Grazing and drought reduce cyanobacterial soil crusts in an Australian *Acacia* woodland

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Abstract

Cyanobacteria-dominant soil crusts are important components of unvegetated interspaces in Australia's semi-arid rangelands. We studied the changes in crust cover and floristics at increasing distances up to 500 m from three stock watering points in western Queensland's Mulga bioregion between 2002 and 2005. Sampling times corresponded with pre-drought (2002), drought (2003), early post-drought (2004) and late post-drought (2005) periods. Cyanobacterial cover increased markedly with increasing distance from water, with the largest changes occurring within 200 m of water. The change in cover with distance from water was most pronounced before the drought compared with during or after drought. Crust composition also changed in relation to distance from water, and the abundance of three cyanobacteria (*Scytonema* sp., *Stigonema ocellatum*, *Porphyrosiphon notarissi*) was greater away from water. The diversity of crust species increased significantly with distance from water, and was greatest in the late post-drought period. Although cyanobacterial crusts were present close to water (<100 m) before the drought, cover close to water had not recovered to pre-drought levels 2 years after drought. Our results indicate that excessive damage by stock trampling has an immediate impact on crusts and reduces their capacity to recover after drought. Changes in the severity or intensity of drought may therefore accelerate degradation processes and compromise the ability of crusts to recover after grazing.
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1. Introduction

In Australia, overgrazing by domestic, feral and native herbivores over the past century has resulted in considerable damage to woodland vegetation communities and their associated soils (Noble and Tongway, 1986). Overgrazing, exacerbated by drought, compacts surface soils, destroying surface aggregates and reducing soil porosity and infiltration. Trampling also reduces niches for water capture and seed germination, and compromises the ability of the surface to capture and store soil water (Eldridge, 1998a). Lower levels of litter cover reduce the rate of mineralisation of organic matter, creating negative feedbacks on litter

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decomposition processes. Excessive trampling reduces the quality of the soil surface, resulting in flow-on effects to plants and animals, and ultimately affecting the long-term stable productivity of woodland soils. Trampling is most evident close to watering points where livestock tend to congregate (Andrew and Lange, 1986; Dougill and Cox, 1995). Gradients radiate out from the water point such that there is often a decline in plant cover and diversity close to the water, depending on stocking intensity, and substantial changes in soil physical and chemical condition (Andrew and Lange, 1986; Tongway et al., 2003). This decline corresponds with an increase in dung density, and the radial gradients are termed the 'piosphere' (Lange, 1969).

Biological soil crusts are complex assemblages of mosses, lichens, liverworts, algae, fungi and bacteria that are found on and below the surface of dryland soils (Eldridge and Rosentreter, 1999). They are essential components of healthy productive ecosystems and a major component of semi-arid soils over much of southern Australia (Eldridge, 2001). Biological crusts contribute to soil carbon and nitrogen levels (Malam Issa et al., 2001), act as biophysical barriers against the erosive effects of wind and water (Eldridge, 1998a; Eldridge and Leys, 2003) and provide a habitat for soil biota. They contrast with physical soil crusts that are typically formed as a response to raindrop impact on the soil surface and result in a degraded surface that inhibits infiltration (Valentin and Bresson, 1992).

The continental distribution of biological soil crusts in Australia is strongly influenced by climatic patterns, particularly the amount and distribution of rainfall (Rogers, 1971). Soil crusts dominated by lichens are most strongly developed in southern Australia where the rainfall is Mediterranean and the soils are calcareous (Eldridge, 2001; Rogers, 1972). However, in areas where summer rainfall is dominant, lichen growth is limited, as their ability to photosynthesise is compromised when thallus hydration coincides with high summer temperatures (Rogers, 1977). In southern Queensland, cyanobacteria (Rogers, 1989), liverworts (Rogers, 1994) and cyanolichens (Eldridge, 2001) predominate at the expense of multi-layered lichens. The bare interspaces between grasses are generally colonised by a crust or mat of cyanobacterial and bryophytes (Hodgins and Rogers, 1997; Rogers, 1994). The cyanobacterial crust is most strongly developed at the leading edge of the interception zones above the groves where there is less competition for resources from grasses, but where moisture is available (Eldridge, 1998b). Positive feedback processes between these soil crusts and grasses lead to a redistribution of water between the crusts and the grasses, reinforcing the high rates of plant production in the groves.

