

Soil nutrients under shrub hummocks and debris mounds two decades after ploughing

Stefani Daryanto · David J. Eldridge ·
Terry B. Koen

Received: 1 June 2011 / Accepted: 24 August 2011 / Published online: 10 September 2011
© Springer Science+Business Media B.V. 2011

Abstract

Aims Shrub removal by ploughing has been used widely to reduce the effects of shrub encroachment into open woodlands and grasslands. Our aim was to demonstrate that soil chemical properties varied markedly among three patch types (shrub hummock, debris mound, interspace) which varied in age, almost two decades after shrub removal by ploughing.

Methods We compared changes in nutrients under 1) young post-ploughing recruits and mature, unploughed shrubs, 2) mature and recently formed debris mounds and 3) ploughed and recovering interspaces at three depths.

Results Irrespective of their age, nutrient concentrations were greater under shrub hummocks and debris mounds than in the interspaces at two sites. Soil in mature shrub hummocks generally had greater levels of labile carbon and nitrogen (total, mineral, mineralisable), but results varied between sites. There were a few, sometimes inconsistent, effects of ploughing on nutrients under debris mounds, and no differences between the interspaces two decades after ploughing. Nutrient effects were most marked in the top 15 cm of the soil, diminishing rapidly with depth.

Conclusions Our results reinforce the importance of hummocks and mounds as resource sinks and indicate the long-lasting effects of disturbances such as ploughing on soil nutrient pools.

Responsible Editor: Tibor Kalapos.

S. Daryanto
Evolution and Ecology Research Centre,
School of Biological, Earth and Environmental Science,
University of New South Wales,
Sydney, NSW, Australia 2052
e-mail: s.daryanto@student.unsw.edu.au

D. J. Eldridge (✉)
Office of Environment and Heritage, c/- Evolution and
Ecology Research Centre, School of Biological, Earth and
Environmental Science, University of New South Wales,
Sydney, NSW 2052, Australia
e-mail: d.eldridge@unsw.edu.au

T. B. Koen
Office of Environment and Heritage,
P.O. Box 445, Cowra, NSW 2794, Australia
e-mail: Terry.Koen@environment.nsw.gov.au

Keywords Blade ploughing · Debris mounds ·
Encroachment · Fertile island · Shrub · Shrub removal ·
Woodland recovery

Introduction

Encroachment of woody plants into grasslands and the conversion of woodland and open savanna to shrubland is a well documented global phenomenon (e.g. van Auken 2009). Evidence worldwide indicates that woody vegetation plays critical roles in modifying the soil's physical and chemical environment

(Shachak et al. 2008) and provides important habitat for plants and animals (Blaum et al. 2007). There is increasing evidence that woody encroachment alters the spatial distribution of soil nutrient sinks by increasing the cover and arrangement of shrub hummocks and reducing the cover and biomass of herbaceous vegetation (Schlesinger et al. 1996). Soil beneath shrubs contains higher levels of potentially limiting resources such as water, organic matter, seed and nutrients than soil from the interspaces (Archer et al. 2001; Wezel et al. 2000), a phenomenon known variously as the ‘fertile island’ or ‘island of fertility’ effect (e.g. Charley and West 1975, Garner and Steinberger 1989, Schlesinger et al. 1990). This shrub-focused resource distribution is reinforced by the deposition of eroded interspace soil in the shrub patches (Okin et al. 2006) and reduced connectivity between shrub patches (McGlynn and Okin 2006). Shrub growth is promoted at the expense of plants in the interspaces as a result of enhanced microbial and faunal activity in the soil beneath shrub canopies.

Shrubs have been shown to have positive (facilitatory) effects on ecosystem processes such as the development of landscape heterogeneity (e.g. Peters et al. 2006) and increased plant diversity and soil function (Maestre et al. 2009, Eldridge et al. 2011). Increasing shrub density, however, also results in declining pastoral productivity (van Auken 2009). Thus a commonly held view is that large aggregations of shrubs are a sign of degradation (Schlesinger et al. 1996, Tighe et al. 2009), mainly because encroachment is typically viewed in the context of pastoralism (commercial grazing). Indeed, the putative loss of soil function resulting from shrub encroachment is generally regarded worldwide as a precursor to desertification (e.g. Schlesinger et al. 1996).

There have been numerous attempts to restore pastoral productivity for domestic livestock in shrub-encroached grasslands by physical removal of the shrubs; often with mixed success (e.g. Herrick et al. 2006). In eastern Australia, burning and mechanical removal by blade ploughing or root ploughing (MacLeod and Johnston 1990) have been used. Burning requires sufficient groundstorey biomass to carry a fire, and is only suitable following periods of high rainfall that generate sufficient fuel. Low frequency fire would likely favour shrubs as their seeds are known to have a greater germination capacity after fire (Hodgkinson 1991). Mechanical

removal, however, has been promoted widely by land management agents over the past two decades, though its effectiveness varies widely (Robson 1995; Daryanto and Eldridge 2010). Despite an initial reduction in the density of shrubs in the ploughed area, mechanical removal of shrubs often has landscape-scale consequences, such as the increase in wind and water erosion (Coffin et al. 1996).

While a large number of studies has examined changes in shrubland plant communities following mechanical disturbance (e.g. Allegretti et al. 1997), relatively few have considered changes in soils or soil processes, under shrubs and associated debris mounds. Mechanical shrub removal has also been shown to induce short-term increases in soil nutrient pools, followed by gradual declines (Bechtold and Inouye 2007; McClaran et al. 2008). Bolling and Walker (2002) for example, showed a markedly diminished fertile island effect around shrubs regenerating after mechanical disturbance, even after 80 years. Similarly, Teague et al. (1999) failed to demonstrate substantial differences in soil carbon (C) and nitrogen (N) between shrub-dominated and shrub-free environments more than two decades after ploughing. Declines in soil C and N following shrub mortality have been recorded for up to 40 years (Kelly and Burke 1997; McClaran et al. 2008). Apart from these studies of shrub effects on soils, we are unaware of any studies looking at changes associated with debris mounds.

The effect of shrub management practices on the development of biogeochemical pools associated with new fertile islands around shrub recruits or debris mounds is largely unknown for Australian shrublands. Shrublands in eastern Australia are characterised by hummocks of variable size, often with relief to 10 cm, supporting shrubs. They are separated by extensive interspaces dominated by either bare ground or surfaces colonised by cryptogamic soil crusts. The interspaces often have a variable cover of debris mounds, often accumulating around fallen timber or shrubs, and resulting from the accumulation of wind- or water-eroded erosion. While similar mounds have been described in open grassland (log mounds, *sensu* Tongway et al. 1989), they have been poorly studied in encroached woodlands.

We used a long-term enclosure study to examine the effects of four shrub removal treatments involving ploughing and grazing on fertile island development

in a shrub–encroached woodland. The four treatments were: ploughing followed by 1) grazing or 2) exclosure, and no ploughing followed by 3) grazing or 4) exclosure. We used the two ploughing treatments (averaged across grazed and ungrazed treatments), which produced two relative ages (young or mature), to examine potential differences in soil nutrients in three landscape elements (shrub hummocks, coarse woody debris mounds, interspaces), yielding six possible patch by age combinations as follows: 1) hummocks and their attendant mature shrubs that were not removed during the ploughing operation (mature hummocks), 2) hummocks supporting young shrubs that recruited after ploughing (young hummocks); 3) mounds of coarse woody debris representing sites of natural breakdown of mature shrubs (mature mounds), 4) mounds of coarse woody debris forming around large shrubs that were killed as a result of ploughing 18 years previously (young mounds), 5) unploughed, relatively undisturbed interspaces (undisturbed interspaces), and 6) interspaces that were recovering from ploughing about 18 years previously (recovering interspaces) (Table 1).

