. Murray	H	bark, rock
T. velifer F. Wilson	H	bark
Thysanothecium hyalinum Nyl.	H	burnt wood, soil
Toninia caeruleonigricans (Lightf.) Th. Fr.	A, SA	soil
Usnea florida (L) Wigg.	SA, H	bark, wood
U. xanthopoga Nyl.	H	bark
Xanthoria ectanea (Ach.) Ras. ex R. Filson	A, SA, H	bark
X. parietina (L) Beltr.	H	bark

APPENDIX 2

LICHENS AT EACH LOCATION

This appendix consists of a list of the lichens present at each location studied. The first number in each line is the location number (as in Fig. 4.1), those following indicate the species present at that location. A key to species numbers appears below.

Unlisted locations were without lichens.

Key to species numbers.

1. *Acarospora schleicheri*
2. *Acarospora smaragdula*
3. *Acarospora* sp.
4. *Aspicilia calcarea*
5. *Aspicilia calcarea* mod. *fruticosa*
6. *?Biatorella* sp.
7. *Buellia epigaea*
8. *Buellia subcoronata*
9. *Caloplaca subpyracella*
10. *Caloplaca* sp.
11. *Chondropsis semiviridis*
12. *Cladia aggregata*
13. *Cladonia foliacea*
14. *Cladonia subsquamosa*
15. *Cladonia verticillata*
16. *Cladonia* cf. *fimbriata*
17. *Cladonia* squamules
18. *Collema ? coccophorus*
19. *Dermatocarpon lachneum*
20. *Diploschistes ocellatus*
21. *Diploschistes scruposus*
22. *Endocarpon pusillum*
23. *Fulgensia bracteata*
24. *Heppia lutosa*
25. *Heppia polyspora*
26. *Heterodea müllerí*
27. *Lecanora atra*
28. *Lecidea coarctata*
29. *Lecidea crystallifera*
30. *Lecidea decipiens*
31. *Lecidea planata*
32. *Lecidea psammophila*
33. *Lecidea* sp.
34. *Parmelia amphixantha*
35. *Parmelia australiensis*
36. *Parmelia conspersa*
37. *Parmelia molliuscula*
38. *Parmelia pulla*
39. *?Rinodina orbata*
40. *Siphula coriacea*
41. *Synalissa* sp.
42. *Toninia caeruleonigricans*

1 : 7, 18, 21, 29, 30, 37, 41.
2 : 18, 19, 30.
3 : 4, 9, 18, 19, 25, 30, 41, 42.
4 : 4, 9, 18, 21, 25, 27, 29, 42.
5 : 4, 9, 18, 19, 21, 25.
6 : 9, 18, 19.
7 : 4, 11, 18, 22, 24, 29, 30, 35, 42.
8 : 11, 19, 20, 22, 25, 29, 30, 35, 37, 41,.
9 : 2, 4, 5, 18, 19, 29, 30, 35, 42.
11 : 18, 19, 21, 23, 25, 29, 30, 42.
12 : 4, 5, 18, 19, 22, 30.
13 : 4, 18, 19, 21, 25, 29.
15 : 4, 18, 19, 22, 24, 25, 30.
16 : 1, 4, 18, 19, 29, 30.
18 : 18, 19, 29.
19 : 4, 18, 19, 21, 22, 25, 29, 30.
20 : 18, 19, 21, 22, 25, 30.
21 : 1, 9, 18, 27, 29, 30.
22 : 9, 18, 19, 21, 22, 25, 29, 30, 42.
23 : 19, 21, 30, 41.
24 : 19, 24, 25, 30, 41.
25 : 41.
26 : 18, 21, 22.
27 : 17.
28 : 18, 19, 29.
29 : 18, 19, 23, 29, 30, 42.
30 : 4, 9, 18, 22, 23, 29, 30, 42.
31 : 19, 21, 22, 29, 30, 41, 42.
32 : 4, 5, 11, 18, 19, 21, 23, 29, 34, 35, 37, 38, 42.
33 : 11, 18, 19, 20, 22, 23, 25, 29, 30, 35, 37.
34 : 5, 9, 19, 20, 21, 23, 29, 30, 35.
35 : 19, 21, 23, 30, 41, 42.
37 : 18.
38 : 4, 22, 29, 30, 42.
39 : 4, 18, 22, 42.
40 : 4, 18, 30, 42.
41 : 6, 9, 18, 21, 39.
42 : 4, 19, 30, 42.
43 : 18, 19, 23, 29, 30.
44 : 18, 19, 21, 22, 30.
45 : 18, 21, 34.
46 : 22, 42.
47 : 18, 19, 21, 23, 29, 30.
48 : 9, 19, 21, 23, 29, 30, 41, 42.
49 : 19, 21, 23, 29, 30, 42,
50 : 18, 22, 29, 30.

51 : 18, 19, 21, 23, 29, 30.
52 : 17, 21, 22, 30, 32, 38.
53 : 12.
54 : 10, 17, 22, 31.
55 : 17, 19.
56 : 8, 10, 21, 22, 27, 28, 30, 32, 34,38, 40.
57 : 17, 18, 19, 21, 23, 29, 30, 42.
58 : 13, 34.
59 : 7, 17, 23, 29, 30, 34.
60 : 15, 18, 21, 23, 30, 31.
61 : 18, 21, 23, 30, 42.
63 : 17, 21, 23, 28, 29, 30, 31, 38, 42.
65 : 17, 18, 21, 22, 23, 29, 30, 42, 19.
66 : 17, 21, 23, 30, 31, 41, 42.
67 : 5, 19, 21, 22, 25, 29, 30, 38, 42.
68 : 11, 19, 23, 29, 30, 34, 35, 42.
69 : 23, 29, 30, 41.
71 : 12.
73 : 18, 19, 24, 41.
74 : 18, 19, 22, 24, 30.
75 : 18, 24.
76 : 5, 19, 22, 29, 30, 41, 42.
78 : 22, 25, 29, 30.
81 : 18, 19, 24, 29.
82 : 1, 18, 19, 22, 24, 25, 29, 30, 41.
86 : 1,19, 22, 24, 25.
102 : 18, 19.
103 : 18, 19, 30.
106 : 18, 19.
109 : 18, 19, 22, 24, 29, 30.
111 : 18, 19, 29, 30, 41 .
112 : 18, 19, 22, 24, 41.
119 : 19, 24.
125 : 4, 19, 22, 24, 30.
129 : 12, 21, 22.
130 : 12, 16.
131 : 18, 19, 21, 22, 30, 41 .
132 : 2, 5, 11, 19, 20, 21, 23, 29, 30, 35, 37, 42,22.
133 : 5, 11, 20, 23, 29, 30, 35, 37, 42,22.
134 : 2, 19, 21, 23, 29, 30, 38, 41.
135 : 2, 17, 21, 22, 23, 29, 30, 42.
136 : 12, 21, 22, 23.
137 : 4, 21, 23, 30, 42.
138 : 4, 22, 23, 29, 30, 41.
139 : 19, 23, 29, 30.
140 : 19, 41, 42.
141 : 19, 22, 29, 42.

