

The effects of shrub removal and grazing on vegetation and soils in a shrub-encroached Australian woodland

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The effects of shrub removal and grazing on vegetation and soils in a shrub-encroached Australian woodland

Stefani Daryanto

A thesis in fulfilment of the requirements for the degree of
Doctor of Philosophy



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Plant communities and soil properties in many dryland ecosystems have changed dramatically over the past century due to the proliferation of woody plants, caused largely by the introduction of livestock grazing, changes to natural fire regimes, and climate. Areas heavily encroached by shrubs are generally regarded as degraded, and this view is largely based on the fact that shrubs reduce pastoral productivity. There have been many attempts to remove shrubs in pastoral systems using chemical, biological and mechanical techniques to improve pastoral production. It remains unclear, however, whether shrubs *per se* or the interactions between grazing and climate are responsible for the putative reductions in pastoral productivity in shrub-encroached areas. This thesis examines the long-term ecological effects of mechanical shrub removal by blade-ploughing, with and without grazing, on vegetation and soils in shrub-encroached woodlands in eastern Australia. The results show that the combination of ploughing and grazing creates dramatic effects on soils and vegetation in this dryland system. Chapter 1 provides an overview of shrub encroachment phenomenon, its common association with degradation, as well as the benefits of shrubs and the overall encroachment effects on ecosystem processes. The chapter also describes the results of previous attempts to control shrubs using mechanical removal techniques. Chapters 2 and 3 examine the changes in vegetation and soil disturbances by animals, respectively, that result from mechanical shrub removal. Chapter 4 compares soil properties between ploughed sites occupied by newly-regenerated shrubs and unploughed sites dominated by mature shrubs. Chapters 5 and 6 describe the changes in the spatial distribution of soil nutrients and infiltration of water in a shrubland resulting from different combinations of ploughing and grazing. Chapter 7 examines the role of shrub-encroached lands as sinks for aboveground and belowground carbon (C) and considers the effects of different landscape elements (e.g. shrubs, log or debris mounds, trees) on C storage. Chapter 8, provides a conclusion, and evaluates the potentially negative effects of shrub removal as part of a land management strategy in this semi-arid system and explores the ecosystem values of shrubs including other possibilities to manage shrublands and suggestions for future research.

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Plant and soil surface responses to a combination of shrub removal and grazing in a shrub-encroached woodland

Journal of Environmental Management 91 (2010): 2639–2648. DOI: 10.1016/j.jenvman.2010.07.038

Authors: Stefani Daryanto and David J. Eldridge

Stefani Daryanto (SD) can claim more than 50% of the work since she undertook all of the field and laboratory work, and 70% of the data analyses that are reported in the paper. She also wrote about 80% of the manuscript. Statistical advice and assistance on the paper was provided by Terry Koen (TBK), a biometrician at the Office of Environment and Heritage, and supervised by Dr David Eldridge (DJE). No other authors will be submitting this work as part of their thesis submissions.

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Chapter 3

Shrub hummocks as foci for small animal disturbances in an encroached shrubland

Journal of Arid Environments 80 (2012): 35–39. DOI: 10.1016/j.jaridenv.2011.12.001

Authors: Stefani Daryanto and David J. Eldridge

SD undertook all of the data analysis, 60% of the field work and wrote 70% of the manuscript. No other authors will be submitting this work as part of their thesis submissions. Advice on statistics was provided by Dr Santiago Soliveres, a post-doctoral fellow working in the Eldridge Lab. The study was conceived by DJE, and supervision was by DJE.

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Chapter 4

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

Plant and Soil 351 (2012): 405–419. DOI: 10.1007/s11104-011-0978-5

Authors: Stefani Daryanto , David J. Eldridge, and Terry B. Koen

SD undertook more than 75% of the manuscript writing, all of the field and laboratory work. Statistical advice and assistance on the paper was provided by TBK. The study was conceived by DJE, and supervision was by DJE. No other authors will be submitting this work as part of their thesis submissions.

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Ploughing and grazing alter the spatial patterning of surface soils in a shrub-encroached woodland

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Chapter 6

Infiltration of water varies with disturbance in a shrub-encroached woodland

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Chapter 7

Managing semi-arid woodlands for carbon storage: Grazing and shrub effects on above- and belowground carbon

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Authors: Stefani Daryanto, David J. Eldridge, and Heather L. Throop

SD undertook more than 75% of the manuscript writing, all of the field and laboratory work as well as all statistical analyses. The study was conceived by Heather L. Throop

(HLT), and supervision was by DJE. No other authors will be submitting this work as part of their thesis submissions.