Crusts are sensitive to trampling (Anderson et al., 1982; Eldridge, 1998a; Memmott et al., 1998) and clearly defined trends in the composition of cyanobacteria (Hodgins and Rogers, 1997; Malam Issa et al., 1999) and lichens (Andrew and Lange, 1986; Rogers and Lange, 1971) have been identified along grazing gradients centred on watering points in extensive pastoral systems. Trampling-induced disturbance to biological soil crusts destabilises the soil surface, altering the movement of resources along the surface, and often leading to a breakdown in spatial heterogeneity and a loss in ecosystem function (West, 1990). Ongoing physical damage to crusts leads to their eventual demise, with concomitant reductions in soil function. Resilience of semi-arid pastoral systems to grazing-induced disturbance and therefore rates of recovery after drought, are critically dependent on the maintenance of a functioning biological soil crust, given the pivotal role that crusts play in maintaining soil nitrogen and carbon pools in semi-arid systems (Evans and Johansen, 1999). Recovery from damage can be extremely slow, often in the order of decades. Similarly, as cyanobacterial crusts are considered as early successional crust types (Harper and Marble, 1989), their persistence, even under adverse environmental conditions such as extended droughts, is critical for the restoration of ecosystem function.

Here, we report on a study designed to document the changes in soil crust cover and composition along a grazing gradient in south-western Queensland, Australia. The gradient was in a large paddock consisting of discrete run-on and runoff zones, which differ markedly in their soil physical, chemical and biological characteristics (Tongway and Ludwig, 1990). The efficient functioning of these landscapes depends on the maintenance of this patchiness, which varies from the scale of individual patches of biological soil crust on the surface to changes across entire catchments. The patchy distribution of vegetation and soil influences the conservation and flow of resources from one part of the landscape to another, and is a useful indicator of landscape stability and productivity.

The aims of the study were to assess changes in cover and composition of a cyanobacterial-dominant crust at increasing distances from water over different climatic phases. We did this by monitoring changes at increasing distances from three newly installed watering points (at the beginning of the study waters had been

in place for 8 years), and confirmed the presence of a grazing gradient by measuring animal dung and basal cover of perennial grasses as surrogates of grazing pressure. Although trampling is known to adversely affect biological soil crusts, few studies have specifically examined grazing-induced changes in crusts dominated by cyanobacteria. A previous study, however, was conducted in the same paddock (Hodgins and Rogers, 1997), but prior to closure of the bore drain which preceded the water points. We predicted that the cover and diversity of the cyanobacterial crust would behave in a similar manner to lichen- and moss-dominated soil crust and therefore increase with increasing distance from water.

2. Methods

2.1. The study site

The study was carried out in the 2000 ha Glencoban Bore paddock (28°10′S; 146°02′E) located 40 km east–south-east of Cunnamulla in semi-arid south-western Queensland, Australia. Glencoban Bore paddock is stocked with sheep and cattle, the mixture and rates dependent on pasture availability and quality (Fig. 1). Annual rainfall at Glencoban is spatially and temporally variable, ranging from <100 to >600 mm annually, with an average annual rainfall of 376 mm (Clewett et al., 2003). Dews are an important source of soil moisture during the cooler months. Drought cycles occur frequently, often broken by significant rainfall and floods.

Much of the Glencoban Bore paddock lies within the Gilruth Land System (Mills et al., 1990), a generally flat landscape with a series of runoff and run-on zones. The runoff zones are characterised by compacted red earth soils (Kandosols; Isbell, 2002), often with large patches of gravely ironstone on the surface. Infrequent heavy rain on the runoff slopes generates sheet water flow that pools in shallow depressions or larger ephemeral swamps ringed by poplar box (*Eucalyptus populnea*) at the lower parts of the landscape (Pickup, 1985). The runoff and depositional zones lead into broad run-on zones aligned on the contour, which are dominated either by groves of mulga (*Acacia aneura*) or scattered poplar box. The runoff zones support a mixture of perennial grasses co-dominated by mulga Mitchell grass (*Thyridolepis mitchelliana*) and greybeard grass (*Amphipogon caricinus*). However, productivity and diversity are greatest in the groved run-on zones. The dense cover of perennial grasses, particularly on the upslope edge (interception zone) of the run-on zones, retains water and nutrients in the groves.
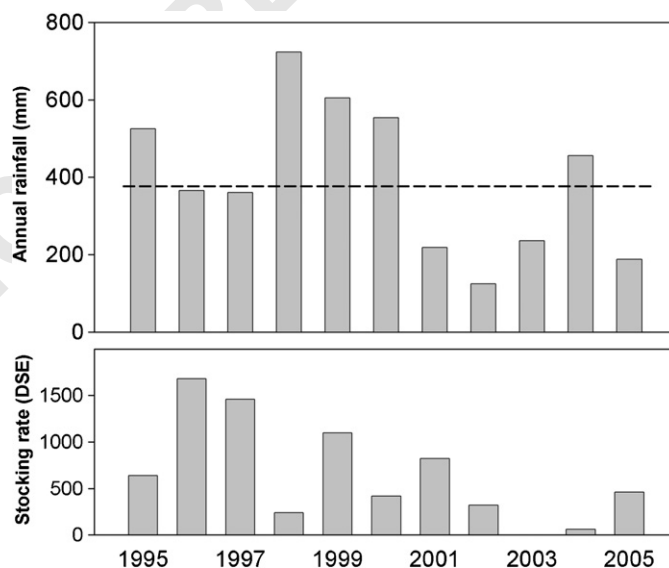