We had three hypotheses about soil nutrients in relation to these three different aged landscape elements. First, in support of the fertile island hypothesis, we expected to detect greater C and nutrient (e.g. N) concentrations under all resource–accumulating elements (shrub hummocks, debris mounds) than in the interspaces, irrespective of their age. Second, we predicted that the soil within hummocks under older shrubs that were present before ploughing (mature hummocks) would have greater concentrations of C and N than younger shrubs recruiting from seed after ploughing, as older (generally larger) shrubs are likely to sequester and accumulate greater C and N pools than younger

shrubs (McClaran et al. 2008; Throop and Archer 2008) and the period of accumulation is greater. Similarly, soil around older debris mounds would be expected to be more nutrient–enriched than that around young mounds, given that larger, older mounds have a greater ability to capture and hold resources and attract microarthropods (*sensu* Tongway et al. 1989). Finally, we predicted that concentrations of soil C and N would be greater in the undisturbed than the recovering interspaces as ploughing disturbs cryptogamic crusts (Eldridge and Robson 1997), which accumulate C and N, and recover very slowly from disturbance (Belnap and Eldridge 2001).

Methods

Study area

The study was conducted at two semi–arid woodland sites in north–western New South Wales, Australia; Wapweelah (29°16'S, 145°26'E) and Bloodwood (29°30'S, 144°45'E) about 140 km north and north-west of Bourke respectively. Summers are hot (mean maximum 36.4°C) while winters are mild (mean minimum 17.9°C) and rainfall at both sites averages about 300 mm annually, with 45% more rain occurs between October and April. The landscape is level to slightly undulating (< 1% slope) and comprises of sandplains of Quaternary alluvium and aeolian sediment (Robson 1995). Wapweelah falls within the Gumbalie Land System and is characterised by sandy red earths with loam to sandy loam surface textures. Bloodwood has calcareous red earths and sandy earths with topsoil textures that are loamy sands and falls within Goonery Land System (Walker 1991).

Table 1 Summary of the four ploughing and grazing treatment scenarios and their extent in eastern Australia. Mature shrub hummocks are ~60 years old, younger shrub hummocks <20 years old

| Scenario | Ploughed | Grazed | Shrub hummock | | Debris mound | | Interspace | |
|---------------------|----------|--------|---------------|-------|--------------|-------|-------------|------------|
| | | | Mature | Young | Mature | Young | Undisturbed | Recovering |
| Unploughed Ungrazed | no | no | yes | | yes | | yes | |
| Ploughed Ungrazed | yes | no | | yes | | yes | | yes |
| Unploughed Grazed | no | yes | yes | | yes | | yes | |
| Ploughed Grazed | yes | yes | | yes | | yes | | yes |

Both sites were dominated by shrubs, which encroach into the bare areas remaining after the removal of perennial grasses by grazing (Daly and Hodgkinson 1996). They supported similar shrub species, though with slightly different composition. Wapweelah supported dense stands of turpentine (*Eremophila sturtii*), green turkey bush (*Eremophila gilesii*) and budda (*Eremophila mitchellii*), at densities up to 7000 stems ha⁻¹ (Daryanto and Eldridge 2010) while Bloodwood was dominated by narrow-leaved hopbush (*Dodonaea viscosa* subs. *angustissima*). Scattered mulga (*Acacia aneura*) trees occurred at both sites. The groundstorey vegetation at both sites was dominated by a range of perennial grasses such as woollybutt (*Eragrostis eriopoda*) and wiregrasses (*Aristida* spp.), with assorted ephemeral forbs from the families Chenopodiaceae and Brassicaceae (Robson 1995; Eldridge and Robson 1997).

Shrub removal design

In 1990, one block (200 m×400 m) was established and divided into four equal plots of 200 m long by 100 m wide. The two central plots were then enclosed in a 6 m high, vertebrate-proof fence. Half of the fenced and one of the unfenced plots were then ploughed, leaving the remaining unploughed (Fig. 1). This design therefore resulted in four combinations: ploughed-grazed, ploughed-ungrazed, unploughed-grazed and unploughed-ungrazed. This experimental setup was repeated at three replicate locations (blocks) separated by distances of 1–5 km. The same design was used at both sites. The grazed plots were grazed by sheep, goats,

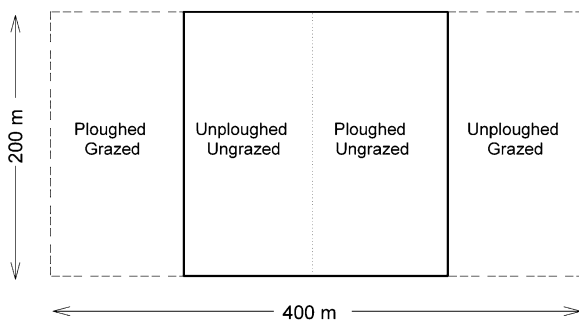


Fig. 1 Layout of the treatments for both sites. The solid line represents a vertebrate-free enclosure and the broken lines outside indicate the extent of the grazed plots

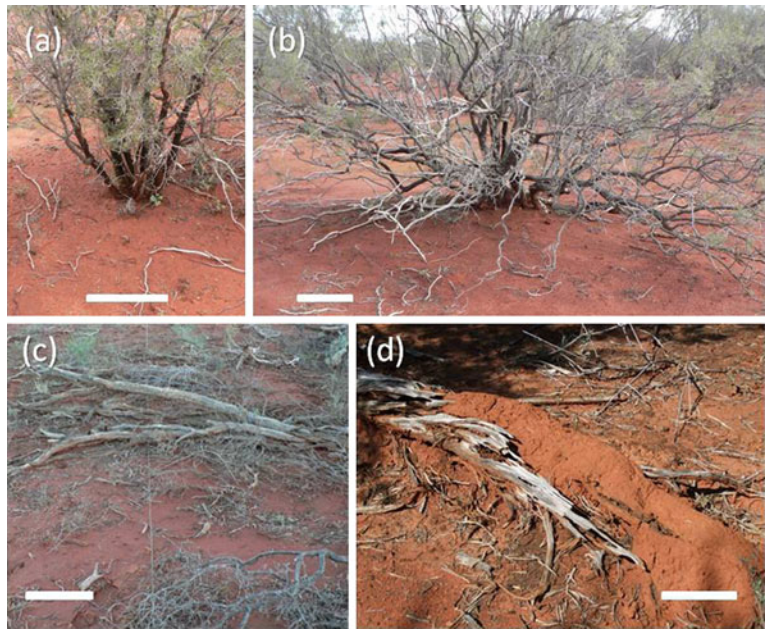
cattle, kangaroos and low densities of rabbits. The ploughing treatment consisted of a single pass with a 4.2 m wide single-tined 'Stationmaster' blade plough pulled by a 90 kW crawler tractor and only shrubs were removed during ploughing (Robson 1995). Trees were not removed during ploughing, though some herbaceous species would have died as a result of soil disturbance. Ploughing severs the roots of woody plants about 20 cm below the surface and has minimal effect on the soil surface. However, hummocks from which shrubs have been ploughed are susceptible to deflation and loss of topsoil while they are unvegetated.

Soil sampling and laboratory analysis

Soils were sampled at both Wapweelah and Bloodwood 18 years after ploughing and enclosure on the three landscape elements: 1) shrub hummocks supporting *Eremophila sturtii* or *Dodonaea viscosa* shrubs, 2) areas of coarse woody debris (termed 'debris mounds'), which comprised the stems of dead shrubs and some accumulating woody debris, and 3) the interspaces. *Eremophila sturtii* and *Dodonaea viscosa* hummocks were chosen because they are the dominant hummock-forming shrubs at both sites. Unlike *Acacia* and *Senna* species, they do not fix N, so any shrub effects on soil nutrients would be due to their resource capturing abilities rather than direct N fixation.