142 : 12, 17, 21, 22, 23, 29, 30.
143 : 23, 29, 30.
144 : 4, 18, 22.
145 : 11, 19, 21, 22, 23, 30, 35, 42.
146 : 7, 11, 19, 20, 23, 29, 30, 34, 35, 37, 42.
147 : 17, 22, 30.
148 : 17, 21, 22, 29, 30, 38, 40, 41.
149 : 12, 17, 21, 22, 34, 40.
150 : 17, 19, 21, 29, 30, 36, 42.
151 : 17, 19, 21, 29, 30, 31, 34, 40.
152 : 17, 19, 21, 22, 28, 30, 34, 36.
153 : 2, 3, 18, 19, 21, 23, 29, 30, 34, 42.
154 : 22.
155 : 22.
156 : 22, 30, 41, 42.
157 : 18.
158 : 18,22, 41.
163 : 19.
164 : 18, 19, 24, 29, 30, 41.
165 : 18, 24,.
167 : 18, 42.
168 : 18.
180 : 6, 18, 19, 22, 25, 30, 31.
181 : 22.
182 : 24.
183 : 8, 22, 25, 28, 30.
184 : 8, 22, 30, 31, 33.
185 : 8, 18, 21, 25, 27, 30.
186 : 4, 19, 22, 30, 31.
188 : 9, 17, 21, 30, 32.
189 : 8, 25, 28, 30, 31, 34.
190 : 8, 21, 31, 34.
191 : 22, 31, 34.
192 : 18, 21, 22, 31.
193 : 4, 18, 19, 22, 25, 30.
194 : 22.
195 : 18, 19, 22.
199 : 19, 24.
200 : 4, 18, 19, 24, 30, 42.
202 : 18, 19, 24, 29.
209 : 18, 22.
210 : 2, 13, 21, 30, 31, 34.
211 : 11, 18, 21, 24, 29, 30, 34, 37.
214 : 22.
215 : 22.
216 : 18, 19, 22, 28, 30.

217 : 19, 30, 34.
218 : 19, 21, 22, 23, 29, 30.
219 : 2, 5, 21, 23, 24, 29, 30, 34.
220 : 11, 17, 21, 22, 34.
221 : 13, 21, 23, 30, 32, 34.
222 : 18, 21, 22, 23, 29, 30, 42.
223 : 18.
224 : 4, 22, 29, 30, 42.
225 : 19, 30, 42.
226 : 18, 19.
227 : 18.
229 : 18, 19.
230 : 17, 18, 19, 21, 23, 29, 30.
231 : 4, 22, 29, 30, 42.
232 : 4, 18, 22, 23, 29, 30, 42.
233 : 18, 19, 21, 23, 24, 29, 30.
234 : 19, 23, 29, 30, 42.
235 : 21, 22, 23, 29, 30, 42.
236 : 19, 21, 23, 29.
237 : 17, 21, 22, 23, 29, 30.
238 : 21, 22, 23, 29, 30.
239 : 17, 19, 21, 30.
241 : 24.
242 : 18, 19, 22, 24.
243 : 5, 18, 21, 22, 23, 29, 30, 42.
244 : 19, 24, 29.
246 : 19, 21, 22, 30, 42.
248 : 22, 25.
249 : 24.
250 : 24.
251 : 9, 19, 25, 30.
270 : 18.
271 : 18, 22, 30.
275 : 19, 24.
282 : 18, 19, 29, 30.
284 : 4, 18, 22.
285 : 19, 29, 30.
286 : 4, 5, 18, 19, 23, 24, 29, 30, 42.
287 : 9, 21, 22.
288 : 3, 4, 18, 22, 25, 29.
289 : 18, 19, 24.
290 : 18, 22, 42.
291 : 2, 21, 22, 29, 30, 34, 42.
292 : 2, 7, 20, 21, 22, 23, 29, 30, 37, 42.
293 : 11, 18, 19, 20, 21, 29, 30, 35, 37, 38, 42.
294 : 17, 21, 27, 29, 30, 32, 37, 42.
295 : 2, 21, 22, 25, 29, 30, 34, 37.
296 : 2, 11, 20, 21, 22, 23, 25, 29, 30, 36, 42.

297 : 2, 5, 17, 18, 20, 21, 22, 23, 29, 30, 38, 42.
298 : 11, 18, 19, 21, 22, 25, 29, 30, 34, 42.
299 : 18, 19, 22, 23, 29, 30, 42.
300 : 19, 29, 30, 42.
301 : 4, 18, 41, 42.
302 : 2, 17, 21, 22, 23, 29, 42.
303 : 4, 9, 17, 18, 19, 22, 25, 29, 42.
304 : 11, 19, 21, 29, 30, 35, 36.
305 : 4, 18, 19, 24, 29, 30, 35, 42.
306 : 18, 22, 35.
307 : 4, 9, 11, 19, 22, 24, 30, 42.
308 : 4, 18, 22, 23, 29, 30, 35.
309 : 11, 18, 22, 24, 29, 35.
311 : 4, 18, 22, 29, 30, 35.
312 : 11, 35.
313 : 11, 22, 23, 25, 29, 30, 35, 37.
315 : 2, 19, 25, 27, 31, 34, 41.
316 : 11, 18, 19.
323 : 18, 19, 29.
324 : 4, 18, 19, 23, 29, 30.
325 : 4, 18, 19, 30.
326 : 18.
327 : 18, 24.
328 : 19.
330 : 12, 17, 21, 22, 26, 28, 30, 31, 38, 42.
331 : 12, 17, 21, 26.
332 : 17, 21, 22, 28, 32.
333 : 12, 17, 18, 21, 22, 28, 30, 38.
334 : 12, 17, 21, 22, 28, 30, 31, 38, 40.
335 : 17, 22, 26, 30, 34, 36, 40.
336 : 17, 21, 22, 28, 30, 32, 34.
337 : 2, 17, 21, 22, 23, 29, 30, 42.
338 : 4, 17, 21, 22, 29, 30, 42.
339 : 14, 17, 21, 22, 31.
340 : 17.
341 : 17, 21, 22, 31, 36, 40.
342 : 12, 17, 26, 40.
343 : 21, 22, 30, 36.
344 : 12, 15, 21, 22, 29, 30, 40.
345 : 17, 21, 22, 34, 40.

APPENDIX 3

INFLUENCE VALUES

This appendix consists of a table of influence values for locations with values other than zero for at least one influence. Blank columns indicate a zero value. The location numbers correspond with those in Figure 4.1; nodal structure was illustrated in Figure 5.1.

