

Dynamics of cryptogamic soil crusts in a derived grassland in south-eastern Australia

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Abstract We examined the dynamics of cryptogamic soil crusts in a derived (disclimax) grassland near Orange in south-eastern Australia. Changes in the cover of cryptogamic crusts and floristics and abundance of the constituent species were measured on four treatments with two levels each of grazing and cultivation. Twenty-two lichens, mosses and liverworts were found at the study site and, of these, 13 were collected in the quadrats. Three moss species (*Barbula calycina*, *Eccremidium arcuatum* and *Bryum pachytheca*) and one lichen species (*Cladonia tessalata*) accounted for 67% of total cover-abundance scores. Generally, cover-abundance was significantly higher in the unvegetated microsites than in the vegetated microsites. Species richness was not significantly different between the four grazing-cultivation treatments but, on average, there were significantly more species in the unvegetated microsites (mean = 3.2 species) than in the vegetated microsites (0.54 species). Grazing and cultivation resulted in significantly greater cover of bare ground and consequently significantly greater crust cover. Averaged across all treatments, approximately half of the area of unvegetated soil was occupied by cryptogams. Overall, the results indicate that lichens and bryophytes are important components of derived temperate grasslands, surviving in even densely vegetated swards. This study suggests that strategies which disturb the soil surface (e.g. grazing and cultivation) will stimulate the abundance and cover of soil crust organisms by increasing the availability of unvegetated microsites.

Key words: cryptogams, derived grasslands, grazing, lichens, mosses, soil crusts.

INTRODUCTION

Cryptogamic crusts and their constituent organisms are common in semiarid and arid areas of Australia (Rogers & Lange 1972; Eldridge 1996; Eldridge & Tozer 1997; Hodgins & Rogers 1997). Soil crusts are complex associations of mosses, lichens, liverworts, cyanobacteria, fungi and bacteria that are intimately bound onto surficial soils (Eldridge & Greene 1994). Crusts, which are often referred to as microphytic or cryptobiotic crusts, stabilize the soil surface against water and wind erosion (Williams *et al.* 1995; Eldridge & Kinnell 1997) and influence water flow across the landscape (Yair 1990; Eldridge *et al.* 1997). Many organisms in the crust can fix atmospheric nitrogen (Belnap *et al.* 1994) and sequester carbon dioxide directly from the atmosphere, storing it as soil organic carbon (Beymer & Klopatek 1993). Crusts also provide a habitat for soil animals (Scarlett 1994) and influence the germination of vascular plants (Zaady *et al.* 1997).

Soil bryophytes and lichens are common compo-

nents of native pastures in the humid and subhumid, as well as the arid and semi-arid rangelands of Australia (Scott *et al.* 1997). Despite occasional references that cryptogams are found in woodlands, forests and non-arable areas with low fertility soils (Scott & Stone 1976; Scott 1985; Downing *et al.* 1991, 1997; Downing 1992; Streimann 1994), there are few studies of soil lichens and bryophytes in humid and temperate native pastures of eastern Australia. This is not surprising given their generally small size, cryptic nature and the fact that a microscope is often required for their identification (Eldridge & Tozer 1996a).

One such area in eastern Australia is the 'Burrendong Country' in central western New South Wales (Vivers 1997). This area traverses two of Anderson's (1968) botanic subdivisions: the central tablelands (with an elevation of >650 m and a humid climate) and the subhumid central western slopes. Infertile, generally acidic, podzolic and solodic soils (Kovac *et al.* 1990) predominate on the undulating to steep landscape. Although the area still retains much of its tree cover, large areas of woodland and forest have been cleared, resulting in soil erosion, particularly along drainage lines, and an increase in the frequency

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of some native shrubs such as *Cassinia arcuata* R. Br. Shrub increase is thought to be a consequence of low fertility soils, the presence of bare ground and the absence and/or poor growth of herbaceous competitor species (Campbell 1990; Semple 1990). Cleared areas now support derived shrublands or grasslands. Grazing rates are low, ranging from 0.6 dry sheep equivalents (DSE) per hectare on *Cassinia arcuata* shrublands (Campbell 1990) to 2–5 DSE/ha on hilly country (Stackman 1997; Vivers 1997). Areas lacking vascular plant cover but often with cryptogams are common, though cryptogams are not highly regarded by graziers (Savory 1988). Stackman (1997), for example, in describing a change in land management from continuous to rotational grazing, reported that ‘most of the bare areas are first colonised by annuals such as vulpia and brome which is a good deal more useful than moss and lichen.’

