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Environmental Factors Relating to the Distribution of Terricolous Bryophytes and Lichens in Semi-arid Eastern Australia

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Abstract. *Bryophytes and lichens associated with soil crusts were sampled over 500,000 km^2 of rangelands in semi-arid eastern Australia. Canonical Correspondence Analysis (CCA) was used to examine the relationships between a range of environmental variables and the distributions of these species from a subset of 130 samples from 87 sites. CCA revealed that bryophytes were related to total annual rainfall, soil pH, calcium carbonate levels, plant cover, texture, organic carbon, and soil texture. Lichens were related to annual rainfall, pH, calcium carbonate levels, plant cover, sheet erosion, organic carbon, and crust cover. Rainfall is a primary determinant of plant cover, which in turn affects light, nutrient availability, and litter levels, and therefore bryophyte and lichen distribution. On the basis of the first two ordination axes, bryophytes and lichens clustered into loose arrangements of species, based on their responses to the environmental variables.*

A common feature of semi-arid environments is the high degree of spatial and temporal variability in plant and soil properties (Tongway & Ludwig 1994). Arid environments often support a low cover of vascular plants, which provide a niche for non-vascular plants such as mosses, lichens, and liverworts. In these environments, bryophytes and lichens are the principal visual components of biological crusts, also known as cryptogamic or microphytic crusts. These crusts, and their constituent non-vascular plants are patchily distributed throughout the landscape, occupying areas of bare ground between individual vascular plants, and in some areas, completely dominating the ground flora (Eldridge 1996; Eldridge & Tozer 1996).

Both biotic and abiotic factors are thought to influence the distribution of soil surface biota in arid and semi-arid environments. Stable substrates are a necessary prerequisite for the establishment and growth of lichens (Rogers 1974). Consequently, they are generally absent from landscapes dominated by unstable sandy soils or cracking clays (Eldridge 1996). Lichens in particular are believed to increase soil microtopography and therefore enhance the capacity of the soil to pond and retain water (West 1990). Mosses, too, are generally restricted to more stable or sheltered microsites. However, some mosses such as *Barbula crinita* are able to survive in aeolian landscapes of extensive sand accretion by flexing back their leaves strongly after rainfall, thus 'swimming up' through the inundating sand after only a few millimetres of rain (Moore 1980; Scott 1982).

The effect of microclimate on the distribution of mosses is typified by the moss *Tortula pagorum,* which grows in small sandy accumulations at the base of, and on the trunks of, arid zone *Callitris* and *Alectryon* trees. These microsites, which are relatively well shaded, receive extra moisture channelled along the bark after rainfall. Similarly, the liverwort *Asterella drummondii* is common in areas below rock overhangs in the arid zone where it benefits from runoff from bare slopes and thrives in areas of low evaporation. Such microclimatological effects have been commonly reported for rock crevices. For example, Kunkel (1975, cited in Scott 1982) showed that rock slope was the single most important factor effecting the distribution of moss species on a desert rock outcrop in Colorado. Similarly, John and Dale (1990) found that elevation and slope were the environmental factors most strongly correlated with the distribution of a saxicolous lichen community on a rockslide in Alberta, Canada. Runoff from rock faces may be sufficient to convert small arid crevices into nutrient-rich mesic microsites capable of supporting a rich suite of non-vascular flora.

Interrelationships between soil and landscape factors are complex, reflecting simultaneous changes in factors such as microtopography, slope, and soil stability. Quantitative studies of how these factors interrelate are rare in semi-arid regions, and studies have concentrated on either saxicolous lichen communities (John & Dale 1990), or on forest bryophytes and lichens (e.g., Cornelissen & ter Steege 1989; Palmer 1986; Wolf 1994). Our understanding of the relative importance of abiotic factors in controlling the distribution of non-vas-

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cular flora is complicated by the high correlation between individual factors. Similarly, the wide differences in floristics of soil crust communities in apparently homogeneous environments may obscure our understanding of the relationships between species and their environments (Wolf 1994). For example, studies of lichens and bryophytes at Mungo National Park in semi-arid eastern Australia have demonstrated the wide variability in both total crust cover and floristics within quadrats at any one site (Downing & Selkirk 1993; Eldridge 1995, 1996).

Ecological and biogeographical studies of soil crust bryophytes and lichens in arid and semi-arid eastern Australia reveal that the major environmental factors influencing their distribution are rainfall amount and distribution (Rogers 1971, 1972), and soil factors such as calcium carbonate content (Downing 1992; Downing & Selkirk 1993; Rogers 1972) and sodium content (Rogers 1972). Apart from these studies, we are unaware of any studies which have systematically examined the influence of abiotic factors, particularly soil physical characteristics, in the distribution of arid and semi-arid soil crust biota.

In this paper we use a canonical ordination technique, Canonical Correspondence Analysis (CCA), to investigate patterns in species data that can be explained by a number of measured environmental variables (ter Braak 1986). We examine the relationships between individual soil surface bryophyte and lichen species, and a range of environmental variables from a large number of sites in a heterogeneous semi-arid and arid landscape in eastern Australia.

STUDY AREA AND METHODS

The study area.—The study was conducted over 500,000 km^2 of rangelands in New South Wales, Australia (Fig. 1). The climate can be classified as arid or semi-arid (Meigs 1953), and rainfall decreases westerly from more than 500 mm yr^{-1} in the east to 220 mm in the west. Seasonal distribution varies between winter-dominant in the southwest to summer-dominant in the northeast. Droughts are a regular feature of the climate. Mean daily temperatures are typically hot in summer (>40°C) and mild in winter (>10°C), and evaporation increases from south to north and from east to west (Cunningham et al. 1981).