SITE	A	B	B_1	B_2	C	C_1	C_2	C_3
1		3	2	1	1			
2		1						
3	1	2						
4	1	3		1	2		1	
5	1	1			1			
6	1							
7		6	2	1				
8		5	4	1				
9		6	3	1				
11		4		2	1			
12		2	1					
13		2		1	1			
15		2						
16		3		1				
18		1		1				
19		3		1	1			
20		1		1				
21	1	2		1	1		1	
22	1	3		1	1			
23		1			1			
24		1						
26					1			
27					1	1		
28		1		1				
29		4		2				
30	1	5		2				
31		3		1	1			
32		7	4	1	3		1	1
33		6	4	2				
34	1	5	3	2	1			
38		4		1				
39		2						
40		3						
41	3				1			

SITE	A	B	B_1	B_2	C	C_1	C_2	C_3
42		3						
43		3		1				
44		1			1			
45		3			2			1
46		1						
47		3		1	1			
48	1	4		2	1			
49		4		2	1			
50		2		1				
51		3		2	1			
52		1			4	1	2	
53					1	1		
54					4	1	1	
55					1	1		
56		1			9	1	6	1
57		4		2	2	1		
58		1			2			2
59		5	1	2	2	1		1
60		2		1	3	1		
61		3		1	1			
63		4		2	5	1	2	
65		4		2	2	1		
66		3		1	3	1		
67		3	1	1	2		1	
68		7	2	2	1			1
69		3		2				
71					1	1		
74		1						
76		3	1	1				
78		2		1				
81		1						
82		2		1				
103		1						
109		2		1				
111		2		1				
125		2						
129					2			
130					2	2		
131		1			1			
132		8	6	2	1			
133		7	5	2				
134		4	1	2	2		1	
135		5	1	2	2	1		
136		2		1	2	1		
137		4		1	1			

SITE	A	B	B_1	B_2	C	C_1	C_2	C_3
138		4		2				
139		3		2				
140		1						
141		2						
142		4		2	2	1		
143		3		2				
144		1						
145		5	2	1	1			
146		9	5	2	1			1
147		1			1	1		
148		2		1	4	2	1	
149		1			5	3		1
150		3		1	2	1		
151		3		1	5	2		1
152		2			4	1	1	1
153		6	1	2	2			1
156		2						
164		2		1				
180	1	1			1			
183		1			2		2	
184		1			2		2	
185		1			3		2	
186		1			1			
188	1	1			3	1	1	
189		2			4		2	1
190		1			4		1	1
191		1			2			1
192					3			
193		2						
200		3						
202		1		1				
210		3	1		4			1
211		4	1	1	3		1	1
216		1			1		1	
217		2			1			1
218		3		2	1			
219		5	1	2	2			1
220		2	1		3	1		1
221		3		1	4		1	2
222		4		2	1			
224		4		1				
225		2						
230		3		2	2	1		
231		4		1				
232		5		2				
233		3		2	1			
234		4		2				

SITE	A	B	B_1	B_2	C	C_1	C_2	C_3
235		4		2	1			
236		2		2	1			
237		3		2	2	1		
238		3		2	1			
239		1			2	1		
243		3	1	2	1			
244		1		1				
246		2			1			
251	1	1						
271		1						
283		2		2				
284		1						
285		2		1				
286		5	1	2				
287	1				1			
288		2		1				
290		1						
291		5	1	1	2			1
292		7	4	2	1			
293		6	4	1	2		1	
294		3	1	1	4	1	2	
295		4	2	1	2			1
296		7	3	2	1			
297		6	3	2	3	1	1	
298		5	1	1	2			1
299		4		2				
300		3		1				
301		2						
302		4	1	1	2	1		
303	1	3			1	1		
304		4	2	1	1			
305		5	1	1				
306		1	1					
307	1	4	1					
308		5	1	2				
309		3	2	1				
311		3	1	1				
312		2	2					
313		5	3	2				
315		2	1		3		1	1
316		1	1					
323		1						
324		4		2				
325		2						
330		2			7	3	2	
331					4	3		
332					4	1	3	
333		1			5	2		

SITE	A	B	B_1	B_2	C	C_1	C_2	C_3
334		1			8	3	2	
335		2			4	3		1
336		2			5	1	2	1
337		5	1	2	2	1		
338		4		1	2	1		
339					3	1		
340					1	1		
341					4	2		
342					4	4		
343		1			1			
344		2		1	4	3		
345		1			4	2		1

APPENDIX 4.1

PRINCIPAL COMPONENTS ANALYSIS LOADINGS - SPECIES

Loadings in this table are multiplied by 100.

	I	II	III	IV	V
Acarospora schleicheri	+13	- 5	+30	+ 9	-11
Acarospora smaragdula	+42	- 7	-21	+ 4	- 1
Acarospora sp.	+13	- 4	+ 9	- 1	- 8
Aspicilia calcarea	+41	-20	+40	- 8	-15
Aspicilia calcarea mod. *fruticosa*	+41	-23	-18	- 1	- 1
?Biatorella sp.	+ 8	+ 2	+30	+ 8	+83
Buellia epigaea	+24	-12	-30	+ 5	+ 8
Buellia subcoronata	+16	+38	+ 9	+60	-10
Caloplaca subpyracella	+27	- 7	+40	+ 9	+29
Caloplaca sp.	+12	+36	-10	+41	- 8
Chondropsis semiviridis	+49	-32	-38	+13	+12
Cladia aggregata	+18	+45	-11	-47	+10
Cladonia foliacea	+ 9	+11	- 7	+16	- 2
Cladonia subsquamosa	+ 6	+ 7	- 1	- 6	+ 2
Cladonia verticillata	+14	+32	- 4	-28	+ 6
Cladonia cf. *fimbriata*	+ 1	+ 6	- 2	-14	+ 4
Cladonia squamules	+45	+50	-10	-27	+ 2
Collema coccophorus	+56	-19	+46	- 7	- 4
Dermatocarpon lachneum	+63	-23	+35	- 9	-12
Diploschistes ocellatus	+47	-34	-52	+13	+18
Diploschistes scruposus	+74	+27	- 2	-10	+ 8
Endocarpon pusillum	+68	+13	+12	- 9	- 5
Fulgensia bracteata	+65	-18	-12	-13	- 4
Heppia lutosa	+26	-16	+32	- 7	-18
Heppia polyspora	+43	- 8	+32	+24	+ 1
Heterodea mülleri	+13	+37	-11	-38	+ 8
Lecanora atra	+21	+23	+17	+51	- 7
Lecidea coarctata	+28	+58	- 3	+14	- 4
Lecidea crystallifera	+77	-23	+ 5	-10	-10
Lecidea decipiens	+88	0	+15	- 5	-10
Lecidea planata	+28	+47	+ 4	+ 9	+ 8
Lecidea psammophila	+21	+38	- 4	+37	- 5
Lecidea sp.	+ 5	+12	+ 5	+26	- 5
Parmelia amphixantha	+41	+29	-18	+24	- 3
Parmelia australiensis	+48	-38	-36	+11	+11
Parmelia conspersa	+22	+16	-12	-16	+ 5
Parmelia molliuscula	+47	-31	-50	+23	+15
Parmelia pulla	+41	+35	-18	- 1	+ 1
? Rinodina orbata	+ 4	0	+26	+ 6	+85
Siphula coriacea	+25	+59	-12	-22	+ 4
Synalissa sp.	+31	- 8	+22	- 5	-12
Toninia caeruleonigricans	+67	-19	+ 6	-12	- 8

APPENDIX 4.2

PRINCIPAL COMPONENTS ANALYSIS LOADINGS - SITES

Loadings in this table are multiplied by 100. Location numbers correspond with those in Figure 4.1.