The aim of the work reported here was to examine the influence of disturbance on the dynamics of a soil crust community in a derived grassland in south-eastern Australia. Specifically, we measured crust cover, richness and cover-abundance of crust species in order to assess the impact of various combinations of grazing and cultivation on the dynamics of lichen and bryophyte crusts. The work reported here forms part of a larger study aimed at understanding more about the impacts of grazing and exclosure on the botanical composition of derived grasslands.

Study area and trial design

The study area is located near Kerrs Creek, approximately 30 km north of Orange, New South Wales

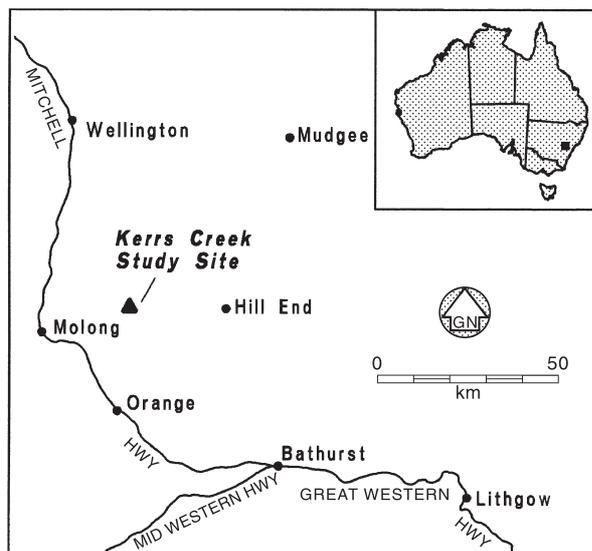


Fig. 1. Location of the Kerrs Creek study area in south-eastern Australia.

(33°01'16'' S, 149°08'23'' E, Fig. 1). It is located within the temperate humid zone of Australia, has a mean annual rainfall of ~780 mm, and an altitude of ~700 m. The site has a westerly aspect with a slope of 10% and supports a derived grassland dominated by the native perennial grasses *Bothriochloa macra* (Steud) S.T. Blake and *Danthonia eriantha* Lindl. The slightly acidic (pH = 6.0) fine sandy loam topsoil is underlain by clay and is typical of red podzolic soils in this locality (Kovac *et al.* 1990).

Domestic and feral animals were excluded from the site in September 1991 for a pasture manipulation experiment involving the effect of cultivation on pasture cover and composition (Semple *et al.* 1997). A cultivation treatment was applied once in September 1991 using a rotary hoe. The size of the exclosure was halved in May 1995 when four blocks of treatments were reopened to grazing. By June 1997 (5.75 years after initial treatment and exclosure), there appeared to be a strong association between the levels of bare soil surface and cryptogam cover within the various levels of disturbance. The two treatments (cultivated and uncultivated control) that had been exclosed for the full 5.75 years (ungrazed control), together with the same treatments that had been reopened to grazing after 3.75 years (grazed), were selected for a detailed examination of groundcover components.

Trial design

The layout of the current trial followed a multistratum incomplete block design. The 16 selected plots were arranged in a 4 × 4 grid on the side of a hill, with plots within blocks running along the contour, and blocks placed down the hillslope to accommodate any potential spatial variation (Fig. 2). Each plot measured

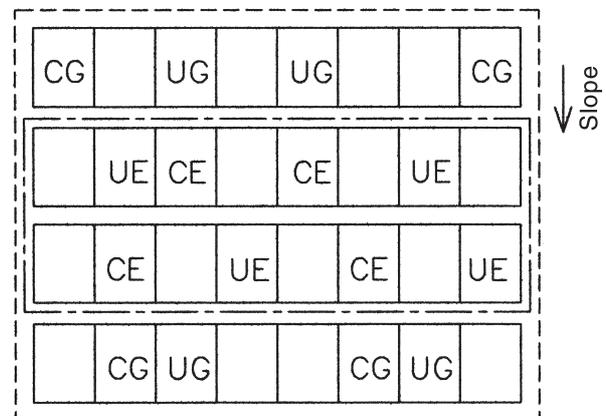


Fig. 2. Layout of the plots at the study site at Kerrs Creek in eastern Australia. UE, uncultivated and exclosed; CE, cultivated and exclosed; UG, uncultivated then grazed; CG, cultivated then grazed. ---, exclosed September 1991 to May 1995; — — —, exclosed since September 1991.