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Introduction

This thesis evaluates the ecological values of shrubs by comparing the long-term effects of the presence or removal of shrubs, in both the presence and the absence of grazing, on soil, vegetation, and properties of small animals using blade-ploughing in an Australian semi-arid woodland. In this chapter, the causes and consequences of shrub encroachment are described, followed by conventional management strategies for controlling shrubs, in particular, mechanical shrub removal. I then evaluate the effects of shrubs on soil and ecological processes, providing insights into the value of shrubs in maintaining these ecological processes. Finally, I outline the structure of the thesis and re-evaluate the notion that shrubs are indicative of degraded ecosystems.

Shrub encroachment in semi-arid ecosystems

Species invasion often comes at a high cost to ecosystems by introducing serious threats to ecosystems by altering ecosystem processes (Liao et al., 2006; Throop and Archer, 2007; Nie et al., 2012; Sala et al., 2012) and therefore altered structure and functions (Grant et al., 2004; Gottschalk et al., 2007). The encroachment of shrubs, particularly native woody species, into former open grassland has increased globally since the late 19th century (Archer et al., 1995; Noble, 1997; Angassa and Oba, 2007; Naito and Cairns, 2011). The scale of encroachment and the number of species involved make shrubs a significant problem in arid areas despite the efforts of practitioners, scientists and governments to control them (Martin et al., 2006). Turpentine (*Eremophila sturtii*), hopbush (*Dodonaea viscosa*) and budda (*Eremophila mitchellii*) are examples of native species that exhibit some invasive qualities in eastern Australian rangelands (Booth et al., 1996a). Their density, which previously had been low for centuries, has increased to a level at which other plant species particularly perennial grasses are suppressed (Noble, 1997). Similarly, in some regions of Europe such as Spain, shrubs have invaded into areas that were once grasslands (Montané et al., 2007). In South America, shrubs of low forage quality have replaced productive grasslands and initiated soil loss (Parizek et al., 2002). In Africa, the same phenomenon has also been observed since the late 1930s (Wigley et al., 2009), reducing the carrying capacity of rangelands for livestock production.

The causes of shrub encroachment

The causes of this phenomenon, variously referred to as shrub invasion, encroachment, or woody thickening, vary and appear to be due to the interaction of several factors (Archer et al., 1995; Van Auken, 2009). Changes in land-use practices from frequent wildfire to controlled, infrequent fire, in addition to increases in stocking rates of both domestic and native animals over large areas of rangelands (Wilson, 1990; Archer et al., 1995) have reduced fire fuel loads. Due to the unpalatability of shrubs, they are often more competitive than grasses under grazing (Booth et al., 1996b). They are also better at withstanding drought, fire, salinity, and frost (Richmond and Chinnock, 1994; Booth et al. 1996b). In this changing climate, variation in rainfall (Fensham et al., 2005) and increases in global CO₂ concentration further benefit C₃ woody species at the expense of C₄ grasses (Polley et al., 1993; Chapin et al., 2002). Since grazing also increases the cover of bare soil surface and consequently erosion, it leads to unfavorable changes in soil chemical and physical properties (e.g. increasing bulk density, decreasing soil infiltrability, and nutrient concentrations; Castellano and Valone, 2007; Stavi et al., 2008). This positive feedback thus reduces the possibility of plant establishment in the interspace and shifts natural vegetation composition from grass-dominated lands to shrub-dominated lands (D’Odorico et al., 2012).

The consequences of shrub encroachment

Although some grassland-obligate animals might experience habitat loss and an increase risk of predation from ground-dwelling predators as shrub cover increases (e.g., Grant et al., 2004; Gottschalk et al., 2007; Klug et al., 2010), most of the other consequences are related to reduced agricultural productivity. The encroachment of unpalatable native shrubs have out-competed palatable pasture species (Page et al., 2000) and threatened livestock health as shrubs form habitat for insects, arthropod pests and parasites such as ticks and tsetse flies (*Glossina* spp.; Teel et al., 1997). Shrubs are also thought to have had adverse effects on forage production and livestock safety because woody plants provide cover for predators (Archer, 2010). The high density of shrubs in addition to the increasing randomness of shrub patterns with grazing (Seifan and Kadmon, 2006), creates difficulties in handling livestock, for example, when

gathering or moving the animals (Archer, 2010). This combination further reduces the economic value of rangelands because it increases the time that could have been spent on foraging (Seifan and Kadmon, 2006).