	COMPONENTS				
LOCATION	I	II	III	IV	V
1	37	-16	-19	6	5
2	45	-14	37	- 9	-11
3	46	-18	52	1	- 1
4	39	-1	39	27	1
5	39	-11	50	5	9
6	24	-11	41	2	15
7	57	-33	5	-3	-7
8	56	-37	-32	18	12
9	55	-31	-2	-4	-6
11	67	-16	28	-6	-8
12	44	-19	20	-8	-10
13	50	-14	42	-2	-9
15	48	-16	52	-2	-18
16	27	-12	36	0	-15
18	43	-21	32	-11	-11
19	62	-11	44	-4	-12
20	55	-26	37	1	-5
21	23	1	35	25	-4
22	59	-11	43	0	7
23	41	-2	22	-9	-10
24	36	-13	38	2	-16
25	12	-4	14	-3	-9
26	43	8	21	-11	0
27	17	28	-7	-19	1
28	43	-21	32	-11	-11
29	63	-24	22	-17	-14
30	55	-18	38	-9	-2
31	60	-7	22	-15	-14
32	44	-20	-28	9	4
33	62	-40	-34	17	14
34	53	-30	-17	4	17
35	54	-10	16	-15	-12
37	21	-10	30	-5	-3
38	54	-14	25	-14	-16
39	42	-14	34	-13	-13
40	44	-17	35	-12	-14
41	13	0	31	6	65
42	45	-18	32	-12	-17

LOCATION	I	II	III	IV	V
43	58	-21	23	-15	-12
44	59	0	31	-13	- 7
45	34	16	3	9	0
46	36	- 4	8	-11	- 7
47	64	-13	20	-16	- 9
48	54	-13	29	- 9	3
49	66	-13	10	-18	-10
50	54	- 9	25	-11	-11
51	64	-13	20	-16	- 9
52	35	38	- 8	10	- 3
53	7	25	- 7	-33	7
54	14	33	0	24	- 4
55	27	17	6	-19	- 3
56	30	58	- 2	55	-10
57	69	- 1	14	-25	- 9
58	88	11	- 8	16	- 2
59	35	4	-21	- 1	1
60	26	24	2	-19	5
61	58	- 1	13	-16	- 5
63	50	42	- 7	- 5	- 2
65	73	2	16	-26	- 9
66	48	21	6	-13	- 3
67	57	- 1	3	- 3	- 4
68	58	-24	-23	7	0
69	42	-13	11	-11	-13
71	7	25	- 7	-33	7
73	29	-16	39	- 9	-18
74	45	-12	41	-11	-17
75	19	-13	33	- 7	-13
76	50	-18	9	-10	-12
78	46	- 6	23	6	- 7
81	38	-16	41	- 9	-17
82	35	-12	43	3	-17
86	21	- 7	35	7	-13
102	32	-16	37	- 8	- 8
103	45	-14	37	- 9	-11
106	32	-16	37	- 8	- 8
109	53	-16	39	-13	-19
111	46	-16	33	-10	-16
112	35	-13	39	-10	-18
119	21	-14	29	- 7	-16
125	42	-13	41	-12	-21
129	23	30	- 5	-34	- 8
130	7	25	- 7	-33	7

LOCATION	I	II	III	IV	V
131	52	- 3	32	-12	-11
132	67	-38	-48	9	12
133	59	-41	-50	11	14
134	52	2	- 4	- 8	- 8
135	61	4	- 9	-17	- 5
136	31	24	- 7	-35	6
137	53	-10	16	-15	-10
138	50	-14	24	-14	-17
139	54	-19	11	-14	-12
140	31	-13	22	- 9	-13
141	55	- 9	21	-13	-13
142	40	2	-17	-10	3
143	49	-14	1	-12	- 9
144	33	- 9	37	-10	-12
145	61	-25	-19	- 2	4
146	54	-32	-51	16	13
147	39	25	3	-19	- 4
148	45	38	- 4	-21	- 3
149	31	53	-14	-30	6
150	43	12	- 1	-23	- 2
151	44	45	- 3	-11	1
152	39	37	- 6	- 6	- 2
153	37	- 5	5	- 2	-10
154	26	7	8	- 7	- 3
155	26	7	8	- 7	- 3
156	41	- 5	18	-10	-13
157	21	-10	30	- 5	- 3
158	29	- 5	27	- 8	-10
163	24	-13	23	- 6	- 9
164	44	-18	39	-11	-20
165	19	-13	33	- 7	-13
167	33	-15	22	-10	- 6
168	21	-10	30	- 5	- 3
180	22	6	32	8	55
181	26	7	8	- 7	- 3
182	10	- 9	21	- 5	-14
183	25	33	13	41	- 9
184	212	32	9	37	- 6
185	27	22	22	54	- 9
186	39	12	26	- 3	- 7
188	28	25	11	15	9
189	27	43	7	44	- 6
190	21	37	10	41	- 3
191	25	31	- 3	13	2
192	34	25	14	- 2	5

LOCATION	I	II	III	IV	V
193	49	-13	48	0	-12
194	26	7	8	- 7	- 3
195	41	- 9	35	-11	- 9
199	21	-14	29	- 7	-16
200	47	-22	46	-14	-21
202	38	-21	37	-11	-17
209	35	- 2	27	- 8	- 4
210	24	18	-10	15	0
211	50	46	- 7	4	- 4
214	26	7	8	- 7	- 3
215	26	7	8	- 7	- 3
216	36	23	17	3	- 9
217	35	8	4	10	- 9
218	66	- 6	12	-17	- 9
219	50	- 8	-11	0	- 8
220	42	16	-23	3	6
221	23	20	- 8	24	- 4
222	70	- 9	15	-18	- 9
223	21	-10	30	- 5	- 3
224	54	-14	25	-14	-16
225	47	-14	20	-11	-12
226	32	-16	37	- 8	- 8
227	21	-10	30	- 5	- 3
229	32	-16	37	- 8	- 8
230	64	4	14	-24	- 7
231	54	-14	25	-14	-16
232	63	-20	28	-18	-16
233	59	-16	28	-16	-15
234	60	-21	12	-16	-14
235	67	- 6	5	-18	- 8
236	15	2	- 2	- 8	1
237	61	14	- 1	-23	- 4
238	62	- 2	3	-15	- 6
239	47	21	8	-20	- 3
241	10	- 9	21	- 5	-14
242	36	-13	40	-11	-16
243	60	-16	2	-14	- 6
244	32	-18	28	-10	-17
246	60	- 1	18	-15	- 8
248	26	0	22	12	- 1
249	10	- 9	21	- 5	-14
250	10	- 9	21	- 5	-14
251	32	- 9	40	11	12
270	21	-10	30	- 5	- 3
271	46	- 2	28	- 9	- 8