5 m × 2.8 m. As a consequence of the design of an earlier more detailed experiment (Semple *et al.* 1997), the four treatments were arranged in pairs of uncultivated excluded (UE)–cultivated excluded (CE) and cultivated grazed (CG)–uncultivated grazed (UG), thereby forming four incomplete blocks with two replicates of two of the treatments (Fig. 2).

METHODS

Groundcover measurements on treatment plots

Ground cover on each of the 16 plots was assessed in June 1997 using two throws of a 2 m × 0.5 m quadrat frame containing 100 points. Duplicate measurements were made in each plot. Cover was assessed as either 'vegetated' (i.e. where the soil surface was covered by live or dead vascular plants, which were mainly grasses) or 'unvegetated' (i.e. where the soil surface was exposed or covered by cryptogams).

Composition, species abundance and cover of cryptogams and size and shape of patches

All measurements reported in this paper were made in June 1997. We laid out a 5.7-m transect along the diagonal of each of the 16 plots and chose the closest patch of unvegetated soil to each of five randomly assigned locations along this transect. As unvegetated patches varied greatly in size, ranging from <1 cm² to many tens of square centimetres, we restricted our selection of patches to those with an area >18 cm² and which supported neither vascular plants nor litter. We repeated this procedure on the nearest patch of ground, within 10 cm of each unvegetated patch, in a predetermined direction, which had >90% cover of vascular plants. This procedure resulted in five paired locations per plot, with each pair comprising a vegetated and unvegetated surface.

Small cores of area 4.2 cm², containing soil and associated crust organisms, were carefully extracted from the centre of each of the 10 patches using a coring device. With this procedure, 20 vegetated and 20 unvegetated cores were collected from each of the four treatments, giving a total of 160 cores, henceforth known as 'quadrats'. Simultaneously on the unvegetated microsites only, the area of each patch was measured and its shape described as either circular, square, rectangular or irregular/linear shaped. Generally, linear shaped patches were twisted and convoluted with relatively small width : length ratios.

Cores of detached soil were carefully removed from the coring device and observed under a dissecting microscope at low magnification. The small size of the quadrats (4.2 cm²) allowed an assessment of crust cover

and composition within the field of view of the microscope. Within each quadrat, cover-abundance of all crust species was measured using a modified Braun–Blanquet (Poore 1955) technique on a scale of 1–7, where 1 = cover <25% and less than five individuals, 2 = cover <25% and six–25 individuals, 3 = cover <25% and 25–50 individuals, 4 = cover <25% and >50 individuals, 5 = cover 25–50%, 6 = cover 50–75%, 7 = cover >75%. A pilot trial, undertaken to calculate species area curves for the site confirmed that five quadrats was sufficient to sample more than 90% of the species present. Species diversity (α -diversity) was calculated as the number of species present within a treatment (Whittaker 1977). The proportion of the surface occupied by moss, lichen and cyanobacteria and the percentage of each quadrat occupied by truly bare soil (i.e. devoid of any cyanobacteria or non-vascular plants) was estimated under the microscope.

Lichens and bryophytes were identified using keys published in Scott & Stone (1976), Filson & Rogers (1979), Catcheside (1980), Filson (1988, 1992) and McCarthy (1991a), as well as more recent generic revisions. Nomenclature followed Streimann & Curnow (1989) for mosses, Scott (1985) for liverworts, McCarthy (1991b) for lichens and, where appropriate, more recent taxonomic revisions.