Shrubs at the two ploughed treatments (ploughed-grazed, ploughed-ungrazed) were less than 18 years old (termed 'young hummocks') as all shrubs had been removed by the ploughing treatment 18 years previously (Fig. 2a). Substantial shrub recruitment about 12 months after ploughing (David Robson, personal observation) suggests that most young shrubs would have been about 17 years old or younger at the time we sampled the soils. Most would have established from seeds but a few may have resprouted from epicormic buds (Daryanto and Eldridge 2010). The debris mounds represented the remains of shrubs that had been pushed over during by ploughing 18 years previously (termed 'young mounds'; Fig. 2c). We selected only debris mounds in the clearly-defined plough lines (which were still evident 18 years after ploughing), thereby ensuring that young mounds were about 18 years old. Debris mounds contained areas of sediment and litter, and

Fig. 2 Images of the shrub hummock and debris mound microsites showing **a** young hummock with *Eremophila sturtii*, **b** mature hummock with *Eremophila sturtii*, **c** young debris mound soon after ploughing and **d** mature debris mound with clear evidence of decomposition by termites. Bars are 30 cm across



covered an area of up to 10 m² (Fig. 2c). The interspaces in the two ploughed treatments were designated as ‘recovering’ from the action of ploughing, and sampling was restricted to areas showing clear evidence of ploughing.

Sampling on the remaining two unploughed treatments (unploughed–grazed, unploughed–ungrazed) was conducted within hummocks under large old shrubs (mature hummocks; Fig. 2b), under large debris mounds (mature mounds, Fig. 2d) and within the interspaces. Mature shrubs are substantially larger (~5 m diameter, 3–4 m tall) and therefore older than ‘young shrubs’ (1–2 m diameter, ~1.5 m tall). Based on data from long-term shrub studies at Fort Bourke near our study sites (Booth and Barker 1981), we expect that mature shrubs probably recruited during the high rainfall years in the early 1950s and were therefore about 60 years old when their hummocks were sampled. Mature debris mounds, representing sites of natural attrition of former large shrubs, were sampled only from the unploughed sites. We used characteristics such as the degree of incorporation in the soil and breakdown by termites (Fig. 2d) to confirm that they were more than about 30 years old. Long-term records of fallen timber from other areas of arid Australia demonstrate the strong relationships between stage of breakdown and age (Sinclair 2004). Finally, the interspaces in the unploughed treatments were designated as ‘undisturbed’.

Across all treatments, soils were sampled from three depths (0–5 cm, 10–15 cm and 25–30 cm) beneath the three landscape elements (shrub hummock, debris mound, and interspace) with a 6.2 cm cylindrical coring device. Samples for shrub hummocks were taken at the mid-canopy to ensure the capture of most soil sediments, including that from the stem flow (Whitford et al. 1997). Interspace soils were sampled within the bare areas and more than 5 m from any plant canopies. For debris mounds, samples were taken from the upslope position. Sampling sites were in an unbiased manner from within transects placed throughout the plots for assessment of vegetation cover. Soils were air dried, passed through a 2 mm sieve, and transported to the laboratory for further analyses. Soil moisture was determined volumetrically, and bulk density calculated after removal of any coarse (> 2 mm diameter) fractions (Throop et al. 2011). Electrical conductivity (EC) and pH were determined using 1:5 soil:water suspension. Labile C was determined using modified permanganate oxidizable C method (Weil et al. 2003). Mineralisable and pre-existing mineral N was determined using salicylate–dichloroisocyanurate method and the Flow Injection Analysis was conducted using Quikchem 8500 at 660 nm (Gianello and Bremner 1986). Total C and N were analysed using high temperature combustion analysis (LECO CNS-2000; LECO Corporation, St. Joseph, MI, USA).

Statistical analysis

A matrix comprising the average value of each soil property for young and mature hummocks and debris mounds, and disturbed and undisturbed interspaces, for each of three blocks ($n=9$) was subjected to Principal Component Analysis using the PRIMER (Version 4) statistical package (Clarke and Warwick 1994). Each variable was normalised by subtracting the mean and dividing by the standard deviation in order to bring the data with mixed measurement scales to a common dimensionless scale. Separate analyses were performed for Wapweelah and Bloodwood. We use a split-plot (mixed-models) ANOVA approach to examine possible shrub effects on soil nutrients. The first stratum considered Blocks ($n=3$), and the second stratum landscape element effects (i.e.

shrub hummock, debris mound, interspace). To determine the age effect, we partitioned the landscape element subplot into a number of single degree of freedom contrasts i.e. differences between young and mature hummocks, young and mature debris mounds, and recovering and undisturbed interspaces. This approach is more consistent with our hypothesis about age effects within specific landscape elements than one that considered all possible, and less meaningful, effects among the three landscape elements by two age units (Table 2). One degree of freedom contrasts for additional grazing effects were largely ignored. The third stratum considered depth effects and their interactions with landscape elements. Again we were only interested in the three interactions among depth, landscape element and age unit, each with two degrees of freedom (Table 2). All data

Table 2 An example of the mixed-models ANOVA structure for total N

| Component | d.f. | <i>F</i> statistic | <i>P</i> -value |
|--|------|--------------------|-----------------|
| Block stratum | 2 | 4.51 | |
| Block.Landscape element stratum | | | |
| Landscape element | 2 | 7.09 | 0.004 |
| Landscape element.Interspace | 1 | 0.4 | 0.533 |
| Landscape element.Mound | 1 | 4.07 | 0.056 |
| Landscape element.Hummock | 1 | 20.13 | <0.001 |
| Landscape element.Interspace.Recovering | 1 | 2.84 | 0.106 |
| Landscape element.Interspace.Undisturbed | 1 | 0.12 | 0.737 |
| Landscape element.Mound.Mature | 1 | 0.27 | 0.611 |
| Landscape element.Mound.Young | 1 | 2.86 | 0.105 |
| Landscape element.Hummock.Mature | 1 | 9.7 | 0.005 |
| Landscape element.Hummock.Young | 1 | 0 | 0.973 |
| Residual | 22 | 1.77 | |
| Block.Landscape element.Depth stratum | | | |
| Depth | 2 | 51.45 | <0.001 |
| Depth.Landscape element | 4 | 4.83 | 0.002 |
| Depth.Landscape element.Interspace | 2 | 0.19 | 0.825 |
| Depth.Landscape element.Mound | 2 | 1.62 | 0.209 |
| Depth.Landscape element.Hummock | 2 | 7.22 | 0.002 |
| Depth.Landscape element.Interspace.Recovering | 2 | 0 | 0.999 |
| Depth.Landscape element.Interspace.Undisturbed | 2 | 1.12 | 0.334 |
| Depth.Landscape element.Mound.Mature | 2 | 1.03 | 0.365 |
| Depth.Landscape element.Mound.Young | 2 | 0.31 | 0.736 |
| Depth.Landscape element.Hummock.Mature | 2 | 6.6 | 0.003 |
| Depth.Landscape element.Hummock.Young | 2 | 0.06 | 0.942 |
| Residual | 48 | | |
| Total | 107 | | |

were checked for normality and homogeneity of variance (Levene's test, Genstat 12th Edition) prior to analyses and *post-hoc* differences in means were examined using Least Significant Difference testing. We calculated the total pools of nitrogen and carbon to 30 cm deep for Bloodwood and Wapweelah separately. Total C and N pools were obtained by integrating the area under the C or N percentage by depth curves for each landscape element and adjusting by the relevant bulk density values. For the unsampled layers (5 to 10 cm, 15 to 25 cm), we used the average bulk density and percentage values of either C or N from the soil layers immediately above and below them. We calculated separate pools for grazed and ungrazed plots.