Seven broad landscape types can be identified in the survey area (Table 1). Crust cover is greatest on calcareous and non-calcareous plains, and on ranges and hills (Eldridge & Tozer 1996). Plains support a mixed woodland dominated by *Eucalyptus populnea-Callitris glaucophylla* or *Casuarina cristata-Alectryon oleifolium.* Ranges and hills are dominated by sparse *Acacia aneura* trees and assorted grasses and herbs. Other landscapes supporting crust communities include footslopes and rolling downs with desert loam soils dominated by the perennial shrubs *Atriplex vesicaria* and *Maireana* spp. Sandplains and dunefields of earthy sands with dense mallee (*Eucalyptus* spp.) shrublands support a variable community of soil crust taxa. Unstable dunes in the northwest and active floodplains with clay soils in the southeast support only sparse crust communities.

The grazing of sheep and cattle on native pastures is the predominant landuse over much of the area, on properties ranging from approximately 20,000 to 80,000 ha in area. Areas of opportunistic mixed farming and irrigation occur in the east and southwest, and smaller areas are dedicated to national parks and nature reserves.

Data collection.—Data were collected from 282 sites scattered throughout the survey area at regular intervals of 25–30 km along major roads and tracks. The intensity of sampling varied according to the proportion of the study area occupied by each of the seven landscape types. At each site, ten 0.5 m^2 quadrats were positioned at 10 m intervals along a 100 m transect. Whilst ten quadrats may seem small given the inherent heterogeneity in semi-arid environments, it was considered the maximum allowable given time constraints both in the field and in the laboratory. Within each quadrat a description of the soil surface morphology and biological features was made. These are shown in Table 2 and described below.

Soil surface morphology.—Position within the landscape was recorded as either ridge, upperslope, midslope, lowerslope, flat, drainage line or closed depression. Slope within the quadrat was classified as 0%, 1–3%, 3–5%, 5–10%, or >10%. Surface microtopography was defined as the vertical distance between the lowest and highest points in the quadrat i.e., <5 mm, 5–8 mm, 8–15 mm, 15–25 mm, or >25 mm. These relate to the potential for retention of rainfall on the surface. Crust coherence gives a measure of the force required to disrupt the soil surface with an object equivalent to the diameter of a pencil. Coherence, which was generally assessed dry under field conditions, assesses the degree to which the surface has the capacity to resist stress immediately upon wetting, or to reform after wetting (Tongway 1994). Crust coherence classes were ranked as sandy (single grained), self-mulching (clay aggregates), break on touch, slight pressure, significant pressure, high pressure, and unbreakable. Increasing number equates to increasing predisposition to hardsetting. The degree of surface cracking measures the percentage of the surface covered with cracks and relates to the capacity of the surface to disintegrate and erode: 0%, <10%, 10–25%, 25–50%, or >50%. Degree of cracking probably also gives an indication of the potential microsites for seed lodgement. Stability of the soil surface to raindrop impact, determined using the Emerson drop test (Tongway 1994), was ranked as stable, moderately stable, unstable, or very unstable. The percentage of the soil surface affected by sheeting, rilling, pedestalling, and scarping (all forms of erosion caused by wind and/or water) was ranked as 0%, <10%, 10–25%, 25–50%, or >50%. The percentage of the surface covered by eroded material (sand, gravel, and stone) was ranked as 0%, <10%, 10–25%, 25–50%, or >50%.

Rainfall and soil physico-chemical data.—Average annual rainfall (mm) for each of the sites was obtained using available meteorological data (Bureau of Meteorology 1986). Soil texture was determined in the laboratory using the bolus method of Northcote (1979). Organic carbon (%) was determined according to the modified Walkley-Black technique (Colwell 1969). The amount of calcium carbonate ($CaCO_3$) was determined by treating the soils with 2 drops of 0.1 N HCl and ranking the effervescence as nil, slight, moderate, high, or very high. Soil pH was measured on a 1:5 soil-water extract using a pH meter.