LOCATION	I	II	III	IV	V
275	21	-14	29	- 7	-16
282	54	-19	33	-11	-13
284	33	- 9	37	-10	-12
285	50	-16	21	-10	-14
286	56	-29	22	-14	-17
287	27	4	25	1	20
288	22	- 8	21	0	-10
289	28	-17	40	- 9	-16
290	42	- 9	23	-12	- 7
291	55	5	- 9	2	- 6
292	51	-23	-43	7	11
293	61	-27	-42	11	14
294	38	17	- 8	35	- 3
295	52	- 5	-19	19	3
296	55	-15	-26	0	8
297	63	- 5	-27	- 7	3
298	66	-10	8	9	- 3
299	68	-20	23	-18	-14
300	55	-19	19	-13	-15
301	34	-16	35	-11	-15
302	55	8	- 9	-16	- 4
303	53	- 5	47	- 5	3
304	43	-12	-20	- 6	7
305	55	-32	24	8	-14
306	33	-19	- 6	2	5
307	47	-22	29	- 1	2
308	56	-26	8	- 7	- 7
309	44	-30	- 8	2	0
311	51	-24	12	- 4	- 6
312	26	-28	-34	12	12
313	55	-32	-30	17	10
315	32	17	12	35	- 7
316	33	24	- 1	3	3
323	45	-14	37	- 9	-11
324	57	-24	34	-15	-17
325	43	-18	45	-10	-16
326	21	-10	30	- 5	- 3
327	19	-13	33	- 7	-13
328	24	-13	23	- 6	- 9
330	36	56	-10	-31	6
331	17	39	-12	-44	10
332	27	46	-41	16	- 4
333	40	50	- 5	-21	2
334	33	63	-10	-30	7

LOCATION	I	II	III	IV	V
335	26	42	-14	-31	5
336	36	48	- 6	20	- 5
337	61	4	- 9	-17	- 5
338	61	7	17	-23	-11
339	16	20	0	- 8	4
340	17	28	- 7	-19	1
341	29	45	- 9	-21	7
342	15	47	-14	-46	9
343	28	14	- 4	-14	2
344	26	39	- 6	- 4	6
345	33	47	-12	-14	2

APPENDIX 5

ENVIRONMENTAL DATA

The values of environmental parameters at each location for the study on lichen distribution. The location numbers are those used to indicate the position of each collecting site in Figure 4.1.

The values given across the table which follows are:

(1) Rainfall

The figure given is the lower value defining a five centimetre class. An asterisk indicates that rainfall at the location shows either a marked seasonal maximum in the summer, or has a uniform precipitation throughout the year.

(2) pH

The pH, reading rounded to one decimal place, of the soil extract.

(3) Calcium concentration

The figure given is milli-moles of extracted calcium x 10^2 / gram of soil

(4) Sodium concentration

The figure given is milli-moles of extracted sodium x10^2 / gram of soil.

(5) The nature of the soil surface

R	Rock	L	Loam
S	Sand	H	Hard-setting
A	Amorphous	C	Clay

(6) Mean maximum daily temperature for January

The figure given is the lower limit of a 3°C class.

Station Number	Rain-fall	pH	Ca	Na	Surface	January Temperature
1	35	7.5	65	61	L	29
2	30	8.4	179	107	L	29
3	20	8.3	64	27	L	29
4	20	8.2	65	50	L	29
5	20	8.4	42	35	L	29
6	20	8.4	42	73	L	29
7	15	8.3	66	34	L	32
8	15	8.4	99	29	L	32
9	15	8.5	58	45	L	32
10	20	8.5	41	26	S	32
11	15	8.6	64	80	L	32
12	20	8.6	78	28	L	32
13	15	8.1	22	106	L	32
14	15	8.6	62	22	S	32
15	15	8.0	48	34	L	32
16	15	7.2	36	40	L	32
17	15	8.0	25	21	S	32
18	15	7.5	54	34	L	32
19	15	7.4	13	61	L	32
20	15	8.4	27	78	L	32
21	15	8.2	26	28	L	32
22	15	8.3	73	13	L	32
23	15	8.0	70	14	L	32
24	15	7.4	63	93	L	32
25	15	7.6	12	77	L	32
26	45	7.4	102	89	H	26
27	45	7.6	392	99	H	26
28	45	8.0	372	31	H	26
29	35	7.6	179	29	L	26
30	30	8.2	175	50	L	26
31	25	7.5	133	38	L	29
32	20	8.4	266	41	L	29
33	20	8.3	162	35	L	29
34	20	8.3	157	35	L	29
35	20	7.7	144	42	L	29
36	20	8.4	109	21	S	29
37	20	8.4	153	15	L	29
38	25	8.3	56	11	L	29
39	25	8.3	173	29	L	29
40	25	8.1	124	31	L	29

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January Temp.
41	25	7.8	125	17	L	32
42	25	8.4	126	10	L	32
43	25	8.3	104	20	L	32
44	25	7.6	57	9	L	32
45	25	8.3	65	7	L	32
46	30	8.5	126	8	L	29
47	30	8.5	140	9	L	29
48	30	7.5	120	15	L	29
49	35	8.5	103	8	L	29
50	35	8.5	107	24	L	29
51	35	8.4	166	30	L	26
52	45	7.7	71	108	H	26
53	55	6.2	29	46	H	26
54	55	7.4	37	58	H	26
55	45	7.7	42	59	H	26
56	40	6.8	601	721	H	26
57	35	8.2	167	62	L	26
58	35	8.0	174	37	S	26
59	35	8.3	139	30	L	26
60	35	8.1	121	24	L	29
61	30	8.4	144	19	L	29
62	25	8.1	142	68	S	29
63	25	8.2	83	32	L	29
64	25	8.1	136	121	S	29
65	25	8.3	99	46	L	29
66	25	8.4	78	15	L	29
67	25	8.6	120	29	L	29
68	25	8.7	137	29	L	29
69	25	8.5	165	22	L	29
70	30	8.4	174	22	H	26
71	40	7.1	161	92	H	26
72	15	8.3	26	17	S	32
73	15	7.8	22	54	L	32
74	15	8.0	28	123	L	32
75	15	8.4	74	576	L	32
76	15	8.6	59	49	L	32
77	15	8.0	16	49	S	32
78	15	7.6	31	22	L	35
79	10	8.7	53	17	A	35
80	10	8.5	34	27	L	35