Data analyses

Data were averaged across the five locations in each of the vegetated and unvegetated microsite units resulting in 32 data units (16 plots by two microsites) for each variable of interest. Statistical analyses of species abundance data were performed using the residual maximum likelihood (REML) directive in Genstat (Payne *et al.* 1993). The block strata definitions were defined for four incomplete blocks, two treatment repeats within blocks and the splitting of plots for microsites. The treatment design allowed for a factorial combination of treatments and microsites. Significant differences between treatment levels and microsites were tested using Wald statistics, assuming a χ^2 distribution, at $P = 0.05$ level of probability, having made logarithmic transformations when necessary to stabilize the variance of treatment means.

Some species which had numerous zero-count data, especially those in the vegetated microsites, were only analysed for differences between treatments. Where appropriate, a relative comparison between microsites was made by comparing the average cover-abundance from the unvegetated sites with the constant zero, a figure very close to the average abundance on the vegetated sites. Similar conclusions were drawn whether we used a Student's *t*-test or a one-sample sign test of the median being different to zero.

RESULTS

Three lichen species, seven moss species and three liverwort species were found within the 160 quadrats and a further six lichen species and three moss species were found in the plots after intense searching (Table 1). Additionally, the lichens *Cladia aggregata* (Sw.) Nyl., *Heppia* sp. and *Heterodea beaugleholei* R. Filson, and the liverwort *Riccia blackii* Na-Thalang, were found adjacent to the study plots.

Three moss species and one lichen species each comprised more than 10% of the total cover and abundance values: *Barbula calycina* (30.4%), *Eccecidium arcuatum* (15.8%), *Bryum pachytheca* (10.1%) and *Cladonia tessalata* (10.8%), respectively (Table 1). The lichens *Endocarpon simplicatum* var. *bisporum* (7.0%) and *Lecidea ochroleuca* (6.9%), made a moderately high contribution to total cover and abundance and along with *Cladonia tessalata* were found in plots from at least three treatments.

The lichen component of the soil crust consisted of squamulose and crustose species. Mosses were dominated by members of the family Pottiaceae (*Barbula calycina*, *Didymodon torquatus*, *Phascum* sp. and *Triquetrella papillata*, which are relatively small, cryptic, dry area species; Zander 1993). *Phascum* sp. and *Triquetrella papillata*, although contributing relatively

little to total cover and abundance (4.9 and 5.5%, respectively), were present on all treatments. The liverworts contributed little to total cover and abundance (Table 1).

Species richness in relation to microsite and treatment

Sufficient non-zero data existed to allow us to examine the effect both of treatment and of microsite for only one variable (total number of species: α -diversity) and two species (*Barbula calycina* and *Bryum pachytheca*).

There was no significant difference in species diversity (α -diversity) nor in abundance of any species among treatments (Table 2). On average, there were significantly more cryptogam species in the unvegetated microsites (mean = 3.2 species) than in the vegetated microsites (0.54 species; $\chi^2_1 = 236$, $P < 0.001$). Cover-abundance of *Barbula calycina* and *Bryum pachytheca* was significantly greater in the unvegetated microsites than in the vegetated microsites ($\chi^2_1 = 120$, $P < 0.001$ and $\chi^2_1 = 20.6$, $P < 0.001$, respectively; Table 3). For the remaining 11 species, the majority of mean cover-abundance data in the vegetated microsites were zero, thus preventing us from testing for statistically significant differences between microsites (though clearly

Table 1. Presence of species within each of the four treatments, and the percentage of total cover and abundance contributed by each species in cryptogamic soil crusts in a derived grassland in south-eastern Australia. Refer to the text for descriptions of the treatments. ϕ = Species found outside the 160 quadrats but present within a treatment and therefore no measurement of cover and abundance