While shrub encroachment is regarded by many as a sign of ecosystem degradation or desertification due to reductions in rangeland productivity from economic perspective (Maestre et al., 2009), it remains unclear, however, whether shrubs *per se* or interactions between grazing and the changing climate are responsible for the such reductions in shrub-encroached grasslands. Indeed, the ecosystem functions in areas encroached by shrubs have changed, for example in their soil water balance (Aguilar et al., 1996) and soil nutrient spatial distribution (Schlesinger et al., 1996). However, the generally negative perception of native shrubs as invaders is highly context-dependent (Colautti and MacIsaac, 2004) and recent studies suggest that encroachment may have positive impact on multiple ecosystem functions (Maestre et al., 2009; Eldridge et al., 2011; Maestre et al., 2012). These ecosystem functions include moderating microclimate (Pugnaire et al., 2011), preserving soil physical and chemical properties by reducing erosion (Ludwig et al., 2005) and enhancing organic matter input via fixation of nitrogen (N) and carbon (C) (Lajtha and Schlesinger, 1986), conserving biodiversity (Maestre et al., 2012) and providing some economic benefits (e.g., C sink, grazing and forestry; Barger et al., 2011; Crossman et al., 2011; Mekuria et al., 2011; Prowse and Brook, 2011). Shrubs may even reverse the desertification process (Maestre et al., 2009), a phenomenon directly associated with the encroachment itself. In extreme conditions, shrubs can act as nurse plants (Pugnaire et al., 2011; Howard et al., 2012) due to their ability to withstand drought, salinity, frosts and fire (Richmond and Chinnock, 1994; Booth et al., 1996a). More importantly, in ecosystems where water is a key factor of productivity (Le Hou  rou et al., 1988; Wang et al. 2012), shrub encroachment has substantial effects on hydrological properties and water balance (Nie et al., 2012; Turnbull et al., 2012).

Mechanical shrub removal

Livestock production in rangelands depends upon grazing, and the presence of shrubs has been associated with the reduction in forage quantity and quality, reduction in

animal growth, decreases in the quality of animal products and most importantly, reduction in the profit margin due to increasing cost (DiTomaso, 2000). There have been many attempts, therefore to promote grass recovery at the expense of shrubs. Stock removal and the establishment of exclosures have been some of the earliest attempts to enhance grass establishment, but it could be decades before these practices of removing grazing pressure have an effect on perennial grasses due to long legacy effects (Valone et al., 2002; Guo, 2004). These practices also often produce mixed results. In some cases, the establishment of exclosures has resulted in increased grass cover (Verdoodt et al., 2010) and improved the soil chemical and physical characteristics (Mekuria et al., 2007). In most other cases, however, stock removal from previously grazed area is not followed by grass recovery, although there are some significant soil improvements (Brejda, 1997; Castellano and Valone, 2007). Instead, shrubs continue to dominate even after complete grazing removal (West et al., 1984; Roundy and Jordan, 1988; Angassa and Oba, 2007; Daryanto and Eldridge, 2010).

Other attempts to control shrubs generally involve techniques such as fire, herbicide, mechanical and biological control agents. Mechanical shrub removal is a common method to treat shrubs in semi-arid rangelands, but it is generally costly due to high fuel and labor costs. It is also difficult to apply in heterogeneous communities as different species may have different re-sprouting ability and therefore react differently to the same treatment. In addition, most mechanical shrub control methods can only be applied on relatively flat landscapes (DiTomaso, 2000). Root (blade) ploughing, a common mechanical treatment to control shrubs in eastern Australian rangelands, is an expensive method and may cost \$A 40–85 per hectare in 1990, depending on soil type, texture and moisture, plough model and tractor type, as well as shrub size and density (Harland, 1993). It is an effective mechanical treatment for controlling undesirable woody species using a horizontal blade dug through the soil at 30 to 40 cm depth which is pulled behind a 74.6–kW or larger crawler tractor (Gonzalez and Latigo, 1981; Cross and Wiedemann, 1985). There have been several modifications for the blade, such as front–end stacking, disc plough, moldboard plough, chisel plough, web plough, and blade plough (Gonzalez and Latigo, 1981; Tanner et al., 1988; Harland, 1993). Blade–ploughing is the most effective method for removing shallow-rooted woody species that do not readily re–sprout (e.g., *Dodonaea* spp.; Harland, 1993) particularly if

it is applied during the dry season (Allegretti et al., 1997). This treatment, however, causes a lot of damage to the soil surface, biological soil crusts, and herbaceous plants including perennial grasses (Scifres, 1980; Morton and Melgoza, 1991; Daryanto and Eldridge, 2010).