Results

Results from Wapweelah indicated that the first two components of the PCA biplot had generally greater

concentrations of total and labile C, and mineral and mineralisable (available) N beneath mature mounds, mature hummocks and undisturbed interspaces. For Bloodwood, however, there were no clearly-defined trends in relation to the landscape elements by age units, and generally greater variability in soil properties among them (Fig. 3). Univariate analyses of individual soil physical and chemical properties indicated significant differences among the landscape units at both sites, with generally lower levels of most attributes in the interspaces than either under shrubs or under debris mounds (Table 3). Effects, however, were not always consistent between sites. For example, average bulk density was greater in the interspaces (1.63 Mg m^{-3}) than either the debris mounds or shrub hummocks (1.49 Mg m^{-3}) at Bloodwood, ($F_{2,22}=12.33$, $P<0.001$), but not at Wapweelah. Similarly, while average concentrations of total N and total C under shrub hummocks and debris mounds at Wapweelah were 2.5–times greater than in the interspaces ($F_{2,22}=7.09$, $P=0.004$ and $F_{2,22}=$

Fig. 3 Principal Component Analysis biplot displaying the first two component axes for sites at Wapweelah (a, c) and Bloodwood (b, d). Interrelationships among soil variables are presented in the top graphics. Sites are coded for age using young shrub hummocks, young mounds and recovering interspaces (*closed circle*) and mature mounds, mature hummocks and undisturbed interspaces (*open circles*). The site codings (*bottom graphics*) are shown separately to aid in the interpretation of the biplots

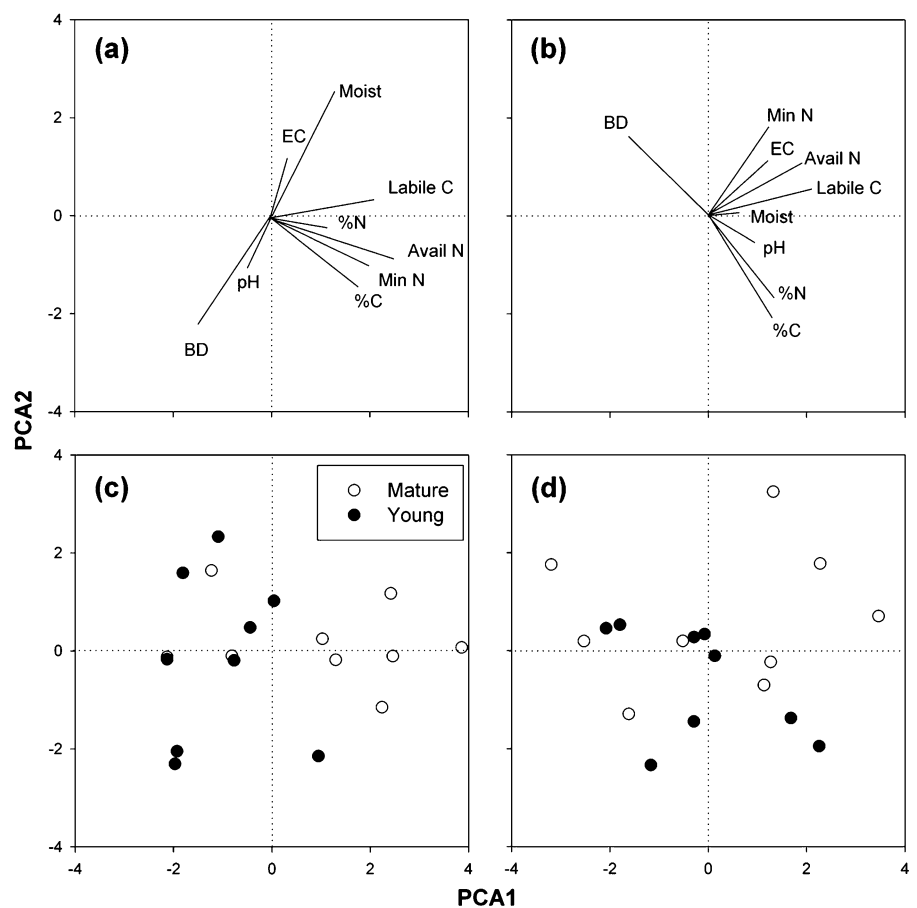


Table 3 Differences in soil physical and chemical properties between different ages and trends among the three landscape elements averaged over the three depths. H=hummock, M=mound, I=interspace. For a given site and landscape element

different superscripts indicate a significant difference in that attribute between mature–young or undisturbed–recovering at $P=0.05$. SE=standard error of the mean

| Soil chemical and physical properties | Landscape element | | | | | | | | | | | | Trend among landscape elements |
|--|--------------------|--------|--------------------|--------|-------------------|--------|-------------------|--------|-------------|--------|------------|--------|--------------------------------|
| | Shrub hummock | | | | Debris mound | | | | Interspace | | | | |
| | Mature | | Young | | Mature | | Young | | Undisturbed | | Recovering | | |
| | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE | |
| Bloodwood | | | | | | | | | | | | | |
| Total N (%) | 0.052 | 0.003 | 0.055 | 0.004 | 0.065 | 0.013 | 0.061 | 0.005 | 0.049 | 0.004 | 0.054 | 0.004 | H=M=I |
| Total C (%) | 0.445 | 0.048 | 0.498 | 0.055 | 0.468 | 0.071 | 0.578 | 0.113 | 0.359 | 0.041 | 0.468 | 0.057 | H=M=I |
| Mineral N (mg kg ⁻¹ soil) | 2.28 ^a | 0.422 | 1.21 ^b | 0.126 | 1.81 | 0.423 | 1.09 | 0.132 | 1.01 | 0.212 | 1.14 | 0.267 | H=M>I |
| Mineralisable N (mg kg ⁻¹ soil) | 8.60 | 0.897 | 7.77 | 1.287 | 8.14 | 1.103 | 7.55 | 1.024 | 4.37 | 0.552 | 3.74 | 0.413 | H=M>I |
| Labile C (mg kg ⁻¹ soil) | 117.2 ^a | 10.980 | 90.8 ^b | 5.468 | 121.8 | 10.954 | 120.1 | 12.554 | 60.1 | 2.697 | 76.4 | 9.266 | M>H>I |
| Bulk density (Mg m ⁻³) | 1.52 | 0.048 | 1.52 | 0.039 | 1.53 ^a | 0.050 | 1.40 ^b | 0.057 | 1.65 | 0.023 | 1.58 | 0.044 | H=M<I |
| Soil moisture (%) | 7.92 | 0.373 | 8.84 | 0.511 | 8.65 | 0.519 | 9.45 | 0.590 | 7.92 | 0.439 | 8.46 | 0.504 | H=M=I |
| pH (1:5 water) | 5.97 | 0.117 | 6.07 | 0.118 | 6.19 | 0.123 | 5.88 | 0.129 | 5.70 | 0.058 | 5.82 | 0.112 | H=M=I |
| EC (dS m ⁻¹) | 0.04 ^a | 0.007 | 0.01 ^b | 0.002 | 0.02 | 0.006 | 0.02 | 0.005 | 0.01 | 0.003 | 0.01 | 0.002 | H=M>I |
| Wapweelah | | | | | | | | | | | | | |
| Total N (%) | 0.064 ^a | 0.005 | 0.047 ^b | 0.002 | 0.057 | 0.005 | 0.049 | 0.003 | 0.047 | 0.002 | 0.044 | 0.002 | H=M>I |
| Total C (%) | 0.710 | 0.0813 | 0.544 | 0.049 | 0.742 | 0.088 | 0.615 | 0.061 | 0.498 | 0.042 | 0.512 | 0.059 | H=M>I |
| Mineral N (mg kg ⁻¹ soil) | 2.06 | 0.295 | 1.79 | 0.412 | 2.74 ^a | 0.600 | 1.45 ^b | 0.147 | 1.33 | 0.172 | 1.06 | 0.130 | H=M>I |
| Mineralisable N (mg kg ⁻¹ soil) | 17.00 ^a | 1.895 | 10.29 ^b | 1.007 | 12.67 | 1.612 | 11.85 | 1.462 | 8.46 | 0.724 | 7.28 | 0.625 | H=M>I |
| Labile C (mg kg ⁻¹ soil) | 378.5 ^a | 22.176 | 324.3 ^b | 17.236 | 329.9 | 18.376 | 304.5 | 9.794 | 288.6 | 11.211 | 296.4 | 11.882 | H>M=I |
| Bulk density (Mg m ⁻³) | 1.42 | 0.035 | 1.43 | 0.041 | 1.40 ^a | 0.042 | 1.60 ^b | 0.060 | 1.51 | 0.044 | 1.52 | 0.054 | H=M=I |
| Soil moisture (%) | 4.29 | 0.154 | 3.98 | 0.129 | 4.05 | 0.148 | 3.57 | 0.139 | 4.03 | 0.151 | 4.06 | 0.193 | H=M=I |
| pH (1:5 water) | 6.26 | 0.084 | 6.33 | 0.122 | 5.99 | 0.128 | 6.22 | 0.062 | 6.09 | 0.118 | 6.40 | 0.256 | H=M=I |
| EC (dS m ⁻¹) | 0.03 | 0.007 | 0.02 | 0.002 | 0.03 | 0.003 | 0.02 | 0.002 | 0.02 | 0.005 | 0.03 | 0.009 | H=M=I |

3.80, $P=0.038$ for N and C respectively), there were no significant N or C effects for Bloodwood (Table 3).