Fig. 1. Annual rainfall (mm) for Glencoban Bore paddock for the period 1995–2005 and the stocking rates (dry sheep equivalents, DSE) for the same period. The broken line indicates average annual rainfall (376 mm) over the past 50 years.

1   Glencoban Bore flowed continuously between 1925 and 1995, and was reticulated through a series of open
earth drains bisecting the paddock which extended 6 km. Glencoban Bore was capped in 1995, and the bore
3   drain system replaced with polyethylene pipe and reticulated to five watering points (troughs), evenly
distributed throughout the paddock.

5
2.2. Field methods

7
We monitored the cyanobacterial soil crust annually from 2002 to 2005. This period corresponded with four
9   distinct climatic phases; pre-drought (2002), drought (2003), early post-drought (2004) and late post-drought
(2005). The late post-drought was, in reality, a seasonal drought, just after the substantial drought of 2002
11   (Fig. 1). At each of the three watering points, we established two permanent 500 m transects, oriented to
provide maximum representation of the landscape features of the paddock. A permanent 30 m transect was
13   established perpendicular to each 500 m transect at intervals of 10, 25, 50, 100, 200, 300 and 500 m from water.
Cover of the cyanobacterial crust, bare ground and basal cover of perennial grasses were recorded to the
15   nearest 1 cm along each 30 m transect using a line-intercept method. As the drought progressed, perennial
grasses were recorded only until we were certain that they would not re-shoot, after which they were recorded
17   as litter, if material was detached.
We counted the number of fresh dung events, defined as discrete clumps of sheep faeces, or patches of cattle
19   dung, but excluding dung from native herbivores (i.e., kangaroos—*Macropus* spp.) within 30 contiguous
2 m × 1 m quadrats placed along each of the 30 m transects. Dung was assessed only in 2002 and 2005. Fresh
21   dung is easily identified by its high moisture content and shows little invasion by termites.
To adequately quantify the diversity of soil crust taxa within different surface microsites (e.g., bare soil,
23   sandy-covered surfaces, litter-covered surfaces), five crust samples (approximately 2.5 cm² in area) were
collected from each of four quadrats placed at representative locations along each 30 m transect. Further
25   samples of lichens and bryophytes were also collected from the general area in order to document site-level soil
crust diversity. For this study, we bulked the five samples from each quadrat to obtain four composite samples
27   for each 30 m transect. No crust collections were made at two of the six transects at 100 m from water in 2003
because cattle had destroyed the surface along the transects and no crust could be seen. Thus, for each distance
29   from water along each 500 m transect we averaged across the five samples in each of the four 0.25 m² quadrats
resulting in a total number of 664 composite samples (4 years × three water points × two transects × seven
31   distances from water × four quadrats; less the data from two unmeasured transects).

33   ### 2.3. Identification of soil crust taxa

35   We examined crust species at two levels of intensity. For all soil samples collected over the 4 years of the
study ($n = 664$), we recorded all species inhabiting the samples collected using a dissecting microscope at
37   10–70× magnification. Identification of individual cyanobacterial species was confirmed using a light
microscope. Abundance was calculated as the percentage of samples examined that contained a given species.
39   We also examined, in more detail, samples from 2003 only. Each soil sample was examined under a dissecting
microscope and the cover of each species determined using a microline-intercept method with the microscope's
41   graticule. Taxonomic descriptions of soil crust taxa are presented in a separate manuscript.

43   ### 2.4. Statistical analyses

45   We used a balanced, split-plot ANOVA with two error terms to examine differences in basal grass cover,
cover of cyanobacteria and bare soil, and the density of dung events in relation to the three watering points
47   and seven distances from water. The whole-plot stratum considered water points, and the sub-plot stratum
distances from water and its interaction with water points. As we felt that it was inappropriate to compare
49   distances at one water point with the same distance at a different water point, given that water points were not
true replicates, we pooled the distance × water point interaction into the second error term. Least significant
51   difference (LSD) testing was used to examine differences in means between the seven distances from water
points. Data were checked for homogeneity of variance, independence and normality using Levene's test and

other diagnostic tools using the Minitab (1997) statistical package. Data were transformed, where necessary (generally $\log_{10}$, square root) to meet these assumptions.