Since the effects of shrub control depend on various factors such as the type of control method used, initial vegetation composition, soil conditions, and climate, subsequent vegetation composition may therefore be similar to, lower than or greater than that of the untreated rangeland. The long-term results of ploughing on a diverse shrub community are usually poor where resprouting shrubs such as *Eremophila* spp. (Wiedemann and Kelly, 2001; Chinnock, 2007) dominate (Roundy and Jordan, 1988; Coffin et al., 1996; Daryanto and Eldridge, 2010), even after grasses are seeded (Scifres, 1980; Gonzalez and Latigo, 1981; Morton and Melgoza, 1991). Examples of soil degradation following the clearing of woodlands is well documented (e.g., Syers et al., 1996). This is likely due to the decrease in resource-accumulating patches and biological crust cover (Daryanto and Eldridge, 2010), as well as the inability of newly regenerated shrubs to accumulate nutrients at similar rate to mature shrubs (Daryanto et al., 2012). Most of the degradation has been associated with organic matter loss shortly after disturbance (Babalola and Opara-Nadi, 1993), though significant losses also occurred due to erosion (Syers et al., 1996). As recovery is dependent on seasonal condition (Miller et al., 2004) and plant inputs (Kelly et al., 1996), it usually takes a long time for the ecosystem to recover to the conditions comparable to that before disturbance (Roundy and Jordan, 1988; Coffin et al., 1996; Daryanto and Eldridge, 2010).

Shrubs and their interactions with ecosystem processes

Development of resource-accumulating patches and spatial heterogeneity

Because most shrubs form a patchy, rather than a continuous layer of canopies and root systems, their presence has commonly been linked to an uneven distribution of resources. Soil under vegetated patches is enriched and modified through a process commonly known as the 'fertile island' effect (Garner and Steinberger, 1989), the mechanisms of which involve biological and physical processes. Though most of the

biological processes are related to the decomposition and mineralisation of litter (more details in the following section), they also include: (i) root sequestration of nutrients and the accumulation of root exudates within the rhizosphere (Schlesinger and Pilmanis, 1998), (ii) symbiosis between certain plant species with N-fixing bacteria (Schortemeyer et al., 2002), (iii) ion passive flow of subsurface moisture towards the shrub root zone, which channels a significant fraction of bulk precipitation to the soil (Whitford et al., 1997), and (iv) shelter or food provided by shrub canopies (e.g., seeds and fruits). They attract various birds, insects and small mammals (Pausas et al., 2006), which enrich the soil via defecation and soil mixing by burrowing, or in the case of arthropods, developing macropores (Archer et al., 2001; Daryanto and Eldridge, 2012). The physical processes that develop ‘fertile islands’ under shrubs include: (i) wind erosion or aeolian transport, which leads to windborne sediments trapped by vegetation (Okin et al., 2006; Li et al., 2009), (ii) rainsplash erosion, which refers to the phenomenon that more sediments are transported beneath the shrubs rather than outward, resulting in soil accumulation to shrub mounds (Parsons et al., 1992) and (iii) ion passive flow with water as a result of plant transpiration (Schlesinger and Pilmanis, 1998).

The degree of resource accumulation, however, may vary, since different shrub species exhibit different morphologies and therefore different abilities to fix N, producing litter of differing quality and quantity, thus productivity (Wezel et al., 2000; Whitford, 2002; McCulley et al., 2004). Shrubs with denser foliage (Wezel et al., 2000) and larger canopy area (Pugnaire et al., 1996), and shrubs with hemispherical shape accumulate more wind-borne particles than shrubs that have a more inverted-cone shape (Whitford, 2002). Similarly, soils under clumped or dense vegetation accumulate more organic C and N compared to soil under single trees (Eldridge and Wong, 2005). Therefore, distinctive shrub features lead to the uneven distribution of soil resources and the development of fertile islands below shrub canopies (Whitford, 2002).