Age effects on soil nutrients

Differences in nutrients with age were not consistent across the two grazing properties (Table 3 and 4). At Bloodwood, there were more C and N under both young hummocks and debris mounds, however there was more C and N under mature hummocks and debris mounds at Wapweelah. Similarly, more C and N was recorded in the undisturbed interspace at Bloodwood, but at Wapweelah, more C and N was found in the recovering interspace. Other inconsistencies were also recorded for some attributes, for

example, we measured twice the concentrations of pre-existing mineral N under mature (2.28 mg kg⁻¹ soil) than young (1.21 mg kg⁻¹ soil) shrubs, but only at Bloodwood. Similarly, we recorded 36% more total N (0.064 cf. 0.047%, $F_{1,22}=7.09$, $P=0.004$) and 65% more available N (17.0 cf. 10.3 mg kg⁻¹ soil, $F_{1,22}=3.10$, $P<0.001$) under mature than young shrubs at Wapweelah, but the differences were insignificant at Bloodwood. Labile C was 29% and 16% greater at Wapweelah and Bloodwood respectively under mature than young shrubs. At Bloodwood, soil electrical conductivity under mature hummocks was four-times that under young shrubs (0.04 cf. 0.01 dS m⁻¹; $F_{1,22}=8.37$, $P=0.008$). There were no significant differences in any soil attributes

Table 4 Areal measures of total C and N (g m^{-2}) for sites at Bloodwood and Wapweelah to a depth of 0.3 m

| Site | Attribute | Mature shrub hummock | | Young shrub hummock | | Mature debris mound | | Young debris mound | | Undisturbed interspace | | Recovering interspace | |
|----------------|-----------|----------------------|-------|---------------------|-------|---------------------|-------|--------------------|-------|------------------------|-------|-----------------------|-------|
| | | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| Total carbon | Bloodwood | 2003.2 | 140.4 | 2160.1 | 46.2 | 1949.0 | 133.1 | 2177.1 | 78.0 | 1751.7 | 144.4 | 2028.5 | 74.8 |
| | Wapweelah | 2841.0 | 445.6 | 2199.9 | 233.7 | 2930.6 | 126.4 | 2886.6 | 213.2 | 2180.2 | 117.0 | 2229.5 | 545.9 |
| Total nitrogen | Bloodwood | 228.0 | 11.1 | 250.6 | 18.2 | 262.4 | 16.8 | 251.6 | 12.7 | 238.2 | 11.7 | 252.3 | 9.7 |
| | Wapweelah | 277.7 | 25.0 | 202.0 | 12.0 | 237.0 | 17.9 | 228.4 | 19.3 | 206.7 | 6.9 | 225.6 | 39.0 |

between undisturbed (unploughed) and recovering (ploughed) interspaces (Table 3).

Depth effects on soil nutrients

Predictably, there were clearly-defined reductions in most attributes (except EC at Bloodwood and pH at both sites) with increasing depth, but the depth profiles differed among the different shrubland elements. While the bulk density of undisturbed interspace soil was relatively high and changed very little with depth at Bloodwood, values at the surface of recovering interspaces were substantially lower and increased markedly with depth (depth \times patch interaction: $F_{2,48}=3.93$, $P=0.026$). Similarly for Bloodwood, there were some ill-defined changes in mineralisable N with depth under mature hummocks, with similar levels at the surface (11.7 mg kg^{-1} soil) and at depth (8.84 mg kg^{-1} soil) under mature hummocks, but marked reductions, from 14.7 to 5.80 mg kg^{-1} soil, under young hummocks (depth \times patch interactions: $F_{2,48}=4.87$, $P=0.012$, Fig. 4).

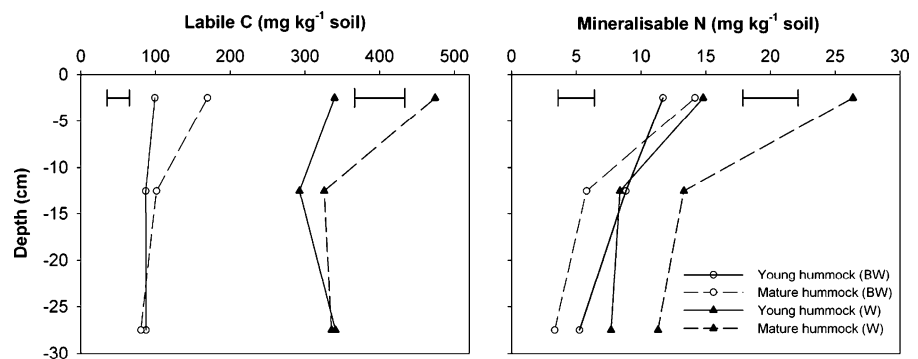
For labile C the trend was somewhat different. There was substantially more labile C under mature

(170 mg kg^{-1} soil) than young hummocks (99 mg kg^{-1} soil) at the surface at Bloodwood ($F_{2,48}=8.80$, $P<0.001$), but similar values below 15 cm depth ($81\text{--}101 \text{ mg kg}^{-1}$ soil; Fig. 4). This trend was similar for Wapweelah, with more labile C at the surface under mature (474 mg kg^{-1} soil) than young hummocks (341 mg kg^{-1} soil), but similar concentrations at depth (335 mg kg^{-1} soil; $F_{2,48}=5.41$, $P=0.008$; Fig. 4). Surface levels of mineralisable N were greater under mature (26.4 mg kg^{-1} soil) than young hummocks (14.8 mg kg^{-1} soil) at Wapweelah, but declines were less pronounced for young hummocks (depth \times patch interaction: $F_{2,48}=6.05$, $P=0.005$; Fig. 4). Similarly, total N at Wapweelah changed very little with depth ($0.06\text{--}0.05\%$) under young hummocks, but there were substantial declines in the uppermost layers ($0.07\text{--}0.04\%$) under mature hummocks (depth \times patch interaction: $F_{2,48}=7.72$, $P=0.002$).

Discussion

Preoccupation with the differences in soil physical and chemical properties between perennial plant

Fig. 4 Depth profiles for labile C and mineralisable N for young and mature hummocks at Bloodwood (BW) and Wapweelah (W). The bars represent the depth by age (young vs mature) LSDs (Least Significant Differences) at $P<0.05$ for Bloodwood (LHS) and Wapweelah (RHS)



patches and their interspaces has dominated the semi-arid literature for more than two decades (e.g. Garner and Steinberger 1989). Although the patchy distribution of soil resources generally leads to increased productivity and diversity in water-limited environments (Titus et al. 2002), little is known about how the capacity of different landscape elements to trap resources might change over time. Knowledge of temporal changes in resources among different elements is important, particularly in shrublands, where the removal of shrubs could have substantial legacy effects by reducing resource pools associated with shrub hummocks (Archer 2009). Our study showed that, although soil beneath older shrub hummocks, and to a lesser extent older debris mounds, contained more resources than young patches, the results were strongly site-specific. The results of our study are relevant to other semi-arid areas where shrubs form small hummocks through the action of wind and/or water erosion (e.g. de Soyza et al. 1997; Bolling and Walker 2002). As indicated below, the exact nature of these hummocks will be dependent on differences in soil texture, and nutrient concentrations and decomposition rates of foliage of shrub species inhabiting the hummocks (e.g. mesquite cf. creosote bush). Furthermore, differences were mostly apparent at the surface, where resources tend to accumulate, attenuating rapidly with depth after 15 cm. Our prediction that undisturbed interspaces would have higher nutrient concentrations than recovering interspaces, even after almost two decades, was not upheld. Together, the results provide further evidence that autogenic recovery of disturbed shrublands is likely to be protracted (e.g. Havstad et al. 1999).