Multivariate analysis was used to examine patterns in diversity and abundance of soil crust taxa for the detailed study of the 2003 data only. Data for locations <100 m from water were not included because crust cover was zero in 3 of the 4 years studied (2003–2005) at 50 m and less from water. A data matrix of 21 columns (crust taxa) by 24 rows (six replicates each of the four distances: 100, 200, 300 and 500 m from water) was converted to a similarity matrix using Bray-Curtis similarity coefficients contained within the primer (version 5) statistical package (Clarke and Gorley, 2001). The similarity matrix was then subject to non-metric multi-dimensional scaling (MDS). Differences in the diversity (number of taxa) and abundance of soil crust taxa between the four distances were determined using ANOSIM which derives a test statistic (Global R) and a significance level. The SIMPER subroutine was then used to determine which of the taxa explained most of the dissimilarity between the four distances. We used the DIVERSE function in primer to calculate four measures of diversity (number of taxa, number of individuals, richness and evenness) for each of the 24 rows. Differences in these measures were tested using ANOVA with the same structure described previously.

3. Results

3.1. Spatial changes in dung and grass cover in relation to grazing gradients

Changes in dung and grass cover were examined to confirm the existence of a grazing gradient corresponding with increasing distance from water. Dung was recorded during the pre-drought (2002) and late post-drought (2005) periods only (Fig. 2), as the paddocks were de-stocked during the drought, and were only restocked in late 2004 (albeit at low rates; Fig. 1). During the pre-drought period, there were marked reductions in the density of dung deposits with increasing distance from water. The density of dung deposits at <50 m from the water point was significantly greater than that found at distances of 200 m or more from water ($F_{6,30} = 30.7$, $P<0.001$, $R^2 = 0.81$; on log–log transformed data). During the late post-drought period in 2005, there was substantially less dung, and although a gradient in dung was still evident out from the water point ($F_{6,30} = 10.0$, $P<0.001$, $R^2 = 0.58$; on log–log transformed data), it was less clearly defined (Fig. 2).

There were significant increases in the basal cover of perennial grasses with increasing distance from water at all four time periods ($P<0.05$; Fig. 3). The pattern in grass cover was opposite to that observed in the dung, reflecting the direct effect of grazing in reducing grass cover. Averaged over all years, the relationships between grass cover and distance from water was best described by an exponential function. In general, the basal cover of grass was substantially greater pre-drought ($6.0\pm0.7\%$; mean$\pm$S.E.) compared with either drought ($2.2\pm0.4\%$), early post-drought ($4.5\pm0.8\%$) or late post-drought ($3.2\pm0.5\%$) which were not significantly different from each other ($F_{3,64} = 1.67$, $P = 0.001$; Fig. 3). Sites with a high basal cover of grasses tended to have an extensive cover of cyanobacteria ($F_{1,166} = 76.20$, $P<0.001$), but grass cover explained only 31% of the variance in cyanobacterial cover.
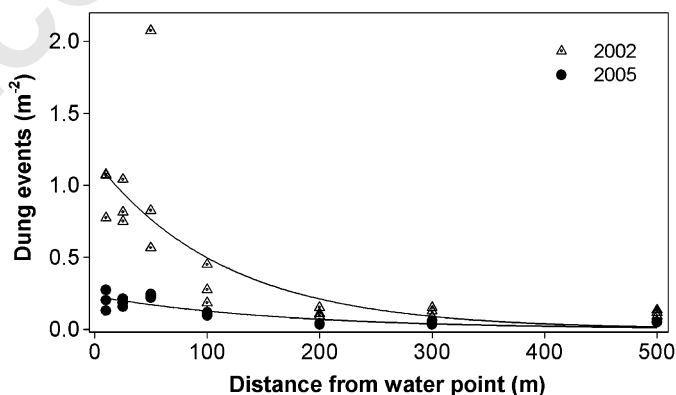

