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Deposition of sand over a cyanobacterial soil crust increases nitrogen bioavailability in a semi-arid woodland

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ABSTRACT

The movement of sand by erosion is a common feature of drylands during droughts and periods of sparse vascular plant cover. We examined the effects of sand deposition on the bioavailability of N in cyanobacterial-dominant soil crusts during and after a severe drought. Crusts were sampled from two depths on stony and stone-free surfaces with and without sandy deposits. All sites supported an extensive cover (up to 51%) of N-fixing cyanobacteria and cyanolichens. During drought, sand-covered crusts had up to three-times more mineral N (NH_4^+ and NO_3^-) and twice the mineralisable N, at both depths, than sand-free samples. Mineralisable N was always greater in the surface soil layer both during and after drought. During the drought, two common N-fixing cyanobacteria (*Scytonema* cf. *hofman-bangii*, *Stigonema ocellatum*) were significantly more abundant on uncovered than sand-covered surfaces. Increased N bioavailability likely results from autolysis and subsequent breakdown of N-enriched cyanobacterial cell material mediated by changes in the soil surface microenvironment. Our work suggests that landscape-level processes of sand deposition have a marked effect on soil nutrient pools by enhancing the accumulation of plant-available N on cyanobacterial crusted surfaces. Inappropriate land management or the loss of cyanobacterial soil crusts during drought would compromise the long-term bioavailability of soil N.

1. Introduction

At large spatial scales arid and semi-arid environments are regulated largely by soil moisture and nutrients (Burke, 1989). At smaller spatial scales, however, processes of wind and water erosion and redistribution of soil, water and nutrients have substantial local effects on soil nutrient pools (Zaady et al., 1998). Microbiotic soil crusts, complex assemblages of cyanobacteria, lichens, bryophytes, algae, bacteria and fungi, are widely distributed at small spatial scales, occupying the interspaces between grasses and shrubs. These crusts are also often strongly associated with non-biological (physical) crusts such as rain-induced, erosional and deposition crusts or chemical crusts (Valentin and Bresson, 1992), with a strong relationship between diversity and soils with a higher silt-clay fraction (Büdel et al., 2009). Microbiotic crusts are common in arid and semi-arid environments, and strongly influence landscape stability and resource flows (Belnap and Lange, 2003). Cyanobacteria, cyanolichens and bacteria in the crusts contribute greatly to soil nutrient pools by producing substantial amounts of bioavailable N in environments where N-fixing plants such as legumes are scarce (Smith et al., 1990; Evans and Ehlringer, 1993; Belnap, 2002; Evans and Lange, 2003). Globally, microbiotic crusts are estimated to assimilate about 40% of biologically fixed nitrogen in terrestrial ecosystems (Elbert et al., 2009). Nitrogen-fixation by cyanobacterial-dominated soil crusts is influenced by variations in light, temperature and oxygen at small spatial scales, and the degree to which they can receive moisture (Belnap, 2002; Dojani et al., 2007).

Redistribution of sand by wind and water erosion processes is a common phenomenon in the grassy woodlands of eastern Australia (McTainsh et al., 1998). The sand originates through natural processes of wind erosion or when grazing-induced trampling by livestock accelerates the disaggregation of surface soil layers (Leys and Eldridge, 1998). These sandy accretions often form depositional crusts that vary in nature, often comprising thin layers of compacted soil with contrasting textures overlying cyanobacterial crusts (Valentin and Bresson, 1992). This deposition is transient in nature, and changes according to droughts, storm run-off and the extent of wind activity. Evidence indicates that the burial of cyanobacterial crusts and other surface biota alters their capacity to fix N (Wang et al., 2007), particularly during dry periods when wind erosion hazard is high and surface plant cover is sparse (McTainsh et al., 1998).