Soil nutrients under shrub hummocks and debris mounds

We detected significantly greater concentrations of labile C, mineralisable N and mineral N in soils beneath shrubs than in the interspaces, consistent with our first hypothesis and with the large body of literature from semi-arid systems (e.g. Bolling and Walker 2002; Schlesinger et al. 1996). Despite recovery from a treatment as severe as ploughing, the soil around small shrub recruits still contained more resources than soil in the interspaces. Soil beneath debris mounds also contained relatively high

concentrations of C (both total and labile) and N (mineral, available) compared with interspace soils, consistently at both sites. Soil restoration studies have demonstrated higher concentrations of organic C, total and mineralisable N, exchangeable K and Ca, greater soil respiration and infiltration, and more stable temperatures under mulga (*Acacia aneura*) branches placed on the surface than in the interspaces, even after only 3 years (Tongway and Ludwig 1996). Greater nutrient concentrations are probably due to a combination of enhanced decomposition rates by macro-invertebrates (e.g. termites; Tongway et al. 1989), trapping of airborne dust (Okin et al. 2006) and deposition of surface sediments (Wood and Javed 1992). Woody debris may even promote the recovery of perennial grasses in cleared shrublands by providing refugia from grazing by native (Bestelmeyer et al. 2007) and domestic (Ludwig and Tongway 1996) herbivores. Retaining woody debris on the soil surface can therefore be an effective way to enhance soil surface heterogeneity in shrub-removed woodlands. Given that even relatively young mounds in our study had more nutrients than interspace soils (Table 3), retention of debris on the surface may compensate, at least in part, for nutrients lost during the shrub removal process.

We found, however, little support for the hypothesis of differences in soil properties between young and old debris mounds, apart from lower bulk density and higher mineral N concentrations in mature mounds at Wapweelah. Given the rapid establishment of nutrient-enriched patches *de novo* under debris mounds (Tongway and Ludwig 1996), it is likely that the small mounds in our study developed nutrient profiles similar to older mounds relatively quickly, particularly at Bloodwood. Breakdown of debris material and mineralisation of nutrients is exceptionally slow in semi-arid environments (Whitford 2002). Evidence for the slow decomposition of coarse woody debris in Australian semi-arid environments is scant, though examination of long-term photographs from arid open woodlands suggests that large logs persist for many decades after dying and collapsing (Sinclair 2004). Consequently, most of the effect under the new mounds was probably due to abiotic capture of sediments rather than decomposition of existing organic material (Abbot and Crossley 1982).

Greater carbon and nitrogen concentrations within older shrub hummocks

Soil under mature hummocks in our study tended to have greater concentrations of mineral N (Bloodwood), labile C (Wapweelah and Bloodwood) and total and mineralisable N (Wapweelah) than soil under young shrubs, though maximum values were concentrated in the top 5–10 cm and tended to converge with depth. Older, generally larger shrubs tend to accumulate more nutrients than younger, smaller shrubs (McClaran et al. 2008; Throop and Archer 2008) and a number of mechanisms could potentially account for this. The denser, wider canopies of larger shrubs (Pugnaire et al. 1996; Wezel et al. 2000) would reduce threshold wind velocities, and increase the deposition of entrained soil particles (Okin et al. 2006). More sediment adhering to the foliage would also increase the potential for sediment transport by stem-flow processes (Whitford et al. 1997) and increase soil deposition under the canopy at the expense of deposition in the interspaces (Parsons et al. 1992). Bigger trees and shrubs would also be stronger nutrient pumps, depositing more nutrients through root sequestration of nutrients and accumulation of root exudates within the rhizosphere.

Larger, mature shrubs would be expected to support higher levels of biological activity, as they provide more habitat (canopy area) and therefore greater resources (e.g. seed, fruit, sap, flowers, leaf-borne invertebrates) for birds and mammals. Indeed *Eremophila sturtii* shrubs close to the study area have been shown to support a greater biomass and richness of sap-feeding insects (Alan Kwok, unpublished data). They also produce more biomass and therefore shed more litter below the canopy, increasing litter depth and probably decomposition (Dowling et al. 1986; Vetaas 1992; de Soyza et al. 1997; Schlesinger and Pilmanis 1998). Levels of total, mineralisable and mineral N, and total and labile C were concentrated in the near-surface layers under shrubs, in an environment where leaf falls were accumulated while decomposition processes were low (Throop and Archer 2007). Soil porosity is greater under mature shrubs due to greater levels of organic matter (Throop and Archer 2008), leading to increased infiltration. Finally, as shrub canopies mature and shading increases, surface temperatures will decline and potentially reduce photo-oxidation of soil organic matter.

Young shrub recruits will undoubtedly trap and retain fewer resources than their mature counterparts. Thus any elevated levels of nutrients associated with young shrubs over and above that in the interspaces are likely due to legacy effects from residual mounds supporting the previous shrub occupants. We recorded substantially more shrub recruits on the edges of residual hummocks (1.4 seedlings and juveniles < 5 cm tall per metre of patch) than in the interspaces or debris mounds (0.19 per metre of patch; $F_{2,20}=13.42$, $P<0.001$, $n=36$; Stefani Daryanto, unpublished data). It is highly likely, therefore, that most of the young shrubs under which we sampled our soils had originally established at the edges of existing hummocks from where mature shrubs had been removed. This suggests therefore that we are measuring recovery of existing hummocks rather than the creation of new hummocks in the interspaces, though we acknowledge that some young shrubs would have established in the interspaces. Shrub regeneration and growth of herbaceous species on residual hummocks would be expected to deplete remaining resources after the original occupants have been removed until the new recruits attain a size large enough to affect the abiotic environment themselves (e.g. Belsky and Canham 1994; Dean et al. 1999) and thus contribute to the development of a resource-rich hummock. That shrub function, in terms of nutrient build-up, is still lower under young shrubs after two decades, even when plants recruit into pre-existing hummocks, further reinforces our view that recovery of soil function is extremely slow. In the absence of human disturbances, similar processes occur adjacent to coarse woody debris and dying shrubs, which accumulate on the surface and becoming sites of shrub recruitment.

Our study was conducted at two different sites with slight differences in soil physical and morphological characteristics (Eldridge and Robson 1997; Daryanto and Eldridge 2010). It is not surprising therefore that there were some inconsistencies in the responses across sites. This inconsistency probably relates to both differences in plant community composition and subtle differences in soil texture. For example, shrub trait would be expected to affect soil nutrient pools by altering foliar decomposition rates (Cornwell et al., 2008). Ploughing has the potential therefore to influence soil nutrient pools by selecting for shrubs with foliage of a high nitrogen content (e.g. *Eremo-*

phila, Burrows 1972) or relatively high C:N ratio (*Dodonaea viscosa*, Ley and D'Antonio 1998; Mack and D'Antonio 2003). For example, *Eremophila* litter produces about 7.25 kg of organic matter per 1000 shrubs, which annually would add 0.14 kg N and 0.008 kg P 1000 shrubs⁻¹ yr⁻¹ respectively (Burrows 1972). Densities of about 8000 *Eremophila* shrubs ha⁻¹ at Wapweelah (Daryanto and Eldridge 2010) would therefore deliver about 1.12 and 0.064 kg ha⁻¹ yr⁻¹ of N and P respectively, in litter inputs, which are relatively high for arid Australian plants (Burrows 1972). In contrast, the density of *Dodonaea viscosa* at Bloodwood was only 5100 shrub ha⁻¹. With a maximum litter production of about 20 kg ha⁻¹ yr⁻¹ and 0.37–0.46% N (Mack and D'Antonio 2003), N inputs into the soils would be about 0.7 kg N ha⁻¹ yr⁻¹. The relatively high (~65 to ~97) C:N ratio of *Dodonaea viscosa* would likely enhance short-term N immobilisation (Wedin 1999).