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January Temp-erature
81	15	8.9	45	67	L	32
82	10	8.6	47	29	L	35
83	10*	8.7	25	23	A	35
84	10*	8.7	35	34	A	35
85	10*	8.5	42	28	A	35
86	10*	7.0	17	19	L	35
87	10*	7.4	10	5	S	35
88	10*	7.8	14	7	S	35
89	10*	7.9	16	3	R	35
90	10*	7.3	17	20	R	35
91	10*	7.6	19	53	A	35
92	10*	8.2	66	65	H	35
93	10*	8.3	18	54	S	35
94	10*	7.8	13	26	S	35
95	10*	8.0	15	16	S	35
96	10*	7.5	20	62	L	35
97	10*	8.2	16	53	S	35
98	10*	7.3	19	48	R	35
99	10	8.0	34	17	S	35
100	10	8.1	23	61	S	35
101	10	8.4	15	80	R	35
102	10	8.6	18	82	L	35
103	15	8.2	455	23	L	35
104	15	8.3	703	69	H	35
105	15	8.6	40	52	R	35
106	15	8.6	47	86	L	35
107	10	8.6	45	47	R	35
108	10	8.7	124	173	H	35
109	10	8.6	83	77	L	35
110	10	8.7	95	74	A	35
111	15	8.4	54	-	L	35
112	15*	8.0	102	262	L	35
113	10	7.9	73	41	L	35
114	10	7.8	98	68	L	35
115	10*	8.0	48	74	L	35
116	10*	7.9	320	105	L	35
117	10*	7.6	85	54	L	35
118	10*	7.4	54	112	S	35
119	15*	7.8	57	160	C	35
120	15*	7.9	35	34	L	35

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January temp-erature
121	15*	7.9	22	44	L	35
122	15	7.9	34	21	L	35
123	15	8.0	27	169	L	35
124	15	8.4	65	39	L	35
125	20	7.9	72	15	L	35
126	25	8.0	98	25	L	35
127	20	8.2	28	26	L	35
128	10*	-	-	-	-	35
129	50	7.3	37	74	H	26
130	50	5.4	46	34	S	26
131	20	7.5	37	121	L	32
132	20	7.8	66	40	L	32
133	20	7.4	73	21	L	29
134	25	8.0	62	18	L	29
135	30	7.8	105	24	L	29
136	35	7.2	60	25	L	29
137	30	7.6	49	18	L	29
138	30	7.6	72	31	L	29
139	40	7.3	171	38	L	26
140	35	7.8	100	16	S	26
141	30	7.6	101	15	S	29
142	30	8.0	105	30	H	29
143	30	7.8	86	78	H	29
144	25	7.9	38	18	S	29
145	25	8.1	116	51	L	29
146	20	8.0	89	16	L	29
147	50	7.7	105	37	H	26
148	45	7.7	91	30	H	29
149	45	7.6	41	29	H	29
150	50	7.5	88	75	H	29
151	45	7.2	35	65	H	29
152	45	7.5	69	56	H	29
153	20	8.6	31	130	L	29
154	15	8.2	107	49	L	29
155	15	8.3	52	34	L	32
156	15	8.2	86	34	L	32
157	15	7.6	67	70	L	32
158	20	7.9	32	53	A	32
159	20	7.8	44	78	A	32
160	20*	8.1	123	78	A	32

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January temp-erature
161	20*	7.6	17	89	H	32
162	20*	7.4	21	44	H	32
163	20*	7.6	32	28	L	32
164	20*	8.0	45	60	L	32
165	20*	8.1	29	72	L	32
166	20*	8.2	65	27	S	32
167	20*	7.7	77	33	S	32
168	20*	8.4	39	39	S	32
169	20*	8.3	56	189	C	32
170	20*	8.0	63	185	C	32
171	20*	8.1	23	216	C	35
172	25*	8.2	38	43	C	35
173	25*	8.0	59	83	C	35
174	25*	7.2	48	34	C	35
175	25*	8.2	76	13	C	35
176	30*	7.4	78	80	C	35
177	30*	7.6	46	18	C	35
178	30*	7.9	53	29	C	35
179	30*	7.4	20	55	C	35
180	30*	6.9	25	19	H	35
181	30*	7.2	15	22	H	35
182	30*	7.4	24	23	H	35
183	30*	6.7	12	7	L	35
184	30*	7.0	13	9	L	35
185	35*	7.4	18	8	L	35
186	35*	7.3	19	9	L	32
187	35*	7.4	12	16	L	32
188	35*	7.5	25	20	L	32
189	35*	7.6	14	12	L	32
190	30*	7.3	10	9	L	32
191	30*	7.3	19	8	L	32
192	25*	7.0	10	9	L	32
193	25*	7.5	50	26	L	32
194	25*	8.0	119	23	L	32
195	20*	7.9	99	12	L	32
196	20*	8.4	16	70	H	32
197	20*	8.3	94	22	H	32
198	20*	7.9	41	17	L	32
199	20*	8.0	125	45	L	32
200	20*	8.1	50	12	L	32

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January temp-erature
201	20*	7.9	88	7	S	32
202	20*	7.5	121	21	L	32
203	25*	8.3	129	29	H	32
204	25*	7.9	43	73	H	32
205	25*	7.9	42	133	H	32
206	25*	8.5	42	138	H	32
207	30*	8.2	31	29	H	32
208	30*	7.9	32	45	H	32
209	30	7.9	59	16	H	32
210	35	7.4	30	10	L	32
211	30	7.7	64	14	H	32
212	30	8.3	44	39	H	32
213	30	7.6	29	94	H	32
214	30	7.7	26	43	H	32
215	30	7.5	35	365	C	32
216	30	7.9	22	40	C	32
217	25	7.9	91	33	C	32
218	25	8.2	156	13	L	32
219	25	8.4	88	13	L	32
220	25	7.6	28	11	L	32
221	25	7.8	27	6	L	32
222	35	8.4	126	24	L	29
223	30	7.9	130	41	S	29
224	35	7.8	108	52	L	29
225	35	8.1	57	7	L	29
226	30	8.4	753	1222	L	29
227	30	8.5	121	94	L	29
228						
229	30	8.5	199	276	L	29
230	30	8.5	158	54	L	29
231	40	8.4	108	24	L	29
232	30	8.4	76	16	L	29
233	35	8.4	120	16	L	29
234	35	8.4	96	13	L	29
235	35	7.8	108	32	L	29
236	45	8.2	107	29	S	26
237	40	8.4	93	63	L	26
238	40	8.5	84	79	L	26
239	40	8.4	267	122	S	26
240	40	8.3	385	96	S	26

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January temp-erature
241	20	7.6	83	155	A	32
242	20	8.4	55	43	L	32
243	20	8.5	84	15	L	32
244	20	8.5	21	59	L	32
245	20	8.5	36	9	L	32
246	20	8.2	32	6	S	32
247	20	8.2	68	89	L	32
248	20	8.3	35	73	L	32
249	20*	7.7	22	36	C	32
250	20*	7.8	58	27	L	32
251	20*	7.2	13	32	H	35
252	20*	8.2	13	25	R	35
253	20*	7.4	11	123	S	35
254						
255	20*	7.7	15	45	H	35
256	20*	7.7	12	10	A	35
257	25*	6.5	10	10	A	35
258	20*	6.7	12	5	A	35
259	20*	6.9	10	9	A	35
260	20*	7.3	14	32	A	35
261	20*	8.2	39	40	A	35
262	20*	8.4	41	79	S	35
263	20*	8.0	8	39	S	35
264	20*	7.6	21	134	H	35
265	15*	8.4	35	31	S	35
266	15*	8.6	34	62	C	35
267	15*	7.4	23	14	S	35
268	15*	7.6	59	28	L	35
269	15*	7.6	38	33	L	32
270	15*	7.6	67	9	L	32
271	15*	8.0	73	19	L	32
272	15*	8.0	34	22	A	32
273	15*	8.2	20	55	A	32
274	15*	8.1	25	80	A	32
275	15*	7.8	20	49	L	35
276	15*	7.9	18	40	S	35
277	10*	8.3	46	103	S	35
278	10*	8.1	31	15	S	35
279	10*	7.5	30	43	S	35
280	10	7.9	47	23	S	35