Sandy deposits alter environmental conditions at micro-scales and may increase cyanobacterial N-fixation (Stal, 1995). Burial time and depth are significant factors in crust survival and function

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(Wang et al., 2007). Although cyanobacteria are known to survive long periods of desiccation (Potts, 1994), the effect of wetting at this time may result in the degradation of exopolysaccharide (EPS) material (outer sheath) and bacterial-mediated consumption, which accelerates decomposition (Hu et al., 2003). Prolonged desiccation can also lead to death of cyanobacteria, the oxidation of proteins, and significant leakage of bioavailable N into the soil (Potts, 1999). Rainfall may release N from cyanobacterial crusts in the form of nitrate and ammonium, and this N can be directly taken up by vascular plants (Veluci et al., 2006; Dojani et al., 2007).

We recorded increases in the size and extent of sandy deposits while undertaking routine rangeland condition monitoring in western Queensland during the 2003 drought. Sand accumulates in small (5–20 cm wide) micro-depressions over the top of the cyanobacterial crusts that dominate the interspaces between perennial grass tussocks. Increasing drought severity is associated with reduced grass cover, and an increase in both the cover and depth of sandy deposits. Observations since 2002 indicated that the crusts below the sand were intact, despite being covered by sand varying in depth from 1 to 10 mm.

Sand could potentially have two markedly different effects on crusts and their capacity to produce N. Depending on its thickness, sand may protect the underlying soil crusts from the effects of livestock trampling during drought, or reduce damage caused by saltating sand grains. However, sandy deposits could compromise the ability of cyanobacteria and cyanolichens to fix N by restricting light penetration (though see Kuhl and Jorgensen, 1994) and moisture absorption, or by altering micro-environmental conditions under the sand. Extended periods of burial at depth could lead to the death of crust organisms, crust decay and the subsequent release of bioavailable N. Here we report on a study of the effects of drought on plant-available N associated with cyanobacterial soil crusts by comparing N bioavailability on sandy surfaces with that on surfaces lacking sand.

2. Methods

2.1. Study site

The study was carried out in Glencoban Bore paddock, which is located approximately 40 km south-east of Cunnamulla in south-western Queensland, Australia (28°10′S; 146°02′E). This low relief, 2000 ha paddock is characterised by two geomorphically distinct zones at the landscape scale; run-on and runoff. These zones have markedly different soil physicochemical and biological characteristics and would be expected to differ in their nutrient responses (Tongway et al., 2003). Run-on zones are densely vegetated groves of *Acacia aneura* F. Muell. ex Benth. or clumps of *Eucalyptus populnea* F. Muell. aligned along the contour on sandy to clayey textured soils. From the air this represents a stippled or banded pattern common to many arid landscapes worldwide (Ludwig et al., 1999). The intervening runoff zones, which make up about 70% of the landscape, are predominantly broad expanses of stony red earths (Kandosols, Isbell, 2002), occasionally dissected by deposition zones at mid-slope or lower slope positions. These deposition zones are shallow depressions where runoff water collects in ephemeral pools following rainfall. The runoff slopes comprise tussock grasslands with a mix of native perennial grasses dominated by *Thyridolepis mitchelliana* (Nees) S.T. Blake, *Amphipogon caricinus* F. Muell., *Enneapogon polyphyllus* (Domin) N.T. Burb and *Eriachne helmsii* (Domin) Hartley.

Average annual rainfall for the area is 370 mm with a distribution skewed towards events of less than a few millimetres (Fig. 1). The predominant land use is grazing of sheep and cattle on native pastures, though the paddock was destocked over the duration of the study. Cyanobacterial soil crusts occur in the unvegetated interspaces between grass tussocks in both runoff and run-on zones, but are more widespread and better established in the runoff zones (Williams et al., 2008). The surface soils of both zones are acidic (pH ~ 5.5) and runoff zone soils comprised 77% sand (36% fine, 41% coarse), with smaller proportions of clay (16%) and silt (7%). Soils in the run-on zones have slightly higher percentages of clay (~22%) and less sand.