Species	% total cover-abundance	Treatment			
		UE	CE	CG	UG
Lichens					
<i>Cladonia tessalata</i> Ahti & Kashwadani	10.8	*	*	*	*
ϕ <i>Collema</i> sp. aff. <i>coccophorum</i>					ϕ
ϕ <i>Diploschistes muscorum</i> ssp. <i>bartlettii</i> Lumbsch					ϕ
<i>Endocarpon simplicatum</i> (Nyl.) Nyl. var. <i>bisporum</i> P. McCarthy	7.0	*	*	*	*
ϕ <i>Heterodea muelleri</i> (Hampe) Nyl.				ϕ	
<i>Lecidea ochroleuca</i> Pers.	6.9		*	*	*
ϕ <i>Neofuscelia</i> sp.					ϕ
ϕ <i>Trapelia coarctata</i> (Sm.) Choisy					ϕ
ϕ <i>Xanthoparmelia reptans</i> (Kurokawa) Elix & Johnston				ϕ	
Mosses					
<i>Barbula calycina</i> Schwaegr.	30.4	*	*	*	*
ϕ <i>Barbula crinita</i> Schultz		ϕ			ϕ
<i>Bryum argenteum</i> Hedw.	< 1		*	*	
ϕ <i>Bryum campylothecium</i> Tayl.			ϕ		
<i>Bryum pachytheca</i> C. Muell.	10.1	*	*	*	*
ϕ <i>Didymodon torquatus</i> (Tayl.) Catches.					ϕ
<i>Eccecidium arcuatum</i> (Hook. & Wils.) C. Muell.	15.8	*	*	*	*
<i>Fissidens aeruginosus</i> (Hook. f. & Wils.) var. <i>arcuatulus</i> I. G. Stone	2.7		*	*	*
<i>Phascum</i> sp.	4.9	*	*	*	*
<i>Triquetrella papillata</i> (Hook. f. & Wils.) Broth.	5.5	*	*	*	*
Liverworts					
<i>Asterella drummondii</i> (Hook. f. & Tayl.) R. M. Schuster	< 1	*			*
<i>Fossombronina microlamellata</i> G.A.M. Scott & D. C. Pike	< 1	*		*	*
<i>Lethocolea squamata</i> (Tayl.) A. Hodgson	4.0	*		*	*

Table 2. Average species diversity (α -diversity), total number of species, coverage of bare soil and cryptogams in each of the four treatments in cryptogamic soil crusts in a derived grassland in south-eastern Australia. Average α -diversity is calculated as the mean number of species per quadrat pooled across the 40 quadrats (cores) in each treatment. SED, standard error of the difference; SEM, standard error of the mean. Different letters within a column indicate a significant difference at $P < 0.05$

Treatment	Treatment code	α -diversity		Ground cover (%)			
		Average	Total no. of species	Nil (bare soil) mean	SEM	Cryptogam-covered soil mean	SEM
Uncultivated with enclosure	UE	1.73	10	0.5 ^a	0.09	0.6 ^a	1.14
Cultivated with enclosure	CE	1.55	10	1.0 ^a	0.21	1.3 ^a	0.19
Cultivated then grazed	CG	2.20	12	10.4 ^b	1.33	12.1 ^b	1.14
Uncultivated then grazed	UG	1.98	14	5.9 ^c	0.99	5.2 ^c	0.84
		SED = 0.51					

Table 3. Average cover-abundance of lichen and bryophyte species on unvegetated and vegetated microsites in cryptogamic soil crusts in a derived grassland in south-eastern Australia. Numbers in parentheses are the number of non-zero data available to calculate the mean. Superscripts indicate insufficient data to allow testing of ^amicrosite effects or ^btreatment effects; ^ctest (t_{15}) that the mean cover-abundance on the unvegetated site is different to zero

Species	Type	Mean cover-abundance		P-value		t_{15}^c
		Unvegetated	Vegetated	Microsite	Treatment	
<i>Barbula calycina</i>	Moss	3.07 (16)	0.35 (12)	< 0.001	> 0.05	
<i>Bryum pachytheca</i>	Moss	0.89 (12)	0.24 (8)	< 0.001	> 0.05	
<i>Cladonia tessalata</i>	Lichen	1.18 (15)	0.04 (1)	^a	> 0.05	< 0.001 ^c
<i>Endocarpon simplicatum</i> var. <i>bisporum</i>	Lichen	0.79 (12)	0.00 (0)	^a	> 0.05	< 0.001 ^c
<i>Ecclremidium arcuatum</i>	Moss	1.71 (15)	0.06 (1)	^a	> 0.05	< 0.001 ^c
<i>Fissidens</i> sp.	Moss	0.25 (7)	0.00 (2)	^a	> 0.05	0.013 ^c
<i>Lethocolea squamata</i>	Liverwort	0.50 (6)	0.00 (0)	^a	> 0.05	< 0.019 ^c
<i>Phascum</i> sp.	Moss	0.45 (10)	0.05 (2)	^a	> 0.05	0.002 ^c
<i>Triquetrella papillata</i>	Moss	0.49 (9)	0.11 (4)	^a	> 0.05	0.013 ^c
<i>Asterella drummondii</i>	Liverwort	0.04 (3)	0.00 (0)	^a	^b	
<i>Bryum argenteum</i>	Moss	0.04 (2)	0.00 (0)	^a	^b	
<i>Fossombronia microlamellata</i>	Liverwort	0.05 (3)	0.00 (0)	^a	^b	
<i>Lecidea ochroleuca</i>	Lichen	0.28 (6)	0.00 (0)	^a	^b	