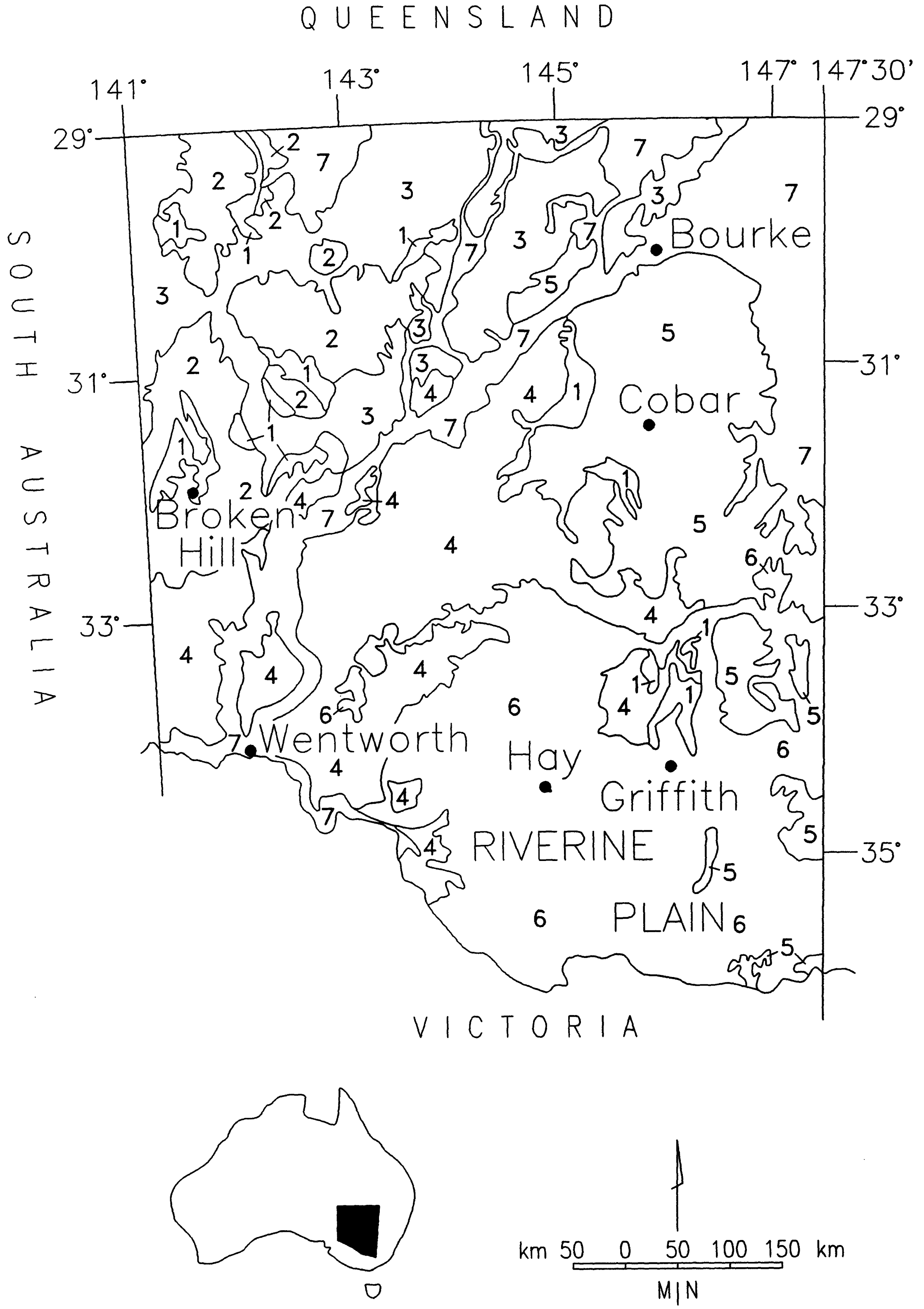

FIGURE 1. Location of the survey area in eastern Australia. Numbers refer to the seven landscape types described in Table 1.

TABLE 1. Description of the seven landscape types in the survey area.[a] Mapping units are shown on Figure 1.[b] Includes bryophytes and lichens.

Mapping unit[a]	Landscape type	Vegetation	Soils	Total no. of species[b]	Mean crust cover (%)	No. of sites
1	Ranges and hills	sparse shrubland with *Acacia aneura*	shallow loams	35	23.9	18
2	Footslopes and rolling downs	sparse shrubland with *Acacia aneura*; chenopod shrubland with *Atriplex vesicaria* and *Maireana pyramidata*	shallow desert loams	51	13.3	39
3	Sandplains and dunefields	mallee shrubland with *Acacia, Eucalyptus* and assorted shrubs	deep earthy sands and sandy loams	53	8.6	56
4	Calcareous plains	woodland with *Alectryon oleifolius* and *Callitris glaucophylla*	calcareous loams clay loams	76	20.9	58
5	Non calcareous plains	woodland with *Eucalyptus, Acacia* and assorted shrubs	clay loams and loams	72	27.7	46
6	Relict floodplains	chenopod shrubland with *Atriplex* spp. and *Maireana* spp.	clays and duplex loams	65	14.6	48
7	Active floodplains	woodland with *Eucalyptus* spp.	clays	25	7.3	17

Electrical conductivity (dS m^{-1}) was measured on a 1:5 soil-water extract. Concentrations (as mg L^{-1}) of soluble and exchangeable cations of sodium, potassium, calcium, and magnesium were determined on a 1:5 soil-water and 1:5 soil-NH_4Cl solutions respectively using a Unicon Solaar 929 atomic absorption spectrophotometer.

Vascular and non-vascular plant data.—Within each quadrat, both vascular plant cover and litter cover were visually estimated as 0%, <10%, 10–25%, 25–50%, or >50% and plant number (number of individual plants) as 0, <5, 5–10, 11–20, or >20. Total crust cover i.e., cover of microphytic crust was estimated by one of us (DJE). Previous studies (Eldridge 1993) verified the accuracy of estimating cover in the field with a consistent observer. The relative proportion of lichen (lic%) and bryophytes (bry%) comprising the soil crust was also estimated.

Soil crust floristics—Samples of soil crust were collected from between two and four of the 10 quadrats at each site. The total number of soil crust collections varied according to landscape type and the variability of the soil crust community at the time of collection. At sites which were apparently devoid of surface crusts, only one sample was taken. Crust samples were transported to the laboratory, loose soil gently allowed to pass through a 2 mm sieve, and all bryophytes and lichens identified, generally to species level, using regional taxonomic keys in Filson (1988, 1992), Filson and Rogers (1979), McCarthy (1991*a*), Catcheside (1980), and Scott and Stone (1976), as well as more recent generic revisions. Two morphological groups of *Collema coccophorum* Tuck. were identified, based on thallus shape. Morphological group A is characterized by an occasionally lobed thallus with conspicuous cylindric isidia, whilst morphological group B has a rosette form with many distinct erect or prostrate lobes (Eldridge 1996). Nomenclature follows Streimann and Curnow (1989) for mosses, Scott (1985) for liverworts, McCarthy (1991*b*) for lichens, and where appropriate, more recent taxonomic revisions.

Analyses.—We used Canonical Correspondence Analysis (CCA, ter Braak 1986) to examine the relationships between the measured environmental variables and the distribution of bryophytes and lichens. CCA expresses species relationships as a linear combination of environmental variables, and combines the features of correspon-

TABLE 2. Biotic and abiotic environmental variables used in the Canonical Correspondence Analyses.