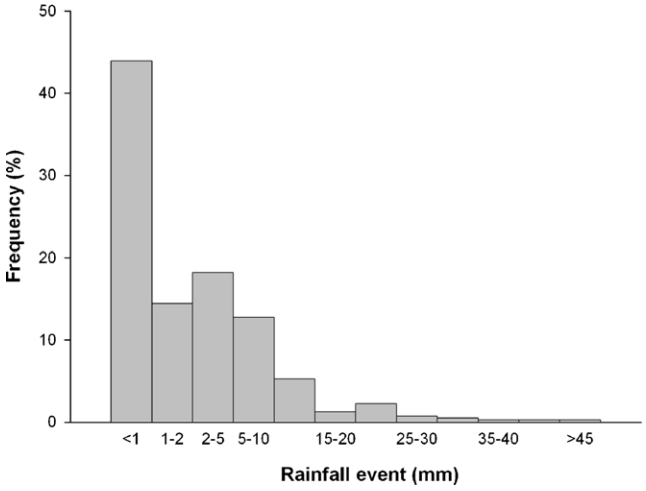

Fig. 1. Frequency distribution of rainfall from the study site between 2001 and 2005.

2.2. Field sampling

Our research focused on the open grasslands of the extensive runoff zones. Cyanobacterial crust samples were collected during two markedly different climatic periods; during a severe drought (August 2003), and a year later, 6 months after significant drought-breaking rains and regional flooding (September 2004). The timing of post-drought sampling was linked to when flood waters had receded. Seasonal and spatial variation is an important consideration when evaluating the potential for cyanobacterial soil crusts to fix nitrogen as the composition of N- and non-N-fixing species in the crust can vary over small spatial scales and in response to changes in temperature and rainfall (Evans and Ehlringer, 1993). We sampled as close as possible to the same time period in the post-drought year.

Using aerial imagery and field survey we stratified the extensive runoff zone in the paddock into three markedly different surface types that occur in patches up to 200 m across. These surface types are (1) stony, characterised by extensive cover of stones to 10 cm in diameter, (2) part-stony, where the surface has a variable cover and (3) stone-free, and dominated by earthy sand. During the drought we sampled three stony, three part-stony and four sandy sites ($n = 10$). Post-drought sampling was carried out in the same areas, but there was one fewer sampling in the sandy site due to flood damage ($n = 9$). Sampling sites were located more than 100 m from livestock watering points where the soil crust is known to be obliterated by stock trampling (Williams et al., 2008).

During previous visits we observed that a thin veneer of sand, varying from 1 to 10 mm thick, covered large areas of cyanobacterial crust on all surface types, and that a significant proportion of the crusts below this sandy veneer were still largely intact. We confirmed the presence of crusts during the drought by gently brushing sand off the surface close to all of our sample areas. As crusts of different colour intensity may be indicative of differences in cyanobacterial crust composition and therefore N-fixation (Belnap, 2002; Johnson et al., 2005), we categorised the crusts into three types: (1) light-coloured, thin crusts with no sandy covering

(2) dark-coloured, thick crusts without the sandy covering and (3) crust overlain by sand.

2.3. Collection of soil samples for N determination

At each of the 10 (drought) or nine post-drought sampling sites we positioned three 1 m × 1 m quadrates at locations that best represented the three crust surfaces. From within each quadrat we selected four 10 cm × 10 cm samples of that crust type from two depths, 0–1 cm and 1–5 cm. The four samples from each depth were bulked mixed and sieved (1.86 mm), stored in airtight bags, and formed the basis for soil chemical analyses. Thus we had 60 drought samples (10 surface type locations by 2 depths by 3 crust types) and 54 post-drought samples (9 surface type locations by 2 depths by 3 crust types). Soil moisture content was <1% at the time of sampling.