Fig. 2. Density of dung events (m^{-2}) in relation to distance from the waterpoint (m) for 2002 and 2005.
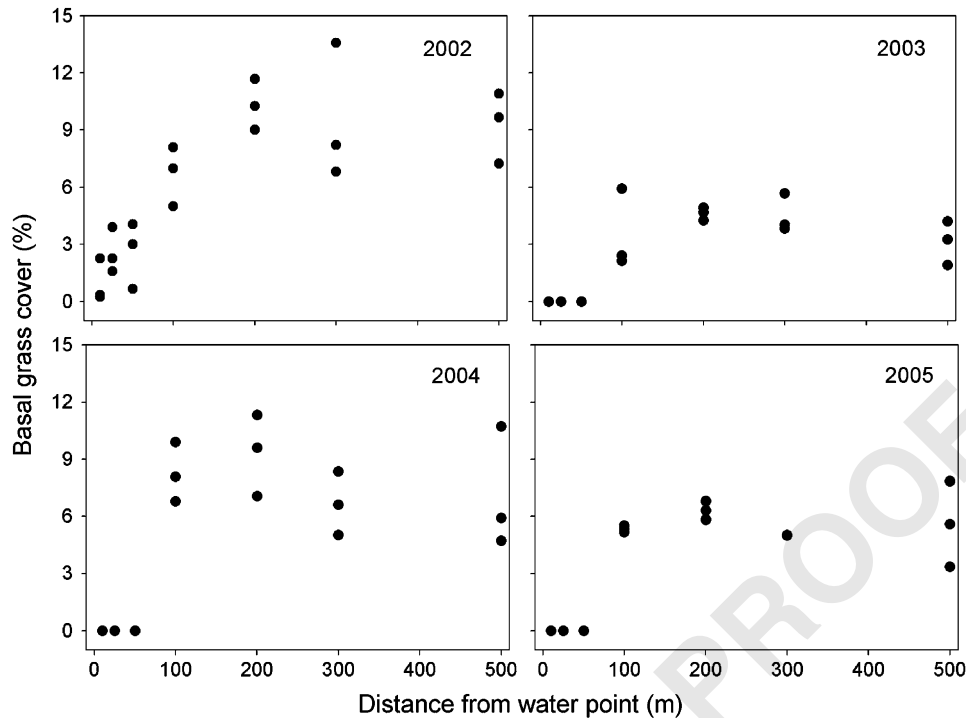
Fig. 3. Basal cover of grasses (%) in relation to distance from water (m) for the periods 2002–2005.

3.2. Spatial and temporal changes in cyanobacterial cover

Before the drought average cyanobacterial cover was <1% within the first 100 m of the watering points, and was not consistently different between water points. Averaged over all distances from water, cyanobacterial cover ranged from 15.8% at one water point to an average of 7.8% at the other two. By the onset of drought in 2003, and continuing to the end of the study, cyanobacterial crusts within the first 100 m of water were so diminished by stock trampling that their cover could not be assessed. Across all watering points there were strong grazing gradients in the cover of cyanobacteria, with clear increases with increasing distance from water during all four climatic phases ($F_{1,40} = 26$–54, $P < 0.001$). Generally, the biggest change in cover from 200 to 500 m occurred in the pre-drought period (Fig. 4).

3.3. Spatial changes in crust taxa

The composition of soil crust taxa varied significantly in relation to distance from the watering point (Global $R = 0.143$, $P = 0.021$), but the difference was only significant between the 100 and 500 m distances (Global $R = 0.45$, $P = 0.014$). Similarity percentage (SIMPER) analysis indicated that half of the difference in abundance between sites close to and far from water was due to only three species (*Scytonema* sp., *Stigonema ocellatum* and *Porphyrosiphon notarissi*; Table 1). All of those taxa explaining about three-quarters of the difference between close and far sites were more abundant at distances of 500 m from water compared with 100 m (Table 1). The MDS biplot clearly shows the distribution of key species in relation to the water point (Fig. 5).

The number of crust taxa recorded in 2003 increased significantly with increasing distance from water ($F_{3,20} = 4.81$, $P < 0.012$; Table 2; Fig. 6). Similarly, there were significantly fewer individuals at 100 m compared with the other distances ($F_{3,20} = 3.48$, $P < 0.004$) but no difference in evenness with increasing distance from water ($P = 0.30$; Table 2). In general, sites with an extensive crust cover tended to support a greater number of crust taxa ($F_{1,170} = 94.1$, $P < 0.001$, $R^2 = 0.35$).
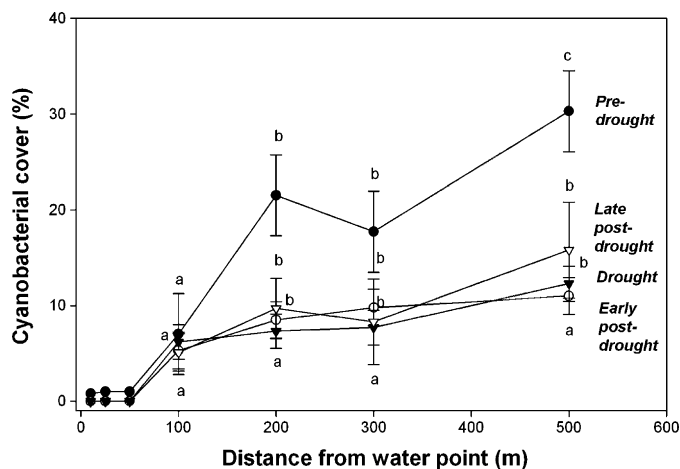
Fig. 4. Mean (±S.E.M.) cyanobacterial crust cover in relation to distance from the water point (m) for each of the 4 years (averaged over the three water points). Within a year, different letters indicate a significant difference in cover at $P < 0.05$. Pre-drought, 2002; drought, 2003; early post-drought, 2004; late post-drought, 2005.