trends were similar to that of *Barbula calycina* and *Bryum pachytheca*).

There were no significant treatment effects for the species *Barbula calycina* and *Bryum pachytheca* (Table 3). For the other 11 species, we examined treatment effects for the unvegetated microsites only, as the mean cover-abundance for the vegetated sites was close to or equal to zero. For seven of these species there were no treatment effects (Table 3). The extremely low number of plants of the remaining four species: *Asterella drummondii*, *Bryum argenteum*, *Fossombronia microlamellata* and *Lecidea ochroleuca*, and therefore the large number of zero values, meant that we could not examine treatment effects for these species.

Proportions of bare soil and crust cover

Averaged across both the vegetated and the unvegetated microsites, and adjusted for vascular plant cover measured on the plots at the time of observations,

there were significant treatment effects on ground cover ($\chi^2_3 = 164.0$, $P < 0.001$) for cryptogam cover. Cryptogam cover on the CG plots was significantly greater than that on the UG plots, which was significantly greater than that on plots which had been excluded (UE and CE; Table 2).

At the level of an individual quadrat (soil core), total cover of cryptogams (moss + lichen + cyanobacteria) was significantly greater on the unvegetated quadrats (mean \pm SEM = $55.1 \pm 3.3\%$) compared with the vegetated quadrats ($4.4 \pm 1.2\%$; $\chi^2_1 = 158$, $P < 0.001$). Increases in crust cover at the quadrat scale were associated with a greater number of crust species ($F_{1,158} = 269.06$, $P < 0.001$, $R^2 = 0.628$; Fig. 3).

Size and shape of unvegetated patches

Analysis of microsites from which the unvegetated quadrats were taken ($n = 80$) revealed a significant difference between treatments for the \log_{10} mean area

Table 4. The total area of bare surfaces corresponding to quadrat locations and the frequency of round, rectangular and linear-shaped areas in cryptogamic soil crusts in a derived grassland in south-eastern Australia. SEM, standard error of the mean. Different letters within a column indicate a significant difference at $P < 0.05$

Treatment	Microsite area (mm ²)		Class frequency (%)		
	mean	SEM	Circular	Rectangular	Linear
Uncultivated with enclosure (UE)	40.7 ^a	8.1	40	35	25
Cultivated with enclosure (CE)	34.6 ^a	7.3	55	15	30
Cultivated then grazed (CG)	359.0 ^b	110.0	30	10	60
Uncultivated then grazed (UG)	101.3 ^{ab}	14.9	30	5	65

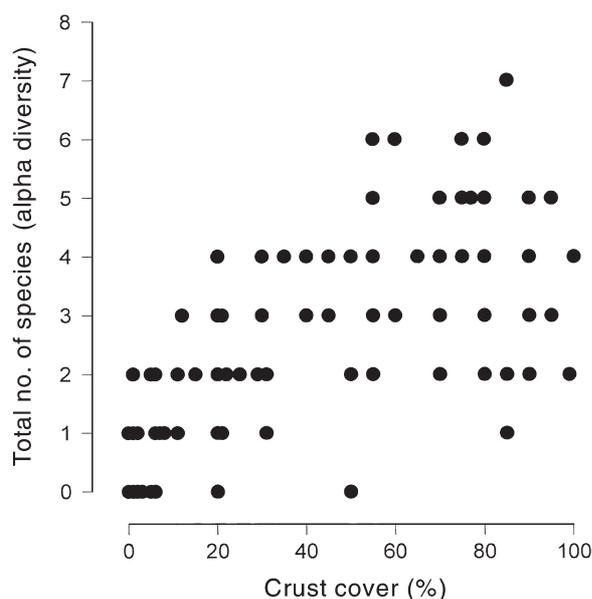


Fig. 3. Scatterplot of species diversity (α -diversity) in relation to crust cover.