2.4. Identification of soil crust samples

For the paddock-level study of crust taxa we examined the 30 drought samples (3 crust types × 10 surface type locations) only, as the post-drought samples were inadvertently destroyed post-transport. Samples of the 0–1 cm layer were used to identify soil crust organisms (including lichens, mosses and liverworts) present on the surface. Initial inspection of the soil crust and the separation of individual species to wet mounts were carried out using an Olympus SZH10 dissecting microscope at 70× magnification. Identification to a species level was performed using Nomarsky differential interference contrast microscopy (Axioskop, MC 80, Zeiss, Jena) using keys in Geitler (1932), Hoffmann (1991) and Komárek and Anagnostidis (1999, 2005). Identifications to species level were based on morphological traits and verified by cyanobacterial experts to the closest known taxa described in the literature, as there are currently no formal identifications of Australian terrestrial cyanobacteria. N-fixing species were identified on the basis of the presence or absence of heterocysts. Heterocystous-forming cyanobacteria are reported to be the major contributors to biologically fixed N (Solheim et al., 1996). Although non-heterocystous species recorded here may have the capacity to fix nitrogen, we treat them as non-N fixers unless evidence to the contrary is reported in the literature. Ten wet mounts were prepared from each of the 30 samples and examined at 400× magnification and the abundance of each species scored on a scale of 1 (rare) to 8 (dominant). Samples of crust for the paddock-scale assessment were examined for the presence of lichens and bryophytes using a dissecting microscope at 70× magnification, and cyanobacteria were identified according to the protocols described above.

2.5. Laboratory analyses

Total C and total N were determined with high temperature digestion using a vario MACRO Elemental Analyser (Elementar). Soils were also analysed for pre-existing mineral N ($NH_4^+ + NO_3^-$) and mineralisable N using Method 4 of Gianello and Bremner (1986). This method measures the amount of N mineralised over a 16 h period of anaerobic digestion at 100 °C, providing us with an index of the potential pool of N available to plants at the time of sampling. The index of mineralisable N cannot be numerically compared with $NH_4^+ + NO_3^-$. Nevertheless, these data are highly correlated with exhaustive aerobic soil incubation for N mineralisation (Gianello and Bremner, 1986).

2.6. Statistical analyses

We used a mixed-models approach (Minitab, 2007) to examine differences in the concentrations of mineral N ($NH_4^+ + NO_3^-$), mineralisable (available) N, total C and N and C:N ratio. Separate analyses were performed for the drought and post-drought data due to the unbalanced nature of the study, i.e. not all surface types were sampled with the same level of intensity during the drought and non-drought. For the drought measurements, the main plots were surface type (stony, part-stony, stone-free) and the sub-plots crust type (crust overlain by sand, light crust, dark crust) and their interaction with surfaces. A third stratum considered depth (0–1 cm, 1–5 cm) effects and its two- and three-way interactions with surfaces and crust type. For the post-drought data, the main plots were four surface factors (i.e. stony, part-stony, stone-free) and the sub-plots crust type and their interaction with the surface factor. The third stratum considered depth (0–1 cm, 1–5 cm) effects and its two- and three-way interactions with surface factor and crust type. For all GLM analyses, data were checked for homogeneity of variance, independence and normality using Levene's test and other diagnostic tools within the Minitab (2007) statistical package and were $\log_{10}$-transformed, where appropriate. In all cases, significant *post hoc* differences between means were compared using least significant difference (LSD) testing.

We used permutational multi-variate analysis of variance (PERMANOVA, Anderson et al., 2008) to test whether cyanobacterial composition for the drought samples varied among surfaces, crust types, and their interactions, using a matrix of nine columns (species) by 30 rows (surface types, crust types). PERMANOVA allowed us to partition the multivariate variation using the structure described above for the univariate analyses. The matrix of abundance data was converted to a similarity matrix using the Bray Curtis similarity coefficients contained within the PRIMER-E statistical package. Pair-wise *a posteriori* comparisons were made, where necessary, using a multi-variate analogue of the *t* statistic, the probability levels being obtained by permutations. Differences in abundance of individual taxa between crust types, surfaces and their interactions were examined using a similar two stratum model as described for the nitrogen analyses.