Table 1

Species, mean abundance, and percentage and cumulative dissimilarity for sites close ($\leqslant 100$ m) and far (500 m) from water

Species	Organism	Mean abundance		Dissimilarity	
		100 m	500 m	%	Cumulative %
Scytonema sp.	Cyanobacterium	0	39.8	25.1	25.1
Stigonema ocellatum	Cyanobacterium	9.3	25.0	13.2	38.3
Porphyrosiphon notarissi	Cyanobacterium	14.4	21.2	12.3	50.6
Peltula spp.	Lichen	4.2	14.6	8.7	59.3
Riccia limbata	Liverwort	8.1	10.1	8.0	67.3
Goniomitrium enerve	Moss	0	10.9	6.9	74.2

4. Discussion

Many studies worldwide have shown that biological soil crusts (including cyanobacteria) are sensitive to trampling by stock (e.g., Anderson et al., 1982; Berkeley et al., 2005; Eldridge, 1998a). In arid South Australia, for example, Andrew and Lange (1986) demonstrated that livestock had a significant impact on the biological soil crusts 2 years after the introduction of a new watering point, although their stocking rates were quite high (200 sheep per water trough). Their results indicated a clear grazing gradient effect on soil crusts, dung and basal cover of grasses. Exponential increases in the cover of cyanobacterial crusts and perennial grasses corresponded with reductions in the density of sheep and cattle dung, and therefore declining stock grazing intensity with increasing distance from water. Our study reinforces the results of these previous studies, but over a larger number of years and over a series of different seasonal conditions from above-average to below-average rainfall, and, in particular, provides insights into the responses of soil crusts to stress brought upon by changing seasonal conditions and grazing.

4.1. Temporal changes in crusts

Our study enabled us to compare our results with those from previous studies conducted within the same paddock. Hodgins and Rogers (1997) found a significant decline in the cover of the cyanobacterial soil crusts with increased grazing pressure (using dung density as a surrogate) close to the old bore drain prior to its closure. Their research followed 4 years of extremely low rainfall. Notwithstanding these results however,
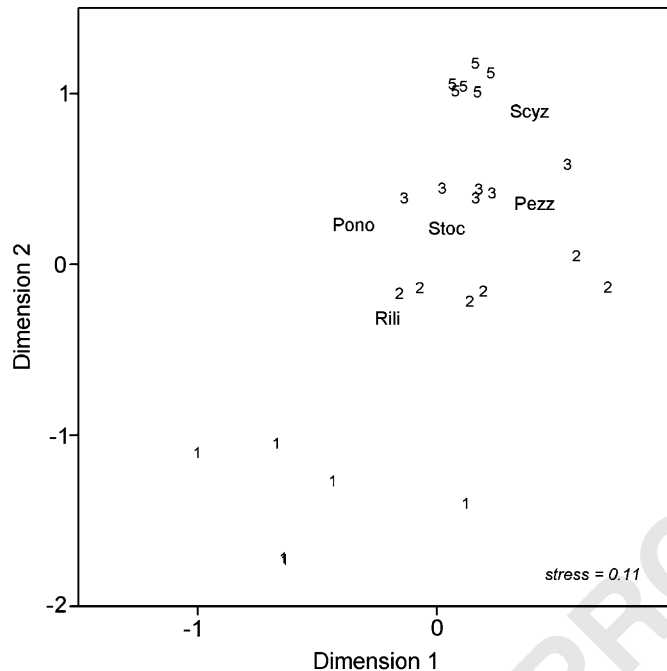
Fig. 5. The first two dimensions of the MDS biplot showing the location of selected species (see Table 1) by distance from water for 2003 only. Numbers indicate distance (× 100 m) from water. Scyz, *Scytonema* sp.; Stoc, *Stigonema ocellatum*; Pono, *Porphyrosiphon notarissi*; Pezz, *Peltula* spp.; Rili, *Riccia limbata*.