Mineralisation and decomposition

Nutrient cycling in dryland ecosystems depends very much on the existing vegetation type. Thus the shift from grasslands to shrublands is generally followed by landscape-

scale changes in decomposition rates (Throop and Archer, 2007). The changes occur not only because of direct vegetation effects (e.g., litter quality and quantity), but also through indirect effects of vegetation on soil hydrology (Turnbull et al., 2012) and solar radiation (Throop and Archer, 2007). At the early stage of the transition, decomposition will increase as a result of higher quantity and quality of the litter (Throop and Archer, 2007). With increasing shrub age and canopy cover, however, net decomposition rate is likely to decrease because of increasing C:N and lignin:N ratios, particularly in litter originating from the stems, which generates a slow release of N (Dossa et al., 2009). The indirect influences of the canopy such as reduced UV radiation (Austin and Vivanco, 2006), physical litter fragmentation by rainfall and soil movement (Barnes et al., 2012) in turn offset the increase in litter quantity (Throop and Archer, 2007), lowering landscape-scale decomposition in the shrublands than grasslands.

Shrub encroachment also increases the fluctuation of woody plant root biomass compared to the foliar litter input, since plants in water- and nutrient-limited system usually invest more in their rooting system rather in their aboveground biomass. As most decomposition takes place near the soil surface due to substrate concentration, higher amounts of soluble salts commonly occurs in the surface soils (Wang et al., 2007; Daryanto et al., 2012), resulting in enhanced nutrient cycling functions around the shrubs. Consequently, the most significant change in soil physical and chemical properties with woody shrub encroachment is the net increase of soil C and N due to higher primary productivity and recalcitrant characteristics of shrub litter (Archer et al., 2001; Liao et al., 2006).

Infiltration of water

The presence of more litter and organic matter, which reduces the formation of physical soil crusts by moderating raindrop impact on the surface (Stavi et al., 2009), also enhances the ability of water to infiltrate (infiltrability) around the shrubs. Litter and vegetated patches prevent rain water runoff, and store a significant amount of water as runon into deeper soil layers (Eddy et al., 1999; Ludwig et al., 2005), with deeper root profiles of shrubs compared to grasses and sometimes even trees (Jackson et al., 1996). More soil resources increase pulses of biological activity (e.g., termites and ants) and

consequently create more macropores around the shrub mounds (Daryanto and Eldridge, 2012). This combination results in changes in physical properties of sub-canopy soils, particularly lower bulk density (Ravi et al., 2007; Stavi et al., 2008; Li et al., 2009) compared with the surrounding interspace.

Water is a key determinant of productivity in semi-arid systems (Le Houérou et al., 1988; Wang et al., 2012), and the encroachment of shrubs substantially affects soil hydrological properties and water balance (Nie et al., 2012; Turnbull et al., 2012). Soils directly under the shrubs have higher rates of infiltration than those at the edge of the canopy (Bhark and Small, 2003; Ravi et al., 2007). The overall net water balance however is generally lower in shrublands than in grasslands, due to mainly the increasing amount of evapotranspiration and decreasing percolation (Nie et al., 2012) in the bare interspaces. Thus maintaining the remaining vegetated patches is essential to increase water infiltration, especially in the disturbed areas where shrubs act as infiltration hot-spots.

Biota activities in shrublands

Shrub encroachment is commonly thought to have negative impacts on biodiversity, particularly for grassland-obligate taxa (Archer, 2010). As food availability for foraging animal species that use the grass matrix of the savanna decreases (Bender et al., 2007), shrub encroachment may lead to habitat loss and fragmentation of plant and animal populations (Grant et al., 2004; Gottschalk et al., 2007). Some grassland birds, for example, experience an increasing risk of predation from ground-dwelling predators as shrub cover increases (Klug et al., 2010). Mammal abundance and diversity are also low in certain areas where shrubs fragment the previously grassy landscape (Blaum et al., 2007a, b).

However, the shift from grasslands to woodlands could increase plant diversity by adding keystone structures and enhancing habitat heterogeneity (Verdú et al., 2000; Hernández et al., 2005). For example, shrubs could provide nesting, perching and foraging sites as well as shelter against predators and extreme climatic conditions (Archer, 2010). Recent studies have suggested that some shrubs provide food and

protection against avian predators (Thiele et al., 2008). Ant diversity also increases with shrub encroachment (Bestelmeyer, 2005) due to the presence of shrub litter which provides habitat for a variety of macro-arthropod taxa. Greater number of individuals, richness and biomass are found in the litter layer compared with in the bare mineral soil. Species composition also varies with depth, where more predators are found on the surface (i.e., in the litter layer), while more soil herbivores are found in the mineral soil closer to plant roots which are their source of food (Doblas-Miranda et al., 2009). Indeed, many desert shrubs, including Australian species, are considered to be hot-spots for soil fungal communities (Diem et al., 2000; O'Connor et al., 2001; Bennet et al., 2009).