3. Results

3.1. Cyanobacterial crust structure across the paddock

Nine cyanobacteria, two cyanolichens, five chlorolichens, three mosses, three liverworts and two algae were recorded in the samples across the paddock. *Porphyrosiphon notarisii* Kützing ex Gomont 1892 was the most abundant cyanobacterium in all crust types, occurring in 37% of samples in the runoff zones. Where they occurred, the N-fixing species *Stigonema ocellatum* (Dillwyn) Thuret ex Bornet et Flahault, *Scytonema* cf. *hofman-bangii* C. Argardh ex Bornet et Flahault 1887 and *Gloeocapsopsis* cf. *dvoraki* (Nováček) Komárek et Anagnostidis 1986 were abundant and accounted for 41–51% of crust composition on all surfaces across all crust types in the runoff zones. Non-heterocystous forming *Schizothrix* cf. *fuscescens* Kutzing ex Gomont 1892 was common to abundant in the sub-surface samples.

3.2. Cyanobacteria associated with nitrogen samples

We detected significant differences in the composition of cyanobacterial species for the drought sampling between the stone-free and the stony (part-stony or stony) groups (pseudo $F_{2,7} = 4.99$, $P(\text{perm}) = 0.037$). This was attributed to almost twice the abundance of *P. notarisii* in the stony than the stone-free surfaces ($F_{2,7} = 15.2$, $P < 0.001$). There was also a significant crust type effect (pseudo $F_{2,14} = 5.01$, $P(\text{perm}) = 0.005$), with differences between the crust overlain with sand and the other two crust types. Abundances of the nitrogen-fixing *S. ocellatum* ($F_{2,14} = 17.6$, $P < 0.001$), the alga *Klebsormidium* ($F_{2,14} = 3.95$, $P < 0.044$) and the

Table 1
Average abundance on a scale of 1 (rare) to 8 (abundant) of soil crust taxa from the three crust types averaged over the three surfaces.

Taxa	Crust type		
	Dark	Light	Sand
Scytonema cf. *hofman-bangii*[a]	4.73[a†]	2.94[b]	2.17[b]
Stigonema ocellatum[a]	3.47[a]	3.36[a]	0.57[b]
Gloeocapsopsis cf. *dvoraki*[a]	0.30[a]	0.40[a]	0.06[a]
Klebsormidium	0.78[ab]	1.29[a]	0.32[b]
Porphyrosiphon notarisii	5.85[a]	5.07[a]	5.59[a]
Schizothrix	4.22[a]	4.25[a]	2.27[b]
Chroococcccus	0.15[a]	0.27[a]	0.17[a]
Phormidium	0.36[a]	0.00[a]	0.00[a]
Microcoleus[a]	0.28[a]	0.00[a]	0.00[a]

† Values followed by the same letter are not significantly different at $P < 0.05$.
[a] Known N-fixers.

non-nitrogen-fixing *Schizothrix* cf. *fuscescens* ($F_{2,14} = 6.54$, $P = 0.010$) were significantly less on the sand-covered samples than either the light-coloured (thin) or dark-coloured (thick) crusts (Table 1). *Scytonema* cf. *hofman-bangii* was also significantly more abundant in the thick crusts ($F_{2,14} = 5.9$, $P = 0.024$). Although *P. notarisii* was the most abundant in samples, there were no significant differences between crust types ($P = 0.09$; Table 1).