Variable	Code	Range of values	Description
slope	SLOPE	1–4	0% (1) to > 10% (4)
microtopography	MICRO	1–5	< 5 mm (1) to > 25 mm (5)
crust coherence	COHER	1–7	sand (1) to unbreakable (7)
surface cracking	CRACK	1–5	nil (1) to > 50% (5) cracking
surface stability	STAB	1–4	stable (1) to very unstable (4)
sheeting erosion	SHEET	1–5	nil (1) to > 50% (5) sheeting ero
eroded sand	SAND	1–5	nil (1) to > 50% (5) eroded sand
plant cover	PLANT	1–5	nil (1) to > 50% (5) cover
bryophyte composition	BRY%	0–100	composition (%)
lichen composition	LIC%	0–100	composition (%)
crust cover	CRUST	0–100	projected foliage cover (%)
rainfall	RAIN	< 200–> 450	annual rainfall (mm)
organic carbon	OC%	< 0.5–> 2.0	(%)
soil texture	TEXT	1–5	sand (1) to clay (5)
calcium carbonate	$CaCO_3$	1–5	nil (0) to abundant (4)
pH	pH	< 6.0–> 8.0	—
electrical conductivity	EC	< 0.01–> 0.30	dSm^{-1}

dence analysis ordination with canonical correlation analysis (Gittins 1985). CCA ordinates species data using axes that are constrained to be linear combinations of the environmental variables. This provides a graphical representation of the relationships between species and environmental variables.

A matrix of 505 rows (samples) by 88 columns (species) resulted from pooling the bryophyte and lichen data across a total of 282 sites. The data set contained a large number (>80%) of zero values. The number of species per sample ranged from 0 to 24, and the number of times a species was found in any one sample ranged from 1 to 318. To increase the clarity and simplicity of this data set, we excluded from the analyses samples containing ≤10 species, and species present in <25 samples. This diminished the influence of anomalous sites and rare and infrequent species, and resulted in a matrix of 130 samples by 39 species. The environmental data were similarly culled, producing a final subset matrix of 130 samples by 35 environmental variables. Bryophyte and lichen data sets were analysed separately.

Of the 35 environmental variables, 18 were omitted from the analyses. These were: degree of rilling, pedestalling, and scarping (all forms of micro-erosion); percentage of eroded gravel and eroded stone; the landscape element units: ridge, upperslope, midslope, lowerslope, flat, drainage line, and closed depression (all categorical variables); concentrations of calcium, magnesium, sodium, and potassium; plant litter and plant number. Plant litter and number were omitted because they were both highly and significantly correlated with plant cover (r^2 = 0.72 and 0.62 respectively). The other variables were omitted for one or more of the following reasons. Firstly, often more than 95% of observations for many variables fell into only one class, thus negating their usefulness as discriminators of species distribution. Secondly, other variables such as rilling and pedestalling produced very short vectors which, in the CCA biplots, were almost inconsequential, and their inclusion did not influence the relationship of the species to the environmental variables. Only those 17 environmental variables used in the final analyses are described in Tables 2, 4, and 5.

RESULTS

Distribution of species.—Among the 505 quadrats (282 sites) sampled, 48 bryophyte and 40 lichen species were identified. The reduced matrix of 130 quadrats (87 sites) by 39 species included 20 bryophytes and 19 lichens. These included 5 hepatics in 2 genera (*Riccia* and *Fossombronia*), 15 mosses in 12 genera, and 19 lichens in 12 genera. The lichen genera *Endocarpon, Catapyrenium* and *Peltula* represented 9 lichen species (Table 3).

Culling of the data had the effect of restricting the analyses to sites on calcareous plains (landscape unit 4) or non-calcareous plains (unit 5), and some footslopes (unit 2), ranges and hills (unit 1), and dunefields (unit 3) in the northwest of the survey area (Table 1). There were few sites from active (unit 7) or relict (unit 6) floodplains used in the analyses because they were poor sites; i.e., they supported few bryophyte or lichen species.

Description of sample sites.—Generally most samples included in the reduced data set came from moderately stable, non-eroding, non-cracking, highly coherent (i.e., hardsetting) soils on surfaces of low slopes (0–1%) and low (5–8 mm) microtopography (Table 4). The soils were generally characterized by low calcium carbonate and electrical conductivity levels, with pH ranging from 6.0 to 8.5. Sites were evenly distributed across all classes of plant cover and annual rainfall, and approximately 50% of samples had total crust cover levels >50% (Table 4). Some of the environmental variables were significantly correlated (Table 5). For example sand erosion was highly correlated with sheeting, and the significant negative correlation between annual rainfall and pH indicates that soil become more alkaline or calcareous as rainfall declines.

TABLE 3. Bryophyte and lichen species included in the analyses. Authorities follow Streimann and Curnow (1989) for mosses, Scott (1985) for liverworts, and McCarthy (1991 *b*) for lichens.

Code	Bryophyte
Acmu	*Acaulon muticum* complex
Alsu	*Aloina bifrons*
Baho	*Barbula hornschuchiana*
Brar	*Bryum argenteum*
Brpa	*Bryum pachytheca*
Crda	*Crossidium davidai*
Crge	*Crossidium geheebii*
Deco	*Desmatodon convolutus*
Dito	*Didymodon torquatus*
Fozz	*Fossombronia* spp.
Gire	*Gigaspermum repens*
Goen	*Goniomitrium enerve*
Phro	*Phascum robustum* var. *robustum*
Pobr	*Pottia brevicaulis*
Pozz	*Pottia* spp.
Rila	*Riccia lamellosa*
Ricr	*Riccia crinita*
Rili	*Riccia limbata*
Rini	*Riccia nigrella*
Stol	*Stonea oleaginosa*
Ctpi	*Catapyrenium pilosellum*
Ctsq	*Catapyrenium squamulosum*
Clzz	*Cladonia* sp.
Coca	*Collema coccophorum* morph. gp. A
Cocb	*Collema coccophorum* morph. gp. B
Dpth	*Diploschistes thunbergianus*
Enpa	*Endocarpon pallidum*
Enps	*Endocarpon pusillum*
Enrg	*Endocarpon rogersii*
Ensb	*Endocarpon simplicatum* var. *bisporum*
Ercr	*Eremastrella crystallifera*
Hede	*Heppia despreauxii*
Leoc	*Lecidea ochroleuca*
Pagl	*Paraporpidia glauca*
Pepa	*Peltula patellata* ssp. *australiensis*
Pezz	*Peltula* spp.
Psde	*Psora decipiens*
Sysy	*Synalissa symphorea*
Xazz	*Xanthoparmelia* spp.