of the unvegetated surface ($\chi^2_3 = 27.7$, $P < 0.001$). Mean area of unvegetated microsites was four- to 10-fold greater on the CG treatment than with the other treatments (Table 4). Further, the unvegetated patches tended to become irregular or linear-shaped as their size increased (Table 4). Smaller, unvegetated patches tended to be circular-shaped rather than linear, probably reflecting the growth habit of grass clumps as they enlarge and coalesce.

DISCUSSION

In the Kerrs Creek study, lichens and bryophytes were a significant component of the ground flora and significant trends were apparent across quadrats and treatments (Tables 1–3). Although not floristically rich, lichens and bryophytes were found on all surfaces, either vegetated or unvegetated, and greater crust cover was associated with grazed plots.

Across all treatments, cryptogam species from the vegetated microsites accounted for <5% of the total

cover-abundance scores, although most species had at least one occurrence in a grassed microsite. The mosses *Barbula calycina* and, to a lesser extent, *Eccremidium arcuatum* and *Bryum pachytheca*, contributed about half of the total cover-abundance scores in the vegetated sites. Cover-abundance scores for individual species were always greater in the unvegetated microsites compared with the vegetated microsites (Table 3).

The general absence of cryptogamic species from the vegetated sites may relate to competition for light and moisture (Richardson 1981) and although little is known about threshold requirements for light and moisture for individual species, cryptogams are generally regarded as being poor competitors for resources. Germination of spores, and elongation of protonema are light-dependent (Richardson 1981). Protonema, the branched filamentous tissue formed on germination of a spore or on regeneration from a propagule (Catcheside 1980), were frequently recorded from quadrats within vegetated areas, suggesting that penetration of light was not limiting in all grass swards.

In our study we found a relatively strong relationship between α -diversity and the proportion of the bare soil covered by crust (Fig. 3), with increases in the area of crusted soil associated with increased diversity. Larger patch size is likely to create greater opportunities for establishment of cryptogams by providing a greater number and variety of regeneration niches (Grubb 1977), thereby favouring a variety of life strategies. This could have occurred through enhanced environmental heterogeneity producing niches suitable for colonization by a range of species reproducing either sexually by spores, or vegetatively by fragments, buds or gemmae (e.g. *Bryum* spp.). One species, *Triquetrella papillata*, was found both on unvegetated surfaces and in dense grass swards. In semi-arid environments such as the Riverine Plain of south-eastern Australia, it occurs under *Atriplex vesicaria* Heward ex Benth. and *Maireana pyramidata* (Benth.) P.G. Wilson shrubs in niches of reduced light intensity but, at the nearby Cocoparra Ranges, forms large mats in the open where light levels are high (D. J. Eldridge, 1999, personal observation). Like *Barbula calycina*, this moss has a wide ecological niche, being able to exploit a variety of habitats.

Role of disturbance

Although there are some studies describing disturbance effects on lichens and bryophytes (including soil-borne forest species; Pharo & Beattie 1997), we know of no studies documenting the relationships between grazing-induced disturbance and soil crust communities in humid and temperate areas of Australia. In the arid and semi-arid rangelands of Australia, Rogers (1977) and Hodgins & Rogers (1997) showed how grazing eliminated lichens, bryophytes and cyanobacteria from areas close to watering points and Eldridge & Bradstock (1994) showed how even a single fire in mallee communities leads to a general loss in crust cover and floristics. European studies, however, indicate that some crust species such as the lichen *Cladonia* and the mosses *Bryum*, *Funaria* and *Ceratodon* spp. tend to be disturbance tolerant (see the terms 'colonists' and 'competitive perennials' of Rogers 1990 and During 1992). Fire, like cultivation and grazing reduces competition from vascular plants and studies involving artificially weeding plots of grasses demonstrated marked increases in the cover and vigour of mosses (Richardson 1981). Studies in Saskatchewan, Canada, revealed a marked decline in floristics and cover of soil lichens and mosses after exclosure (Looman 1964). These and similar studies in Canada demonstrate that after prolonged exclosure, only *Cladonia* spp. are capable of coexisting with dense perennial vegetation.