Shrublands as alternative stable state

Ecosystem functions in semi-arid system can only be maintained if the proportion of resource-accumulating patches or the 'sinks' (e.g., vegetated areas) is greater than the interspace area or the 'source' (Merino-Martín et al., 2012). Therefore, the recovery of degraded woodlands or grasslands depends on: (i) the resistance of shrubs to any subsequent disturbance (Maestre et al., 2009) such as fire (Richmond and Chinnock, 1994) or physical removal (Chinnock, 2007), and (ii) the ability to resist environmental variation such as drought, salinity, and frost (Richmond and Chinnock, 1994; Booth et al., 1996a). Recolonisation of grazed areas by shrubs provides a more rapid recovery of soil and species composition compared to by perennial grasses alone (Howard et al., 2012). The ability of shrubs to regrow rapidly is driven by: (i) the high seed viability of most shrubs (e.g., *Eremophila* spp.) over prolonged periods of time (Richmond and Chinnock, 1994), and (ii) the high seedling survival rate, as they are show little effects due to disturbance by grazing, predators, or diseases (Booth et al., 1996b).

While shrub encroachment is not necessarily a threat to ecosystem functions, it does reduce the carrying capacity of rangeland for commercial livestock production (Archer, 2010). Instead of controlling or eliminating shrub encroachment, an alternative approach may be to capitalise on the ability of shrubs to sequester C since higher leaf area index, annual net primary productivity and plant biomass have been recorded in wooded communities than in the remnant grasslands (Brantley and Young, 2007;

McCulley et al., 2004; Liao et al., 2006). Indeed, the invasion of woody vegetation into semi-arid grasslands with mean annual rainfall > 336 mm (Barger et al., 2011) has been linked to the increase in the amount of C and N stocks in the system (Hibbard et al., 2001; McKinley and Blair, 2008; Svejcar et al., 2008). Thus shrub-encroached lands should not be regarded as degraded system with poor productivity and nutrient cycling, but rather a potential and fully-functioning land-based C sink (Crossman et al., 2011; Mekuria et al., 2011; Prowse and Brook, 2011).

Shrublands show greater resilience to disturbance than grasslands, particularly under positive feedbacks such as erosion-vegetation feedback and fire-grass feedback (D'Odorico et al., 2012). In these feedbacks, nutrient-rich soils are eroded and redistributed from the interspaces to the shrubs, preventing grass regeneration in the interspaces. In the absence of continuous grass cover, fire which could prevent shrub proliferating, is unlikely. Additionally, such fire can only be applied successfully during the early stages of encroachment (Ravi et al., 2009), because once established, mature shrubs generally develop some fire-resisting mechanisms (e.g., thick bark and epicormic buds). Shrubs are therefore expected to maintain their domination even where grasses are allowed to recover, due to variability in climatic and biological factors that may constrain passive recovery rate of grasses (Valone et al., 2002; *but see* Lewis et al., 2010). Land managers could therefore view shrublands not as a degraded environment that is unsuitable for livestock production, but as a resource that has a potential C storage value. However, altered land management practice, government policies, and subsidies are needed to support a viable industry based around utilizing shrublands as a viable C sink (Archer et al., 2001).

Thesis objectives and structure

The main objective of this thesis is to evaluate the effects of blade-ploughing on soil and ecological processes in an Australian shrub-encroached woodland, and to understand how these processes have changed in relation to shrubs and grazing.

This thesis is written as a series of manuscripts with separate Abstracts, Introductions, Results, Discussions, and References. Each chapter is designed therefore to be read as a separate body of work.

Chapter 1 provides an overview of shrub-encroachment phenomenon and its perceived association with degradation, the effects of encroachment on soil and ecological processes and the ecological benefits of maintaining those shrubs.

Chapter 2 compares the shift in landscape functions, soil surface morphology, and vegetation composition among sites experiencing four combinations of ploughing and grazing treatments (i.e., ploughed-grazed, ploughed-ungrazed, unploughed-grazed, and unploughed-ungrazed). The chapter examines the effects of these treatments on shrub density and composition. This work has been published in *Journal of Environmental Management*.