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January temp-erature
281	10	8.1	20	30	S	32
282	15	8.2	25	81	L	32
283	15	8.4	43	27	L	32
284	15	8.3	37	41	L	29
285	15	7.7	60	24	L	29
286	15	8.9	59	16	L	29
287	20	7.7	55	11	L	29
288	20	7.5	64	10	L	29
289	20	8.6	72	47	L	29
290	15	7.9	44	74	L	29
291	20	7.5	50	29	L	29
292	20	8.1	47	26	L	29
293	20	8.4	65	20	L	29
294	20	7.4	47	83	L	29
295	20	8.0	40	41	L	29
296	15	8.2	79	18	L	29
297	15	8.2	82	17	L	29
298	15	8.7	64	20	L	29
299	15	8.5	67	34	L	29
300	20	8.3	58	32	L	32
301	20	8.5	72	20	L	32
302	20	7.6	66	60	L	32
303	20	8.3	44	29	L	32
304	20	7.9	46	46	L	32
305	20	8.3	17	46	L	32
306	25	7.8	70	11	L	32
307	20	8.2	27	51	L	32
308	20	8.1	46	25	L	32
309	20	8.3	39	16	L	32
310	20	7.1	21	11	S	32
311	15	7.6	47	9	L	32
312	20	7.9	53	13	A	32
313	20	7.9	53	8	L	32
314	15	8.0	42	7	S	32
315	15	8.0	26	33	L	32
316	15	8.4	50	69	L	32
317	10	7.8	25	54	L	35
318	10	8.0	12	32	L	35
319	10	7.9	49	104	L	35
320	10	7.7	238	1026	L	35

Station Number	Rain-fall	pH	Ca	Na	Sur-face	January temp-erature
321	10	7.3	1515	4989	L	35
322	10	7.7	656	2254	L	35
323	15	7.6	165	500	L	35
324	20	8.3	47	641	L	35
325	20	8.6	35	122	L	32
326	25	8.6	47	65	L	32
327	25	8.6	53	23	L	32
328	30	8.6	58	82	L	29
329	25	8.5	84	34	L	29
330	50	7.4	30	63	H	26
331	50	6.7	23	33	S	26
332	50	7.2	53	16	H	26
333	45	7.3	23	19	H	26
334	45	7.2	45	15	H	26
335	55	6.9	148	123	H	26
336	45	7.4	23	25	H	26
337	35	7.4	84	16	L	26
338	40	7.7	55	14	S	26
339	45	7.8	25	17	S	26
340	50	7.3	15	13	S	26
341	55	7.2	19	15	H	26
342	55	7.2	13	20	H	26
343	50	7.2	26	13	H	26
344	40	7.0	61	22	L	26
345	40	7.4	27	24	H	26

APPENDIX 6

LOCATIONS FROM WHICH *CHONDROPSIS SEMIVIRIDIS* HAS BEEN COLLECTED

Listed by State, then in alphabetical order of collector, and chronological order of collection. Abbreviations are AD, State Herbarium of South Australia; ADU, Herbarium of the Botany Department, University of Adelaide; MEL, National Herbarium of Victoria. Collections without herbarium citation are in the private herbarium of the collector.

Collections of *Chondropsis semiviridis*

WESTERN AUSTRALIA

Forrest, *A.M. Baird* Aug. 1930 (MEL 6279); Eucla *J.D. Batt* 1886-96 (MEL 5848): Dundas Rocks, south of Norseman, *A.C. Beauglehole 14798*, 18/9/1965 (MEL 14331): 42 miles east of Balladonia, *A.C. Beauglehole 14839*, 22/9/1965 (MEL 22858): Abra Kurri Cave, ca. 30 miles from Eucla, *A.C. Beauglehole 14883*, 23/9/65 (MEL 14330): 11 miles west of Mundrabilla, 370m. east of Norseman, *A.C. Beauglehole 14859* 23/9/1965 (MEL 14334): 20m west of Madura *G.C. Bratt 67/277* Oct. 1967: 15m west of Caiguna, *G.C. Bratt 67/240* Oct. 1967: 68m west of Caiguna, *G.C. Bratt 67/249* Oct. 1967: 27m west of Balladonia, *G.C. Bratt 67/267* Oct. 1967: Lake Cowan near Norseman, *G.C. Bratt 67/282* Oct. 1967: Wave Rock, near Hyden, *G.C. Bratt 67/338* Oct. 1967: 54m west of Coolgardie, *G.C. Bratt 67/506* Oct. 1967: 30m south of Coolgardie, 50m east of Balladonia *N.N. Donner 3103* (AD): 13m north of Mt. Ragged *N.N. Donner 3096* (AD), *R. Filson 8873 & A.S. George* 16/9/66 (MEL 27630): Frazer Range, *R. Helms* Oct. 1891 (MEL 5849, MEL 5850, 7 ADU).

SOUTH AUSTRALIA

Koonamore Vegetation Reserve, *B.S. Barrien,* 1944 (MEL 5851, ADU): 23m south-east of Wirrula, Eyre Hwy, *A.C. Beauglehole 14963* 29/9/1965 (MEL 22850): 26m west-south-west of Koonalda, Nullarbor region, *A.C. Beauglehole 14907* (MEL 22843): 17m east of Kimba, *G.C. Bratt 67/150* Oct. 1967: 10m west of Ivy Tanks, Eyre Hwy, *G.C. Bratt 67/184* Oct. 1967: 30m west of Nullarbor H.S., *G.C. Bratt 67/190* Oct. 1967: Bunyung Station, 20m north of Morgan, *J.B. Cleland* 23/7/1966 (AD): Bulgunnia Station, north of Morgan, *J.B. Cleland* 23/7/1966 (AD): 47m North west of Pt. Augusta, *N.N. Donner 1851* (AD): Refuge Rockholes, 45m west of Whyalla on road to Kimba, *N.N. Donner 2195* (AD): 15m west of Whyalla, *N.N. Donner 2202* (AD): Blanchetown, *M. Fagg 127* (AD): vicinity of Koonalda Cave, Nullarbor region, *R. Filson 9424* 28/12/1966 (MEL 25376): vicinity of Weeks cave, Nullarbor region, *R. Filson 9430* 29/12/1966 (MEL 25364): The Catacombs cave, Nullarbor region, *R. Filson 9441* 4/1/1967 (MEL 25369): Knowles cave, Nullarbor region, *R. Filson 9452* 5/1/1967 (MEL 1000 447): 11 miles north-west of Nullarbor H.S., *R. Filson 9490* 11/1/1967 (MEL 25373): fissure near South Diprose Cairn, Nullarbor region, *D.S. Hemsley* 5/1/1962 (MEL 6282): Chowilla Station, *R. Kuchel 2291* (AD): Nullarbor H.S., 5m south of Malbooma, *B.G. Lay* 26/9/1970 (R.W. ROGERS 1888), *T.R.N. Lothian 3629.* (AD), Murray River *F. von Mueller* Feb. 1851 (MEL 5847 ISOTYPE, MEL 5859): Yudnapinna Station, 50m north of Pt. Augusta, *R.W. Rogers 54* 26/6/1965: 17m north of Pt. Augusta, *R.W. Rogers 61* 26/6/1965: Lincoln Gap Station, 20m west of