The retention of C and N in the soil is strongly influenced by clay mineralogy (Barret and Burke 2002) and to a lesser extent, groundstorey cover, so we would expect a greater N effect on the finer soils at Wapweelah than in the coarser Bloodwood soils. Bloodwood supported low cover and biomass of groundstorey species, even under exclosure (S. Daryanto, unpublished data). Its soils tended to be more hardsetting, due to the small percentage of silt in the surface layers (Eldridge and Robson 1997) and a sparse cover of cryptogamic crusts (<12%, Eldridge and Robson 1997) compared with Wapweelah (to 31%; Daryanto and Eldridge 2010), which likely exacerbated surface sealing. Other inconsistencies between the sites could also relate to subtle differences in hummock orientation and geomorphic setting between Gumbalie and Goonery Land Systems (Walker 1991). Our study therefore suggests that the consequences of shrub removal for soil nutrient retention will be soil surface- and texture-dependent. Soil disturbance and shrub removal are likely, therefore, to have a greater effect on nutrient retention on coarser-textured soils, which are generally dominated by the N-poor litter of *Dodonaea viscosa*.

Similar nutrient pools in disturbed and undisturbed interspaces

The similarity in soil nutrient concentrations between undisturbed and recovering interspaces is surprising

given the substantially (three to five-fold) greater cryptogam cover at the undisturbed sites (Daryanto and Eldridge 2010). Cryptogams are known to increase soil aggregation and enhance soil nutrients by accumulating C and N (Barger et al. 2006). The lack of an age effect could relate to potential differences in crust composition between disturbed and undisturbed interspaces. Cryptogamic crusts are a diverse group of microorganisms and individually have markedly different effects on ecosystem functions (Bowker et al. 2010). We did not assess crust composition, which might have explained differences in the capacity of crusts to produce and retain nutrients. For example, while mosses are important for stability, cyanobacteria are critical for N fixation. Knowledge of the composition of crusts is requisite to an improved understanding of the capacity of the crust community to produce nutrients. Biological activity is also likely to be lower in the interspaces than the shrub patches (e.g. Archer et al. 2001). Higher rates of photo-oxidation of litter at open sites (sensu Austin and Vivanco 2006) might explain the lack of differences in the interspaces.

Conclusions

Ploughing has been used extensively in the semi-arid woodlands of eastern Australia to reduce shrub densities (Robson 1995; Tighe et al. 2009). Our study indicates that it has the potential to change the distribution of soil nutrient pools by removing established shrubs and partly redistributing their resource islands, though some of this may be offset by enhanced resources associated with multiple-aged debris mounds. Ploughing could also alter soil nutrients by changing the distribution of plant species and thus foliar nutrient concentrations. The surface distribution of resources such as labile C and mineralisable N was substantially truncated at both sites, even under mature shrubs, suggesting that any surface disturbance is likely to have substantial effects on near-surface nutrient pools. The generally slow recovery of soil processes in semi-arid environments is likely to be exacerbated by the tendency for land managers to allow livestock to graze sites soon after ploughing.

The major differences in response between our two study sites may relate to differences in their surface

texture, which would affect their capacity to sequester nutrients. Modeling of landscape-level changes in soil nutrients in shrub-encroached woodland should therefore consider not only differences in shrub species, age, patch type and size, but also site-level differences such as surface texture and geomorphology. Our study suggests that shrubs are important elements in semi-arid systems by providing sinks for soil nutrients, even when small (Shachak et al. 2008). Removal of shrubs and their attendant hummock islands therefore comes at a long-term cost associated with loss of nutrients. While the main management goal is the broad-scale removal of shrubs (e.g. Robson 1995), the retention of strips or patches of mature shrubs may be necessary in the short-term to reduce the landscape-scale removal of resources by erosion.

Acknowledgements The exclosures were originally established by David Robson under funding from the NSW Environmental Trust Fund Scheme. We are grateful to the owners and managers of ‘Wapweelah’ and ‘Bloodwood’ for allowing us access to their property and for maintaining the exclosures. We thank Niki Huang and Alexandra James for assistance in field sampling and Erin Roger, Alan Kwok, Samantha Travers and Heather Throop for comments on an earlier draft and two reviewers for helping us to refine the manuscript. This study was supported by a PhD scholarship from AusAID (UNSW).

References

- Abbot DT, Crossley DA Jr (1982) Woody litter decomposition following clear-cutting. *Ecology* 63:35–42
- Allegretti LI, Passera CB, Robles AB (1997) Short- and long-term effects of shrub management on vegetation in the Monte, Argentina. *J Arid Environ* 35:685–693
- Archer SR (2009) Rangeland conservation and shrub encroachment: new perspectives on an old problem. In: du Toit J, Kock JR, Deutsch J (eds) *Wild Rangelands: Conserving Wildlife while Maintaining Livestock in Semi-Arid Ecosystems*. Wiley-Blackwell, West Sussex, pp 53–97
- Archer S, Boutton TW, Hibbard KA (2001) Trees in grasslands: biochemical consequences of woody plant expansion. In: Schulze ED et al (eds) *Global Biogeochemical Cycles in the Climate System*. Academic, San Diego, CA, pp 115–137
- Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 442:555–558
- Barger NN, Herrick JE, Van Zee J, Belnap J (2006) Impacts of biological soil crust disturbance and composition on C and N loss from water erosion. *Biogeochemistry* 77:247–263
- Barret JE, Burke IC (2002) Nitrogen retention across a soil organic matter gradient in semiarid ecosystems. *Ecol Appl* 12:878–890
- Bechtold HA, Inouye RS (2007) Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. *J Arid Environ* 71:122–132
- Belnap J, Eldridge DJ (2001) Disturbance and recovery of biological soil crusts. In: Belnap J, Lange OL (eds) *Biological soil crusts: structure, function and management*. Springer-Verlag, Berlin Heidelberg, pp 363–383
- Belsky AJ, Canham CD (1994) Forest gap and isolated savanna trees. *Bioscience* 44:77–84
- Bestelmeyer BT, Khalil NI, Peters DPC (2007) Does shrub invasion indirectly limit grass establishment via seedling herbivory? A test at grassland–shrubland ecotones. *J Veg Sci* 18:363–370
- Blaum N, Rossmann E, Schwager M et al (2007) Responses of mammalian carnivores to land use in arid savanna rangelands. *Basic Appl Ecol* 8:552–564
- Bolling JD, Walker LR (2002) Fertile island development around perennial shrubs across a Mojave Desert chronosequence. *West Nth Amer Naturalist* 62:88–100
- Booth CA, Barker PJ (1981) Shrub invasion on sandplain country west of Wanaaring, New South Wales. *J Soil Conserv Serv NSW* 37:65–70
- Bowker MA, Maestre FT, Escolar C (2010) Biological crusts as a model system for examining the biodiversity–ecosystem function relationship in soils. *Soil Biol Biochem* 42:405–417
- Burrows WH (1972) Productivity of an arid zone shrub (*Eremophila gilesii*) community in south-western Queensland. *Aust J Bot* 20:317–329
- Charley JL, West NE (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *J Ecol* 63:945–963
- Clarke KR, Warwick RM (1994) Similarity-based testing for community pattern: the 2-way layout with no replication. *Mar Biol* 118:167–176
- Coffin DP, Lauenroth WK, Burke IC (1996) Recovery of vegetation in semiarid grassland 53 years after disturbance. *Ecol Appl* 6:538–555
- Cornwell WK, Cornelissen JHC, Amatangelo K et al (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol Lett* 11:1065–1071
- Daly RL, Hodgkinson KC (1996) Relationships between grass, shrub and tree cover on four landforms of semi-arid eastern Australia, and prospects for change by burning. *Rangeland J* 18:104–117
- Daryanto S, Eldridge DJ (2010) Plant and soil surface responses to a combination of shrub removal and grazing in a shrub-encroached woodland. *J Environ Manage* 91:2639–2648
- Dean WRJ, Milton SJ, Jeltsch F (1999) Large trees, fertile islands, and birds in arid savanna. *J Arid Environ* 41:61–78
- Dowling AJ, Webb AA, Scanlan JC (1986) Surface soil chemical and physical patterns in a brigalow–Dawson gum forest, central Queensland. *Aust J Ecol* 11:155–162