Species-environment plots.—Separate analyses

TABLE 4. Distribution of the 17 environmental variables from the reduced matrix of 130 samples included in the CCA. Class ranges are given on the first line and the number of samples on the second line.

A. Slope (%)						
0	0–1	1–3	3–5	5–10	> 10	
3	116	10	1	0	0	
B. Microtopography (mm)						
< 5	5–8	8–15	15–25	> 25		
7	90	28	5	0		
C. Crust coherence (from 1 = sand to 7 = unbreakable)						
1	2	3	4	5	6	7
0	0	0	17	49	55	9
D. Surface cracking (%)						
0	< 10	10–25	25–50	> 50		
88	23	9	7	3		
E. Surface stability (from 1 = stable to 4 = very unstable)						
1	2	3	4			
29	93	8	0			
F. Bryophyte composition (%)						
0–25	26–50	51–75	76–100			
23	38	35	34			
G. Lichen composition (%)						
0–25	26–50	51–75	76–100			
59	42	21	8			
H. Crust cover (%)						
0–10	11–25	25–50	> 50			
9	19	38	64			
I. Sheeting erosion (%)						
0	< 10	10–25	25–50	> 50		
93	21	14	2	0		
J. Eroded sand (%)						
0	< 10	10–25	25–50	> 50		
98	23	8	1	0		
K. Plant cover (%)						
0	< 10	10–25	25–50	> 50		
9	28	30	36	27		
L. Surface soil texture (1 = sand to 5 = clay)						
1	2	3	4	5		
2	35	39	47	7		
M. Rainfall (mm)						
< 200	201–250	251–300	301–350	351–400	> 400	
5	42	24	34	23	2	
N. Organic carbon (%)						
< 0.5	0.5–1.0	1.0–1.5	1.5–2.0	> 2.0		
21	66	22	12	9		
O. Electrical conductivity (dS m^{-1})						
< 0.01	0.01–0.1	0.1–0.2	0.2–0.3	> 0.3		
4	85	31	7	3		
P. pH						
< 6.0	6.1–7.0	7.1–8.0	> 8.0			
37	39	29	25			
Q. Calcium carbonate content (0 = nil to 4 = abundant)						
0	1	2	3	4		
1	96	17	4	12		

TABLE 5. Correlation coefficients between the environmental variables. Only values significant at $p < 0.01$ are shown.

	Slope	Micro	Coher	Crack	Stab	Sheet	Sand	Plant	Bry%	Lic%	Crust	Rain	OC%	Text	Carb	pH	EC
Micro	0.281																
Coher	—	—															
Crack	—	—	0.301														
Stab	—	—	−0.282	—													
Sheet	—	—	—	—	0.446												
Sand	—	—	—	—	0.383	0.720											
Plant	—	—	—	—	—	—	−0.305										
Bry%	—	—	—	−0.265	—	—	—	0.242									
Lich%	−0.231	−0.247	0.301	0.297	—	—	—	−0.248	−0.638								
Crust	—	—	0.228	—	−0.361	−0.437	−0.375	—	—	—							
Rain	—	—	—	0.300	—	—	—	−0.342	—	—	—						
OC%	—	—	—	—	—	—	—	—	—	—	0.258	0.399					
Text	—	—	0.240	—	—	—	—	—	—	—	0.300	0.388	0.475				
$CaCO_3$	—	—	—	—	—	—	—	—	—	—	—	−0.297	—	—			
pH	—	—	—	−0.358	—	—	−0.251	0.427	0.336	−0.276	—	−0.647	—	—	0.534		
EC	—	—	−0.262	−0.253	—	—	—	0.338	0.319	−0.521	—	−0.274	0.393	—	0.354	0.471	

were performed on bryophyte and lichen data. The first three unconstrained ordination axes for bryophytes and lichens accounted for 32%, 13%, and 8% (total 53%), and 40%, 13%, and 12% (65%) respectively of the variation in species distributions. The species-environment biplots for bryophytes (Fig. 2) and lichens (Fig. 3) demonstrate the relationship between the 39 species and the 17 environmental variables. The length of the vectors indicates the relative importance of the variable in determining the axes, and the angle between an arrow and axis is an inverse measure of their correlation (ter Braak 1986).

For the bryophytes, total annual rainfall, soil pH, calcium carbonate levels, plant cover, and texture were strong determinants of Axis I. The second axis (II) was generally correlated with slope and organic carbon content of the soil, although other variables were also influential. For the lichens, rainfall, pH, calcium carbonate, and plant cover were determinants of Axis I, and sheeting and crust cover strongly influenced Axis II.

DISCUSSION

Few environmental variables represent simple unimodal gradients, and each may affect several primary determinants of species composition (John & Dale 1990). Plant cover for example probably influences light and nutrient availability, levels of litter, and is probably related to moisture availability, soil organic matter, and infiltration capacity.

In the present study, the CCA indicates the complex array of environmental variables correlated with the distribution of bryophytes and lichens in soil crusts in arid and semi-arid eastern Australia. Both lichens and bryophytes were most strongly associated with total annual rainfall, soil pH, and calcium carbonate levels (Figs. 2, 3). To a lesser extent, distribution of lichens was associated with sheet erosion, crust cover, and plant cover, and distribution of bryophytes was associated with plant cover, soil texture, and organic carbon levels of the soil. Although the species did not cluster into well-defined groups, loose arrangements of species can be identified which were associated in a similar way with the environmental variables.