Chapter 3 assesses changes in the density, abundance, richness and composition of surface disturbances made by a range of soil disturbing animals (e.g., ants, beetles, goannas, etc) under the four grazing–ploughing treatments in two different shrubland systems, and whether the effects of the treatments and therefore shrubs are consistent in these different environments. This work has been published in *Journal of Arid Environments*.

Chapter 4 examines differences in soil properties (total N, total C, mineral N or inorganic N, mineralisable N or net N mineralisation capacity, labile C, soil moisture, bulk density, pH and electrical conductivity) in the unploughed and ploughed sites in relation to differences in: (i) the age and size of the shrubs, (ii) the degree of decomposition of log or debris mounds, and (iii) the extent of recovery of the biological soil crust in the interspaces. This chapter also compares differences across two contrasting environments to assess whether the effects of ploughing and shrubs are consistent in these two systems. This work has been published in *Plant and Soil*.

Chapter 5 describes the changes in the spatial patterns of shrubs and litter and biological soil crust cover, labile C, inorganic N, and net N mineralisation capacity with ploughing and grazing treatments. This work has been published in *Geoderma*.

Chapter 6 compares changes in the spatial patterns of bulk density, bare ground cover and soil infiltrability with ploughing and grazing treatments and has been published in *Geomorphology*.

Chapter 7 examines difference of soil organic C with different landscape elements (e.g., shrubs, log or debris mounds, trees) and calculates, at a landscape level, the amount of aboveground and belowground C accumulating on sites experiencing different treatments. This work has been published in *Agriculture, Ecosystems and Environment*.

Chapter 8 summarizes the main findings of this research and its implication, and suggests directions for future research.

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Plant and soil surface responses to a combination of shrub removal and grazing in a shrub-encroached woodland

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Abstract

Shrub encroachment into open woodland is a widespread phenomenon in semi-arid woodlands worldwide. Encroachment or woody thickening, is thought to result from overgrazing, changes in fire regimes and increased atmospheric carbon dioxide concentrations. Eighteen years after one-off shrub removal by ploughing we assessed the effects of four different land management systems resulting from two levels each of grazing (grazed, ungrazed) with and without ploughing, on the cover of landscape units, soil surface condition, diversity of understorey plants and density of shrubs. We recorded 2–7 times more patches under conventional conservation (unploughed–ungrazed) than the others treatments, and plant cover and diversity were greater on the two conservation (ungrazed) plots, irrespective of ploughing. Soils under shrubs and log mounds had greater indices of infiltration, stability and nutrients. Shrub density under the active pastoral (ploughed–grazed) treatment was two and a half times greater than that in other treatments, but results were not significant. The effects of different treatments on shrubs were largely species-specific. Overall, our results suggest that ploughing does not provide long-term control of encroaching shrubs.

Keywords: shrub encroachment, mechanical shrub removal, shrub control, thickening, shrublands, grazing

Introduction

The encroachment of native woody plants into former open grassland or open woodland is an increasing global phenomenon that has been likened to the spread of exotic plants (Noble, 1997; Van Auken, 2000; Archer et al., 2001; Maestre et al., 2009). The encroachment of snakeweed (*Gutierrezia* spp.) (Sterling et al., 1999), mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentata*) in western United States rangelands (Buffington and Herbel, 1965), and turpentine (*Eremophila sturtii*), budda (*Eremophila mitchellii*) and narrow-leaf hopbush (*Dodonaea viscosa* var. *angustissima*) in eastern Australian rangelands (Hodgkinson, 1979) are examples of native species that exhibit some invasive qualities. The causes of this phenomenon, variously referred to as shrub invasion, encroachment or woody thickening, are varied, and appear to be due to the interaction of several factors (Archer et al., 1995). Changes in land-use practices from frequent wildfire to controlled, infrequent fire are exacerbated by increases in stocking rates of both domestic and native animals over large areas of rangelands (Wilson, 1990; Harrington, 1991; Archer et al., 1995), which have reduced fire fuel loads. Variation in rainfall (Fensham et al., 2005) and increases in global CO₂ concentrations are thought to have benefited C₃ woody species at the expense of C₄ grasses (Polley et al., 1993; Chapin et al., 2002), and studies within long-ungrazed exclosures suggest that climate change may be responsible, at least in part, for some changes in shrubland communities (Grover and Musick, 1990).