Table 2
Measures of diversity and abundance for soil crust taxa at increasing distances from water for the detailed study of taxa in 2003 only

Distance from water point (m)	No. of taxa		No. of individuals		Richness		Evenness	
	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
100	5.3[a]	1.49	59.0[a]	17.30	1.1[a]	0.39	0.85[a]	0.04
200	8.5[b]	0.85	92.5[b]	3.02	1.7[ab]	0.18	0.76[a]	0.02
300	9.8[bc]	1.19	83.2[b]	5.69	2.0[ab]	0.25	0.78[a]	0.03
500	11.0[c]	0.73	90.2[b]	4.44	2.2[b]	0.17	0.79[a]	0.03

Within a column, different superscripts indicate a significant difference in diversity and abundance measures in relation to distance from water at $P < 0.01$.

Cowley (2001) did not detect any gradient in cyanobacterial crust cover or grass cover out from new troughs over a 4-year period immediately after the bore drains were decommissioned and new watering points established. Cowley's surveys were carried out during average or above-average seasons where the development of grazing gradients might not have been as pronounced.

In the present study, when the waters had been in place for 7–10 years, development of a clearly defined grazing gradient initially coincided with a drier than average year immediately preceding drought conditions, particularly during 2003, together with periods of relatively ineffective rainfall. Although gradients were apparent during all measurement periods, they became less pronounced as pastoral conditions improved. We conclude, therefore, that the response of the soils and vegetation emanating from the watering point is influenced not only by stock grazing pressure, but also by its interaction with rainfall patterns. The strength of the grazing gradient was reinforced by declining rainfall. Of particular interest was the fact that the seasonal drought in late 2005 moved some of the measures such as crust cover or grass cover (Fig. 2) back to similar levels existing during the drought in 2003. We believe that this was a restocking effect, exacerbated by low
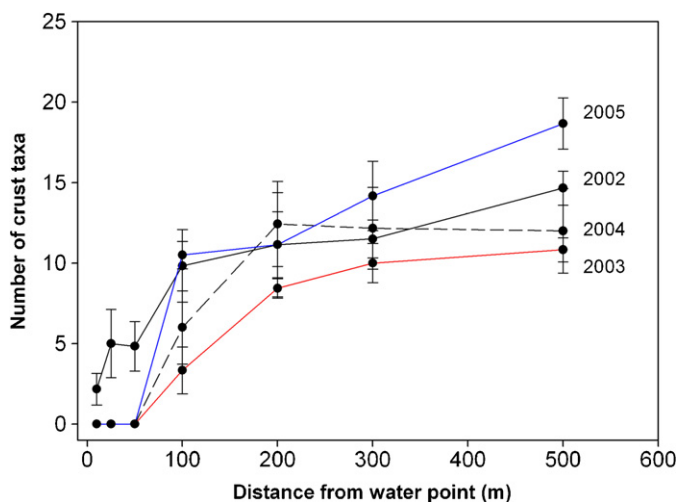
Fig. 6. Mean (±S.E.M.) diversity of soil crust taxa in relation to distance from water for 2002 (pre-drought), 2003 (drought), 2004 (early post-drought) and 2005 (late post-drought).

rainfall levels for 4 of the 5 years since 2001 (Fig. 1). Although the paddock is well managed, there may have been insufficient time for grasses to recover after the drought, and the concentration of stock close to water resulted in the high utilisation of perennial grasses and therefore their low levels of basal cover.

4.2. Functional effects of changes in soil crusts

In our study, the effect of stock trampling was clearly greatest within 100 m of the watering point, due largely to the congregation of grazing animals at the water point, particularly during droughts, when they are fed supplements. A number of biotic and abiotic changes occur in this 'sacrifice' zone. These include removal of vascular plants, reduction in plant cover, deposition of large amounts of dung and therefore alteration to soil nutrient concentrations and plant chemistry, increased soil erosion, breakdown in soil surface integrity, and declines in ecosystem function and stability (Andrew and Lange, 1986; Dougill and Cox, 1995; Tolsma et al., 1987; Turner, 1998). This effect is exacerbated by the sparse cover of vascular plants, which are frequently dominated by weedy 'increaser' species.

While some crust species such as cyanobacteria and some cyanolichens (e.g., *Collema coccophorum* and *Heppia despreauxii*) are able to tolerate relatively high levels of disturbance (Rogers and Lange, 1971), other crust components such as foliose lichens are not (Eldridge and Rosentreter, 1999). The result is a change in species composition favouring those species with physiological or morphological adaptations to survival in a disturbed environment, and a general reduction in diversity, which was apparent in our study (Table 2; Fig. 6). The presence of greater numbers of the liverwort *Riccia limbata* closer to water (i.e., at 100 m) could be due to dispersal of spores in floodwater, similar to that observed in *Riccia blackii* (Rogers, 1994). *R. limbata* may also be structurally more efficient at resisting the ongoing effects of trampling, and its ability to retract the anthocyanin-rich scales gives the underlying photosynthetic material a greater degree of physical protection. Our observations suggest that *P. notarissi* in particular, appears to play an important role in recolonising the newly created soil surfaces, particularly during the post-drought recovery phase. It has extremely mobile filaments, and the sheaths are carotene-rich, giving it high-quality ultraviolet protection in exposed, highly eroded areas.