Bryophytes.—The thallose liverwort *Riccia nigrella* (Rini), which occurred as an outlier on the CCA biplot (sector 2 of Fig. 2), tended to be associated with smooth surfaces (i.e., low microtopography), extensive sheet erosion, and sparse lichen-dominated soil crusts. Eroded surfaces, which also have sparse cover of vascular plants, are likely to have poor infiltration and hence high runoff rates. Species associated with bryophyte-dominant crusts and stable surfaces of high microtopography

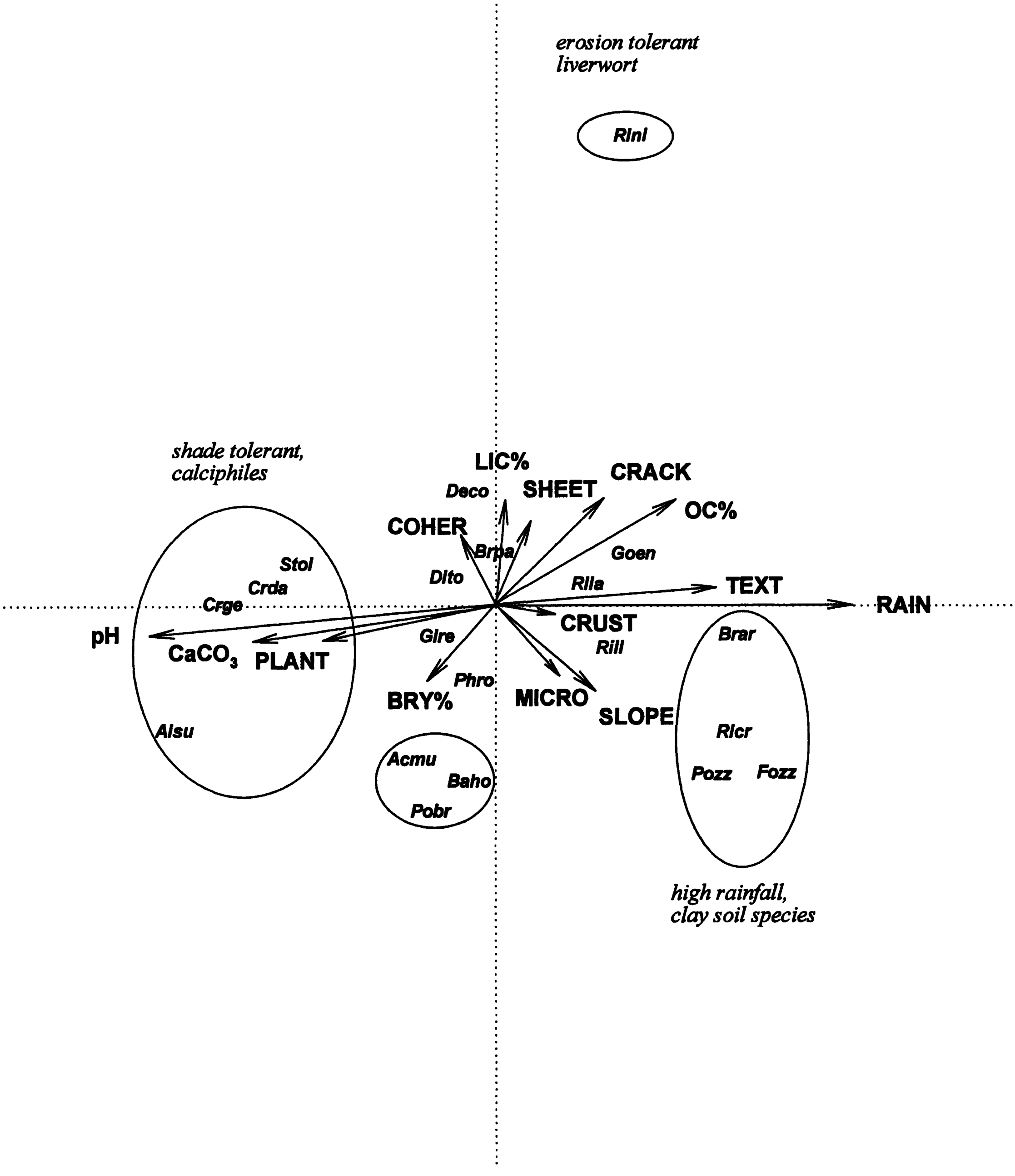

FIGURE 2. Species-environment biplots for axes I and II for the CCA for bryophytes. Vectors show the direction of maximum variation in the measured environmental variables. Vectors for stability, sand, and EC are obscured by other vectors and are omitted from the biplot for reasons of clarity. Species codes are given in Table 3.

are found in sector 4 of Fig. 2. These include the mosses *Pottia brevicaulis* (Pobr), *Pottia* spp. (Pozz) and members of the *Acaulon muticum* complex (Acmu). Surfaces which have high levels of microrelief have a greater capacity to trap and retain water (West 1990). These soils would therefore be likely to have moderate infiltration rates.