3.3. Soil nitrogen and carbon

There were no significant differences in mineral N ($NH_4^+ + NO_3^-$) between any of the stony or stone-free surface types either before or after drought ($P > 0.24$). During the drought, mineral N concentrations were three-times greater in the sand-covered crust than either the light or dark sand-free crust ($F_{2,14} = 4.59$, $P = 0.029$ on $\log_{10}$-transformed data; Fig. 2). Trends were similar after the drought, with about a four-times greater concentration of mineral N in the sand-covered crust compared with the other crust surfaces ($F_{2,16} = 10.06$, $P = 0.001$ on $\log_{10}$-transformed data); however there was an overall reduction in mineral N concentrations (Fig. 2). Mineral N concentrations declined by about 35% with depth during the drought ($F_{1,21} = 12.64$, $P = 0.002$ on $\log_{10}$-transformed data) and by about 20% after the drought ($F_{1,24} = 53.14$, $P < 0.001$ on $\log_{10}$-transformed data; Fig. 2).

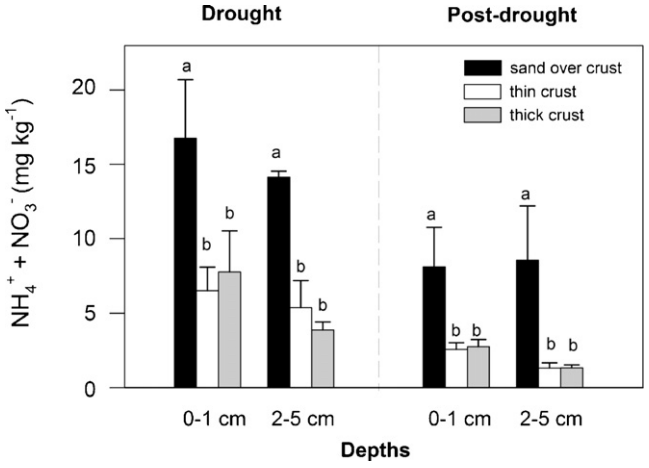

Fig. 2. Mean (±SE) mineral N ($NH_4^+ + NO_3^-$) concentration in relation to depth and crust types for both drought and post-drought periods on the runoff zones. Depth effects were significant for both periods. For both periods, concentrations of mineral N were always greater in the sand over crust type (SC) compared with the light crust (LC) or dark crust (DC). Different letters within a depth and season indicate a significant difference in mineral N concentration at $P < 0.05$. SE = standard error of the mean.

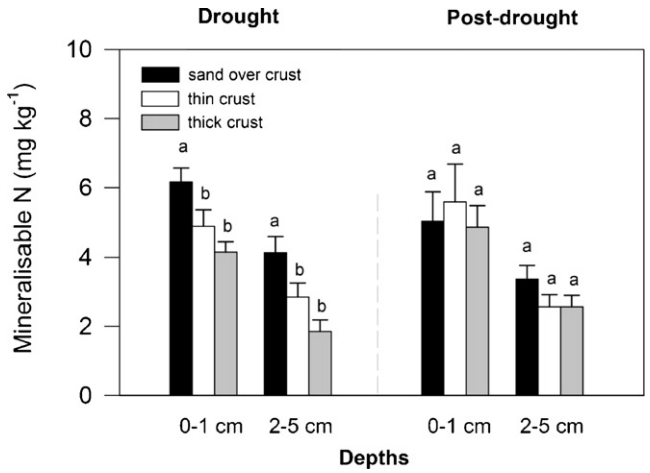

Fig. 3. Mean (±SE) mineralisable nitrogen concentration in relation to depth and crust types for both drought and post-drought periods on the runoff zones. Depth effects were significant for both periods. For the drought period only, mineralisable N was greater in the sand over crust type (SC) compared with the light crust (LC) or dark crust (DC). Different letters within a depth and season indicate a significant difference in mineralisable N at $P < 0.05$. SE = standard error of the mean.

There were no significant two- or three-way interactions either before or after the drought ($P > 0.05$).