- Eldridge DJ, Robson AD (1997) Bladeploughing and enclosure influence soil properties in a semi-arid Australian woodland. *J Range Manage* 50:191–198
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford AG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett* 14:709–722
- Garner W, Steinberger Y (1989) A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *J Arid Environ* 16:257–262
- Gianello C, Bremner JM (1986) A simple chemical method of assessing potentially available organic nitrogen in soil. *Commun Soil Sci Plan* 17:195–214
- Havstad KM, Gibbens RP, Knorr CA et al (1999) Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. *J Arid Environ* 42:155–166
- Herrick JE, Havstad KM, Rango A (2006) Remediation research at the Jornada: past and future. In: Havstad KM, Schlesinger WH, Huenneke LF (eds) *Structure and function of a Chihuahuan Desert ecosystem: the Jornada Basin LTER*. Oxford University Press, UK, pp 278–304
- Hodgkinson KC (1991) Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *J Appl Ecol* 28:60–70
- Kelly RH, Burke IC (1997) Heterogeneity of soil organic matter following death of individual plants in shortgrass steppe. *Ecology* 78:1256–1261
- Ley RE, D'Antonio CM (1998) Exotic grass invasion alters potential rates of N fixation in Hawaiian woodlands. *Oecologia* 113:179–187
- Ludwig JA, Tongway DJ (1996) Rehabilitation of semiarid landscapes in Australia. 2. Restoring vegetation patches. *Restor Ecol* 4:398–406
- Mack MC, D'Antonio CM (2003) The effects of exotic grasses on litter decomposition in a Hawaiian woodland: The importance of indirect effects. *Ecosystems* 6:723–738
- MacLeod ND, Johnston BG (1990) An economic framework for the evaluation of rangeland restoration projects. *Aust Rangel J* 12:40–53
- Maestre FT, Bowker MA, Puche MD et al (2009) Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecol Lett* 12:930–941
- McClaran MC, Moore-Kucera J, Martens DA et al (2008) Soil carbon and nitrogen in relation to shrub size and death in a semi-arid grassland. *Geoderma* 145:60–68
- McGlynn IO, Okin GS (2006) Characterization of shrub distribution using high spatial resolution remote sensing: ecosystem implications for a former Chihuahuan Desert grassland. *Remote Sens Environ* 101:554–566
- Okin GS, Gillette DA, Herrick JE (2006) Multi-scale controls on consequences of aeolian processes in landscape change in arid and semi-arid environments. *J Arid Environ* 65:253–275
- Parsons AJ, Abrahams AD, Simanton JR (1992) Microtopography and soil-surface materials on semi-arid piedmont hillslopes, southern Arizona. *J Arid Environ* 22:107–115
- Peters DPC, Mariotto I, Havstad KM, Murray LW (2006) Spatial variation in remnant grasses after a grassland-to-shrubland state change: implication for restoration. *Rangeland Ecol Manag* 59:343–350
- Pugnaire FI, Haase P, Puigdefabregas J et al (1996) Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos* 76:455–464
- Robson AD (1995) The effects of grazing exclusion and blade-ploughing in semi-arid woodland vegetation in north-western New South Wales over 30 months. *Rangeland J* 17:111–127
- Schlesinger WH, Pilmanis A (1998) Plant-soil interactions in deserts. *Biogeochemistry* 42:169–187
- Schlesinger WH, Raikes JA, Hartley AE et al (1996) On the spatial pattern of soil nutrients in desert ecosystem. *Ecology* 77:364–374
- Schlesinger WH, Reynolds JF, Cunningham GL et al (1990) Biological feedbacks in global desertification. *Science* 247:1043–1048
- Shachak M, Boeken B, Groner E et al (2008) Woody species as landscape modulators and their effects on biodiversity patterns. *Bioscience* 58:209–221
- Sinclair R (2004) Persistence of dead trees and fallen timber in the arid zone: 76 years of data from the TGB Osborn Vegetation Reserve, Koonamore, South Australia. *Rangel J* 26:111–122
- de Soya AG, Whitford WG, Martínez-Meza E et al (1997) Variation in creosotebush (*Larrea tridentata*) canopy morphology in relation to habitat, soil fertility and associated annual plant community. *Am Midl Nat* 137:13–26
- Teague WR, Foy JK, Cross BT et al (1999) Soil carbon and nitrogen changes following root-plowing of rangeland. *J Range Manage* 52:666–670
- Throop HL, Archer SR (2007) Interrelationships among shrub encroachment, land management and litter decomposition in a semidesert grassland. *Ecol Appl* 17:1809–1823
- Throop HL, Archer SR (2008) Shrub (*Prosopis velutina*) encroachment in a semidesert grassland: Spatial-temporal changes in soil organic carbon and nitrogen pools. *Global Change Biol* 14:2420–2431
- Throop HL, Archer SR, Monger HC, Waltman S (2011) When bulk density methods matter: implications for estimating soil organic carbon pools in soils. *J Arid Environ* (in press)
- Tighe M, Reid N, Wilson B et al (2009) Invasive native scrub and soil condition in semi-arid south-eastern Australia. *Agr Ecosyst Environ* 132:212–222
- Titus JH, Nowak RS, Smith SD (2002) Soil resource heterogeneity in the Mojave Desert. *J Arid Environ* 52:269–292
- Tongway DJ, Ludwig JA (1996) Rehabilitation of semi-arid landscape in Australia. 1. Restoring productive soil patches. *Restor Ecol* 4:388–397
- Tongway DJ, Ludwig JA, Whitford WG (1989) Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia. *Aust J Ecol* 14:263–268
- van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. *J Environ Manage* 90:2931–2942
- Vetaas OR (1992) Micro-site effects of trees and shrubs in dry savannas. *J Veg Sci* 3:337–344
- Walker PJ (1991) Land Systems of Western New South Wales. Soil Conservation Service of New South Wales
- Wedin DA (1999) Nitrogen availability, plant-soil feedbacks and grassland stability. In: *Proceedings of the VI Interna-*

- tional Rangeland Congress. D.Eldridge and F. Freudenberger (eds). Vol.1, 193–197. Townsville, Queensland, Australia
- Weil RR, Islam KR, Stine MA et al (2003) Estimating active carbon for soil quality assessment: A simplified method for laboratory and field use. *Am J Alternative Agr* 18:3–17
- Wezel A, Rajot JL, Herbrig C (2000) Influence of shrubs on soil characteristics and their function in Sahelian agro–ecosystems in semi–arid Niger. *J Arid Environ* 44:383–398
- Whitford WG, Anderson J, Rice PM (1997) Stemflow contribution to the 'fertile island' effect in creosotebush, *Larrea tridentata*. *J Arid Environ* 35:451–457
- Whitford WG (2002) *Ecology of desert systems*. Academic, San Diego, California
- Wood MK, Javed N (1992) Hydrologic responses to fuelwood harvest and slash disposal on a pinyon–juniper dominated grassland site in the Gila National Forest. In 36th Annual New Mexico Water Conference—Agencies and Science Working for the Future. WRRRI Report, Las Cruces, New Mexico, pp 25–30