The mosses *Aloina bifrons* (Alsu), *Crossidium geheebii* (Crge), *Crossidium davidai* (Crda) and *Stonea oleaginosa* (Stol) are associated with calcareous loamy to sandy-loam soils characterized by an extensive cover of vascular plants (sectors 1 & 4 of Fig. 2). These surfaces would be expected to have higher levels of canopy interception by light, high litter levels, and therefore abundant populations of macroinvertebrates (Whitford 1996). De-

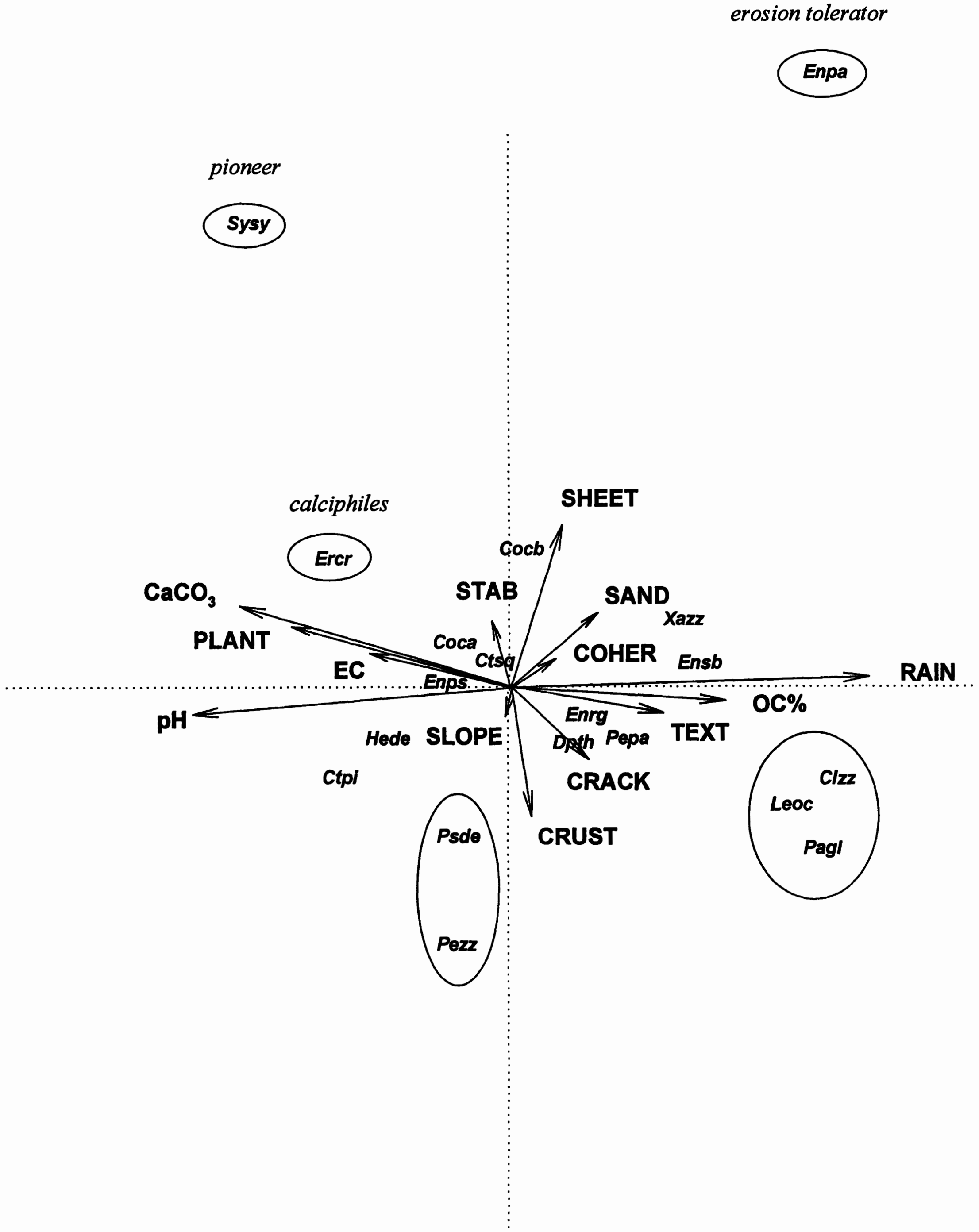

FIGURE 3. Species-environment biplots for axes I and II for the CCA for lichens. Vectors show the direction of maximum variation in the measured environmental variables. Vectors for microtopography, %lichen and %bryophyte are obscured by other vectors and are omitted from the biplot for reasons of clarity. Species codes are given in Table 3.

spite the low rainfall, the favorable soil physical properties and probably high levels of aggregation suggest that these surfaces would have moderately high infiltration rates. *Stonea oleaginosa* is common on landscapes dominated by sandy soils (Eldridge & Tozer 1996), and being small and having reddish-colored leaves and costa, is often inconspicuous among the large iron oxide-rich sand grains which it resembles (Stone 1978). The proposition that the mosses *Crossidium geheebii* and *Aloina bifrons* are often found in similar environments (Catcheside 1980) is supported by the CCA, which suggests that they have similar biotic and abiotic preferences, in particular, rainfall and pH levels. As a group, these mosses are generally found on calcareous soils in association with a moderately dense cover of forbs and perennial grasses, and could therefore be broadly termed shade-tolerant calciphiles. Their position away from the crust cover vector indicates that they are less likely to be found closely associated with areas of continuous soil crusts, but more likely in small more isolated tufts. Furthermore, the group's position in relation to the bry% vector indicates that where sparse and discontinuous areas of soil crust exist, crusts are likely to be dominated by bryophytes.