Cyanobacteria fix atmospheric nitrogen, and rates of up to $68 \, kg \, N \, ha^{-1} \, year^{-1}$ have been reported in the literature (e.g., Aranibar et al., 2003; Rychert et al., 1978). In our study, the known nitrogen-fixing cyanobacteria *Scytonema* sp. and *Stigonema* sp. were significantly more abundant at 500 m compared with 100 m from the watering point (Table 1). Soil nitrogen pools are low in arid and semi-arid rangelands (Stafford Smith and Morton, 1990), and at distances from water these nitrogen-fixing cyanobacteria would be expected to contribute substantially to the nitrogen balance within the paddock (Russow et al., 2005), particularly in

1 areas where native (e.g., *Acacia* spp.) or naturalised (e.g., *Medicago* spp.) nitrogen-fixing plants are a minor component. Locally elevated levels of NH_4–N sometimes occur near watering points as a result of defecation

3 and urination by grazing animals (Tolsma et al., 1987). Cattle typically act as nutrient 'conduits' (Dougill and Cox, 1995; Dougill and Thomas, 2004; Ruess, 1987), grazing on plants out along a grazing gradient and

5 transporting nitrogen close to the watering point in the form of dung and urine. Overall, however, nutrient levels are generally depleted close to water points (e.g., Tongway et al., 2003; Turner, 1998), with the

7 breakdown in spatial arrangement of productive nutrient-rich patches, reductions in cryptogam cover, and the truncation of nutrient-rich layers in the immediate topsoil (Tongway et al., 2003) leading to nutrient losses

9 which far outweigh any increase in nutrients associated with animal dung.

11 *4.3. Land management considerations*

13 Cyanobacteria-dominant soil crusts are crucial components of arid land ecosystems that moderate essential processes such as nutrient cycling and landscape stability. Land managers should therefore attempt, where

15 practicable, to consider the important of cyanobacterial soil crusts as part of their routine land management practices. The effectiveness of multiple watering points scattered across the 2000 ha paddock (as opposed to

17 the single, linear bore drain), was most obvious during the drought, when grazing gradients were strongly evident in the cyanobacterial soil crusts. When compared with the previously recorded extensive gradients

19 from the bore drain (Hodgins and Rogers, 1997), there was less land sacrificed around the watering points. Management of total grazing pressure (including feral and native animals) at critical periods during droughts,

21 and a gradual re-stocking gives the paddock a crucial 'resting' period. The subsequent rapid recovery of the cyanobacterial soil crusts and strong post-drought recovery of perennial grass cover (data not shown) may not

23 have been as robust if domestic stock were reintroduced to capacity immediately after feed became available.

   Excessive damage by stock trampling has a long-term impact on crusts, and their subsequent capacity to

25 recover after disturbance and repeated damage is likely to lead to a reduction in the nutrient status and long-term viability of the soil surface. Strong links between grazing-induced disturbance and the generation of bare

27 soil patches are well established (Braunack and Walker, 1985; de Soyza et al., 1998). At low to intermediate levels of grazing disturbance, bare patches provide suitable niches for soil crusts, and the maintenance of

29 crusted surfaces within a matrix of perennial grasses is maintained by feedback processes moderated by the crusts themselves. Crusts are known to shed water, nutrients and organic matter to adjacent grass-dominated

31 microsites, enhancing the capture of water by grasses and maintaining landscape structure and productivity (Eldridge et al., 2002). However, removal of grasses by grazing, and destruction of, and therefore alteration to,

33 the connectivity of hydrophobic crusts alters the efficiency with which crusts redirect water to the grasses. This is characteristic of the early stages of landscape degradation, leads to a breakdown in landscape heterogeneity,

35 and ultimately a loss of productivity.

   Diversity of species within the biological soil crust could be an important indicator of soil surface function

37 in areas where crusts are a natural component of the ground layer. The recovery process highlights the importance of land management strategies that not only incorporate cyanobacterial soil crusts into

39 management decisions, but also monitor their cover and diversity over time. Rapid recovery appears to have occurred during a period of light or delayed stocking. Our study has shown that both grass cover and

41 cyanobacterial cover responded to changes in grazing intensity out from water. Further studies are required to understand the extent to which grass cover can be used as a surrogate for cyanobacterial cover to enable

43 landholders to better detect changes and improve their management of these wooded rangelands.

45 Q1 **Uncited reference**

47 Noble and Crisp (1979).

49 **Acknowledgements**

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