For the runoff areas only, average mineralisable N concentrations were about 26% greater during the drought (4.03 ± 0.24 mg kg^{-1}; mean ± SE) compared with after the drought (3.20 ± 0.28 mg kg^{-1}), though the design of our study precluded us from testing this statistically. Mineralisable N concentrations during the drought were significantly greater on the sand-covered crust ($F_{2,14} = 8.09$, $P = 0.005$) compared with the other crust types. However, this trend was not apparent after the drought ($P = 0.74$; Fig. 3). Mineralisable N was always greater in the surface soil layer both during the drought ($F_{1,21} = 133.2$, $P < 0.001$) and after the drought ($F_{1,24} = 167.42$, $P < 0.001$ on $\log_{10}$-transformed data). The significant crust by depth interaction indicated that although there was a 75–85% greater concentration of mineralisable N in the topsoil compared with the subsoil in the light and dark crusts, the increase was much less (~40%) for the sand on crust surface ($F_{2,24} = 6.04$, $P = 0.008$ on $\log_{10}$-transformed data).

There were no significant effects on total C, but predictably, total N was always significantly greater in the topsoil (0.06 mg kg^{-1}) than the subsoil (0.05 mg kg^{-1}) both during ($F_{1,21} = 25.08$, $P < 0.001$) and after ($F_{1,24} = 14.85$, $P = 0.001$) drought. Carbon to nitrogen ratios of ~15 suggested functional soil mineralisation processes. Deeper soils tended to have a slightly greater C:N ratio both during (14.8:1; $F_{1,21} = 15.74$, $P = 0.001$) and after the drought (15.9:1; $F_{1,24} = 21.82$, $P < 0.001$).

4. Discussion

In our study, the sand-covered cyanobacterial crust contained three-times the concentration of mineral N and twice the concentration of mineralisable (available) N as cyanobacterial crusts without a sandy covering. The significant N result was obvious both during and after drought (but only for mineral N) in both the immediate surface and at depth, suggesting the presence of a general pattern rather than any depth- or season-specific effect. Significant quantities of N are produced by microbiotic soil crusts in arid and semi-arid regions worldwide, and values range from 0.7 to 100 kg N ha^{-1} yr^{-1} (Evans and Lange, 2003). Biological fixation of N by crusts in arid Australian soil is estimated to be in the vicinity of 1.3 kg N ha^{-1} yr^{-1} (Rychert et al., 1978), and has been linked to the presence of both cyanobacteria and cyanolichens in surface

crusts (Rogers and Lange, 1966; Smith et al., 1990). Free-living, N-fixing bacteria are also important contributors to N pools in desert soils (Smith et al., 1990; Hawkes, 2003), which typically support complex soil microbial communities (Garcia-Pichel et al., 2003). In this study, mean total N concentrations in surface soils were comparable to values reported for Australian arid zone soils (Charley, 1972).

Two principal mechanisms that could account for increases in N bioavailability in sand-covered crusts are (1) cell lysis and release of N following the decomposition of buried cyanobacterial crusts (Evans and Lange, 2003; Hu et al., 2003; Wang et al., 2007), and (2) inhibition of denitrifying bacteria under the sand (Thomas et al., 2008). While evidence from marine systems suggests that many cyanobacteria are adapted to repeated cycles of deposition under soft sediments (Stal, 1995), the survival of cyanobacteria under sandy deposits in terrestrial systems has been little studied and is therefore poorly understood. In our study, *S. ocellatum* was almost absent from our sand-covered samples but relatively abundant in the sand-free crusts, suggesting that it may be unable to survive long periods of inundation during drought.

The most likely explanation for the presence of enhanced N pools under sand is through the death and autolysis of cyanobacterial cell material, which is rich in carbon (Zulpa de Caire et al., 1997), nitrate and ammonium ions (Veluci et al., 2006). Microtopography and prolonged inundation at depth not only limit light and water infiltration, leading to death of cyanobacteria, but can also change the crust formation between organic and inorganic layers (Hu et al., 2003). Autolysis of cyanobacteria results in significant reductions in EPS (Wang et al., 2007). High temperatures and precipitation alter the rheological properties of glycan (a major component in EPS), allowing water to penetrate the cell membrane (Potts, 2001; Shaw et al., 2003). Cells lacking sufficient light to activate photosynthesis are vulnerable to autolysis. Although the reasons are poorly understood, the EPS relinquishes its ammonium within minutes of wetting, which would explain the release of cyanobacterial-mediated N into the soil (Potts, 2001). Post-drought uptake of N by vascular plants would account for our observations of reduced mineral N pools.