Within sector 3 of Figure 2 are the liverworts *Fossombronia* spp. (Fozz) and *Riccia crinita* (Ricr), the mosses *Pottia* spp. (Pozz) and the cosmopolitan moss *Bryum argenteum* (Brar) which tend to be associated with clay soils of enhanced organic carbon, on sites of higher annual rainfall. Distributional data (Eldridge & Tozer 1996) confirm that these species are common in the eastern fringe of the survey area where rainfall is greater, often on cracking clays. The liverworts (*Riccia* spp. *Fossombronia* spp.) separate along a continuum of slope–microtopography–surface coherence. The CCA biplot suggests that *Riccia nigrella* (Rini) favors moderate hardsetting and flat surfaces of low slopes, whereas *Riccia crinita* (Ricr) and *Fossombronia* spp (Fozz) favor cracking sites on relatively higher slopes with a greater development of soil microrelief. *Riccia nigrella* and *Fossombronia* spp. have different strategies for surviving in an arid environment. *Riccia nigrella* is typical of a group of thallose liverworts which have large plate-like scales along their ventral surfaces. As the plant dries out the sides of the thallus curl inwards, drawing the densely-pigmented scales over the green photosynthetic surface, protecting it from high light and temperature levels which would result in desiccation (Scott 1982). This enables these plants to survive in relatively open areas. Although *Fossombronia* is a thallose liverwort, it is distinctly leaflike in appearance, and lacks the characteristic scales of the *Riccia* spp. Instead it relies on anthocyanin-pigmented leaves to shield it from scalding by the sun (Scott 1985), or avoids desiccation by growing in favored microsites such as in drainage lines or under rock ledges which receive supplementary water.

Lichens.—Sites characterized by high rainfall, high levels of organic carbon, low pH (and hence low calcium carbonate levels), and surprisingly, sparse vascular plant cover occur in sector 3 of Figure 3. These sites are likely to have enhanced levels of soil aggregation, due to a combination of finer soil textures and higher rainfall, and probably support an active soil macroinvertebrate population (Whitford 1996). Their position along the texture and rainfall vectors suggests that these sites occur predominantly in the eastern sections of the study area. The dominant lichens in this sector are *Paraporpidia glauca* (Pagl), *Cladonia* sp. (Clzz), and *Lecidea ochroleuca* (Leoc), and their positions in relation to sites of sparse plant cover probably relate to competition for light and nutrients. In a semi-arid woodland dominated by *Callitris glaucophylla,* Eldridge (1996) found that sterile *Cladonia* sp. squamules favored sites either in the open or under trees where competition for light and moisture precludes a strong cover of vascular plants. Similarly at Koonamore Vegetation Reserve in South Australia, sterile *Cladonia* sp. squamules were found predominantly in bare microsites under trees (Rogers 1974).

In sector 1 of Figure 3 is the pioneering lichen *Synalissa symphorea* (Sysy) which is associated with sites of low rainfall, low organic carbon, high pH, sandy soils, extensive plant cover, and relatively smooth non-cracking soil surfaces. *Synalissa symphorea* is an inconspicuous and ubiquitous lichen on semi-arid soils, and is often the only lichen occurring in degraded and recovering sites where crust cover is sparse (Filson & Rogers 1979), hence its position in the opposite direction to the crust vector in Figure 3. Along with the lichens *Heppia despreauxii* (Hede) and *Collema coccophorum* (Coca/Coab) which are also cyanolichens and therefore capable of nitrogen fixation, they are primary colonizers, occurring in disturbed or degraded sites, or areas of poor nitrogen status. The distribution of *Eremastrella crystallifera* (Ercr) is strongly tied to soils of high pH, hence its position on the calcium carbonate axis. In the study area, specimens were restricted almost exclusively to highly calcareous soils (pH > 9.0) in the far southwestern corner of the state (Eldridge 1996).

Peltula spp. (Pezz) and, to a lesser extent, *Psora decipiens* (Psde) are the dominant lichens on surfaces characterized by highly developed crust cover, sparse sheet erosion, and extensive cracking (sector 4, Fig. 3). Greater crust cover means that these surfaces have an increased capacity to trap and retain water. Soils would therefore have moderate infiltration rates, despite high values of slope (up to 5%). Cracking surfaces are thought to increase sites for lodgement of vascular plant seeds by providing entry points for seeds lacking structures such as awns, and may enhance water availability for growing vascular plants (St Clair et al. 1984). The association of these species on the crust cover vector suggests that they are more likely to be found as components of well-developed crusts than as isolated individuals. Extensive crust cover is associated with more stable sites in terms of water erosion (Eldridge & Greene 1994*a*; Eldridge & Kinnell 1997) and eroded material is likely to be dominated by coarse sediments rather than fine silts and clays (Eldridge & Greene 1994*b*).

Sites with sparse crust cover and extensive sheet erosion are located in sector 2 of Figure 3. The dominant species in this quadrant is *Endocarpon pallidum* (Enpa) which is common on hardsetting red earth soils (Eldridge 1996). The association of this lichen with sites of low crust cover is supported by field evidence that suggests that these lichens typically occur as isolated individuals. Overgrazing leads to increased soil surface compaction producing surfaces which are physically crusted and hardsetting, and which have low infiltration rates (Greene et al. 1994). These hardsetting sites are often associated with reduced levels of essential soil nutrients such as nitrogen and phosphorus (Tongway & Ludwig 1990). Reduced soil microrelief suggests that there is little opportunity for water to pond on the surface. Any ponded water would probably be either shed as runoff, or lost through evaporation due to the low infiltration rates.

Although the CCA indicated some strong correlations between the distributions of species and the environmental variables, other factors may be equally important. For example, the small scale variability in soil pH or calcium carbonate may affect bryophyte and lichen distribution. Similarly, other unmeasured microhabitat variables such as aspect, insolation, light intensity, micro-infiltration, soil porosity, soil moisture, and soil fertility (e.g., nitrogen and phosphorus levels) may account for much of the unexplained variation in bryophyte and lichen distribution. Dispersal limitations and competition may also be important.

Soil crust bryophytes and lichens in semi-arid eastern Australia are correlated with a complex array of factors related to the status of the soil surface and the vascular plant community. Land management practices such as grazing, burning, clearing, and cultivation which impact upon these factors are likely to lead to changes in the distribution of these species and ultimately to changes in soil stability, soil hydrology, and soil fertility.

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