In our study, disturbance increased the amount of bare ground and, consequently, the cover of cryptogams (Table 2). This disturbance was largely due to grazing, though the residual effect of cultivation combined with grazing lead to increased bare ground and therefore greater cryptogam cover. As a result, cryptogam cover was significantly greater on the CG plots (12.1%) than on the UG plots (5.2%) and was significantly reduced on the exclosed plots (UE and CE) (mean = 1.0%; Table 2).

In the present study, *Cladonia tessellata* was recorded from all sites, and accounted for 11% of total cover-abundance scores (Table 1). *Cladonia* spp. have widespread continental distributions in the Northern and Southern Hemispheres (Archer 1992) and commonly exist in two morphological forms which employ markedly different reproductive strategies. In areas of higher rainfall, *Cladonia* spp. possess podetia, within which the spores are produced, enabling them to reproduce sexually. In dry areas, however, they rarely possess podetia and consequently rely on vegetative reproduction through fragmentation of the primary thallus which has a foliose or squamulose structure. Very few fertile *Cladonia* spp. were observed at Kerrs Creek, suggesting that fragmentation is the primary means of dispersal to new sites. In the Northern Hemisphere, *Cladonia* spp. often invade abandoned pasture and crop lands. Early studies by Robinson (1959) indicated that

Cladonia spp. reach a peak in abundance and frequency at between 10 and 40 years after disturbance, after which they succumb to shading and competition from grasses and litter. Similarly, Brodo (1961) recorded a reduction in cover of *Cladonia* spp. after only 10 years of recovery through shading by the grass *Andropogon*.

Implications for management of native pastures

This study reinforces the notion that areas devoid of vascular plants and generally regarded as 'bare', frequently support a floristically rich community of non-vascular organisms. On average, about half of the area of unvegetated or 'bare' soil in each treatment supported lichens, mosses or cyanobacteria (Table 2). The occupation of bare soils by cryptogamic organisms is significant for two reasons. Firstly, as bare soil increases, so does the cover of soil crust organisms (Table 2). Given that small areas of cryptogam-inhabiting soil occur amongst grass swards on well-vegetated surfaces, these sites are likely to be permanently occupied by cryptogams. They will probably act as sites from which propagules will disperse when an opportunity arises, such as when pasture cover declines. Thus management strategies which attempt to eliminate these crust organisms in an effort to promote grass growth are likely to be counter-productive. However, it is conceivable that, once developed, cryptogams might prevent the germination and establishment of vascular plants. If this were the case then management strategies such as strategic trampling (e.g. short-duration grazing and trampling) might reduce the dominance of cryptogamic crusts and allow the re-establishment of grasses. We believe, however, that land managers have a better chance of reducing cryptogam cover and restoring an extensive cover of perennial vascular plants by adopting strategies that do not disturb the soil surface.

Occupation of bare soils by cryptogams is important, secondly, because of the impact they have on soil and ecological processes (Eldridge & Greene 1994). There is abundant evidence to support the view that lichens and bryophytes alter soil surface morphology, enhancing the lodgement of vascular plant seeds (St Clair *et al.* 1984; West 1990; Zaady *et al.* 1997). The roughened surfaces of crusts and mats of lichens and mosses allow small amounts of water to accumulate on the soil surface. Cyanobacteria, either free-living or as the algal component of the lichens, are able to fix atmospheric nitrogen (Eskew & Ting 1978; Belnap *et al.* 1994) which is often used by developing vascular plants (Harper & Pendleton 1993; Belnap & Harper 1995). Decomposition of mosses in particular can contribute large amounts of nutrients, particularly N and P, which may account for enhanced survival of vascular plants (van Tooren 1988). Furthermore, the presence of these organisms prevents the breakdown on the soil

surface by raindrop impact (Valentin 1995), which would normally decrease the ability of vascular plants to establish and germinate.

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