Pt. Augusta, *R.W. Rogers 73* 13/1/1966: 18m north of Pt. Augusta, *R.W. Rogers 139* 22/2/1966: Mt. Mary, 80m north-east of Adelaide, *R.W. Rogers 238* 8/3/1966: 8m west of Morgan, *R.W. Rogers 249* 8/3/1966: 4m east of Swan Reach, *R.W. Rogers 441:* 11/5/1966: 13m south-west of Iron Knob, *R.W. Rogers 566* 1/10/1966: 23m south-west of Iron Knob, *R.W. Rogers 572* 1/10/1966: 35m north of Cowell near Whyalla road, *R.W. Rogers 643* 1/10/1966: 12m south of Whyalla *R.W. Rogers 652* 1/10/1966: Canegrass Station near Morgan, *R.W. Rogers 1073* 17/5/1967: Quondong Station, *R.W. Rogers 1135* 18/5/1967: 25m north-west of Iron Knob, along road to Yardea, *R.W. Rogers 1173* 22/5/1967: 55m north-west of Iron Knob along road to Yardea, *R.W. Rogers 1190* 22/5/1967: near south-west corner of Lake Gairdner, *R.W. Rogers 1206* 23/5/1967: 85m south of Kingoonya, *R.W. Rogers 1219* 23/5/1967: 70m south of Kingoonya, *R.W. Rogers 1235* 23/5/1967: Mt. Whyalla, *R.W. Rogers 1756* 10/8/1969: 72m east of Wirrula, *D. Scoles 47* (AD): Loveday, Nullarbor region, *E.J. Vickery* July 1951 (MEL 5855): Colona Station near Fowlers Bay, *J.H. Willis* 27/8/1947 (MEL 5853, MEL 5857): Nullarbor H.S., *J.H. Willis* 29/8/1947 (MEL 5852): 11m east of Koonalda, *J.H. Willis* 18/10/1961 (MEL 6289); 16m north of Lord's Well Station, *R.W. Rogers 1153* 18/5/1965.

VICTORIA

Kulkyne National Forest *A.C. Beauglehole 1153* 1947 (MEL 5858): Walpeup near the Pink Lakes, *P. Bibby* 1947 (MEL 5856): Hattah Lakes district *R. Filson 7334* 14/6/1965 (MEL 11082): Rocket Lake, 24m west of Nowingie, *R. Filson 7375* 9/8/1965 (MEL 11081), 6m west of Redcliffs on the Thurla road *R. Filson 7999* (MEL 11082): Head of McArthur's lease, Sunset Country, *D.W. Goodall* 4/11/1951(MEL 24802): Sandhills near Hattah Lakes, *J.H. Willis* Sept. 1940 (MEL 5846): Thurla, *J.H. Willis* Sept. 1940 (MEL 5854) Lendrook Plain, Kulkyne National Forest, *J.H. Willis* 27/8/1955 (MEL 6293).

NEW SOUTH WALES

Road to Triple Chance Mine, Broken Hill *Marie Allender* 7/9/1967 (MEL 1000241): Between Michelago, Cooma and Dalgety, *J.J. Collett* 20/6/1968 (MEL 27926): 9m east of Cooma on the Numeralla Road, *R. Filson 7876* 2/12/1965 (MEL 1001963), Numeralla *D. McVean* Mt. Hope *D. McVean* 52m west of Balranald, *R.W. Rogers 845* 2/11/1966: 10m west of Goolgowi, *R.W. Rogers 814* 2/11/1966: Beltrees, near Scone *H.L. White* 22/8/1906 (SYD).

QUEENSLAND

Mueller Range, 60m south-west of Winton, *Birch* ca. 1877 (MEL 5860).

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Table 5.4

TABLE 5.4

The relationship between the final Species-Groups A, B, C, D and E, and the groups resulting from the various methods of analysis

Species-Group	Species	Principal Components Analysis: Axes II, III, IV				Axes III, IV				Axis V	Influence Analysis									Regional Grouping				
		Cladia	*Lecanora*	*Chondropsis*	*Collema*	*Cladia*	*Lecanora*	*Chondropsis*	*Collema*	*Caloplaca*	Node C	C1	C2	C3	Node B	B1	B2	Node A	Ungrouped	I	II	III	IV	V
A	*Siphula coriacea*	+				+					+	+								+				
	Cladonia squamules	+				+					+	+									+			
	Cladia aggregata	+				+					+	+								+				
	Heterodea mulleri	+				+					+	+								+				
	Cladonia verticillata	+				+					+	+								+				
	Diploschistes scruposus	+				+					+													+
	Parmelia conspersa	+				+													+	+				
	Cladonia subsquamosa	+				+														+				
	Cladonia fimbriata	+				+					+	+								+				
	Parmelia pulla	+				+							+							+				
B	*Lecidea coarctata*	+					+				+		+								+			
	Lecidea planata	+					+				+										+			
	Buellia subcoronata		+				+				+		+								+			
	Lecidea psammophila		+				+				+		+								+			
	Caloplaca sp.		+				+				+		+							+				
	Lecanora atra		+				+				+		+									+		
	Lecidea sp.		+				+				+		+								+			
	Parmelia amphixantha		+				+				+			+								+		
	Cladonia foliacea		+				+				+			+								+		
C	*Parmelia australiensis*			+				+							+	+							+	
	Diploschistes ocellatus			+				+							+	+							+	
	Chondropsis semiviridis			+				+							+	+							+	
	Parmelia molliuscula			+				+							+	+							+	
	Aspicilia calcarea mod. *fr.*			+				+							+	+							+	
	Buellia epigaea			+				+							+	+							+	
	Acarospora smaragdula			+				+							+	+							+	
	Lecidea crystallifera			+					+						+		+						+	
	Toninia caeruleonigricans			+					+						+								+	
	Fulgensia bracteata			+		+									+		+						+	
D	*Dermatocarpon lachneum*				+				+										+					+
	Collema coccophorus				+				+										+					+
	Heppia lutosa				+				+										+					+
	Aspicilia calcarea				+				+										+			+		
	Heppia polyspora				+				+										+			+		
	Synalissa sp.				+				+										+				+	
	Acarospora schleicheri				+				+										+					+
	Acarospora sp.				+				+										+					+
	Lecidea decipiens				+				+						+									+
	Endocarpon pusillum	+							+										+					+
E	*Caloplaca subpyracella*				+				+	+								+				+		
	Biatorella ?	+							+	+								+			+			
	Rinodina ?	+							+	+								+					+	

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