Variable layers of sand could also alter micro-scale environmental conditions sufficiently to inhibit denitrifying bacteria (Westerman and Tucker, 1978; Johnson et al., 2007). Reduced populations of denitrifying bacteria in the immediate surface layers would result in incomplete N turnover and therefore accumulation of N in a bio-available form (Johnson et al., 2005). Our results are also consistent with observations that the sand layer not only reduces oxidisation, but also inhibits denitrifying bacteria, ultimately resulting in a net export of ammonium and nitrate from the crusts to the underlying soil (Johnson et al., 2007).

Sandy deposits could also have other effects. Sand could protect the underlying soil crust from splash erosion by functioning as an armouring layer during high intensity storms, which are common at the end of droughts. Sand could also reduce the vigour and size of perennial grasses, particularly during droughts, reducing effective competition for N and water. A portion of the increased N could be derived from other disturbed upwind sites from which cyanobacterial crusts have been stripped through wind erosion (McTainsh et al., 1998), a possible consequence of stock trampling (Williams et al., 2008).

The most parsimonious explanation for enhanced N pools is, however, decomposition of some cyanobacterial species trapped under sand, leading to the liberation of extracellular N (Fogg et al., 1973; Russow et al., 2005). The typical precipitation pattern in semi-arid Australia is one that is highly skewed towards rainfall events of only a few millimetres (Stafford Smith and Morton, 1990). While these are generally insufficient to promote vascular plant growth, they promote a rapid response by cyanobacteria and heterotrophs in soil crusts, and provide sufficient moisture for cyanobacterial crusts to maintain their biological functions (Lange et al., 1994). Soil drying and rewetting in our study area would be expected to promote cycles of desiccation and rehydration in cyanobacteria. Some mineral N will be released during these small rainfall events largely from N stored in rainwater (Zaady et al., 1998). The small frequent wetting events during drought will increase bacterial activity in the immediate vicinity of the crusts accelerating the degradation of EPS (Wang et al., 2007). The processes observed in our soils are consistent with the model proposed by Charley (1972), which demonstrates the stepped increase in N mineralisation associated with wetting, followed by the gradual accumulation of the N pool. Even though photosynthesis can commence in these small wetting events, as demonstrated in cyanobacterial crusts in the Kalahari Desert, moisture penetration into the soil can be insufficient to initiate bacterial activity (Thomas et al., 2008).

5. Conclusions

Increased bioavailability of N during drought appears to be largely independent of abundance or survival of N-fixing cyanobacteria in our crusts. Rather, our data suggest that it is related to the disintegration and lysis of cyanobacterial material under a layer of sand. In the absence of native or naturalised N-fixing plants, cyanobacterial soil crusts are likely to be significant contributors to soil N pools, particularly during drought. Indeed, naturally abundant cyanobacterial soil crusts in these ecosystems seem well adapted to cycles of drought and inundation by sand.

The demise of N-fixing cyanobacteria and the ability of *P. notarisii* to survive inundation may be critical for post-drought recovery of soil function in many Australian semi-arid and arid grasslands. Nitrogen production processes could be compromised if crust diversity is reduced, droughts increase in frequency and duration, or there is ongoing destruction by stock trampling (Williams et al., 2008). Similarly, while short-term increases in available N may occur, as in our study, there is potential for long-term declines in the capacity to produce N with the demise of N-fixing cyanobacteria. Protection of the soil surface by maintaining adequate ground cover and reducing disturbance will be critical issues for sustaining soil N pools.

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