The generally negative perception of native shrubs as invaders is highly context-dependent (Colautti and MacIsaac, 2004) and based largely on the effects that shrubs have on reducing pastoral productivity in agricultural, production-based landscapes. It is unclear, however, whether shrubs per se or interactions between grazing and climate are responsible for the putative reductions in pastoral production in encroached woodlands and grasslands. Woody shrub encroachment into grasslands is known to alter the balance between runoff and infiltration (Rostagno et al., 1991) and transpiration and

evaporation (Aguilar et al., 1996), affect the spatial distribution of soil nutrient pools (Schlesinger et al., 1996) and produce far reaching effects on ecosystems. These putative negative effects are, however, not universal. Shrubs are important for moderating a range of ecosystem services because they influence micro-climate, reduce erosion and nutrient loss, increase water holding capacity, maintain soil structure and stability, and provide habitat for a range of taxa (Maestre et al., 2009). Shrubs intercept solar radiation, lowering soil surface temperatures, reducing evapotranspiration and increasing soil moisture contents compared to the interspaces (Vetaas, 1992). Shrubs also regulate pathways of nutrient flow by acting as nutrient pumps (Vetaas, 1992). Recovery rates of heavily grazed systems are faster with the presence of shrubs than with perennial grasses alone (Mazzarino and Bertiller, 1999). Shrubs are not only more resistant to drought (Richmond and Chinnock, 1994; Booth et al., 1996), but they can also tolerate extremes of fire, salinity and frost (Richmond and Chinnock, 1994) and under grazed conditions, have a competitive advantage over perennial grasses (Maconochie, 1982; Booth et al., 1996). Shrub encroachment in Mediterranean systems has recently been shown to be associated with reversal of desertification process, a sign of improved ecosystem function (Maestre et al., 2009).

There have been many attempts to transform shrublands back to their putative original grassland–woodland matrix through programs of destocking, exclosure, or by using mechanical, biological and chemical techniques. Stock removal through exclosure produces conflicting results (Trodd and Dougill, 1998; Angassa and Oba, 2007) and in most cases, shrubs continue to maintain their dominance even after complete grazing removal (West et al., 1984; Eccard et al., 2000; Valone et al., 2002; Guo, 2004; Mengitsu et al., 2005; Angassa and Oba, 2007). Mechanical removal of shrubs generally produces only short-term changes in plant community structure (Morton and Melgoza, 1991; Robson, 1995; Allegratti et al., 1997), often stimulates shrub regrowth, and leads to the eventual persistence and dominance by woody shrubs (e.g., Ruthven III et al., 1993). Post-treatment management of stocking rates is rarely considered by land managers, and many failures are thought to be due to the suppression of grass growth due to overgrazing (Cox et al., 1984). Similarly, landscape-level processes often overwhelm smallscale shrub manipulation treatments, limiting the success of many restoration programs (Herrick et al., 2006).

Here we consider the effects of four land management treatments on the structure and composition of a shrub-encroached woodland. Our study site is typical of encroached woodlands in eastern Australia, which are characterised by dense native shrubs, sparse perennial grasses, and an extensive cover of bare, eroded soil. The four treatments represent different land management scenarios that reflect how managers in eastern Australia manage shrubs within the context of both pastoral production and conservation. The ‘conventional pastoral’ option involves set stocking and no shrub removal, while the ‘active pastoral’ treatment involves the removal of shrubs followed by the maintenance of current grazing practices. ‘Conventional conservation’ is a strategy practiced by managers of national parks and conservation reserves whereby livestock are removed but shrubs are not controlled. ‘Active conservation’ involves the removal of livestock and some shrub removal in order to meet some specific conservation objectives such as altered habitat for key plant or animal species (Table 1). While most of the semi-arid grazing land in eastern Australia falls within the conventional pastoral scenario, increasingly larger areas of shrubland and woodland are being ‘treated’ (shrub removal) through incentives programs driven by community-based land management agencies such as Catchment Management Authorities (<http://cw.cma.nsw.gov.au>) under a scenario of continued livestock grazing. Apart from localised removal of shrubs to improve management of conservation reserves (e.g., removal along fences and tracks), we are unaware of any large scale ‘active conservation’ in the context of physical removal of shrubs.

We used a long-term exclosure experiment to test three predictions about the response of soil surfaces, groundstorey vegetation and shrubs along a gradient in disturbance resulting from a one-off shrub removal by blade ploughing (*syn.* root ploughing) followed by either grazing or exclosure. Blade ploughing has been promoted widely by agencies in eastern Australia since the late 1970s for control of shrubs (Robson, 1995), though anecdotal evidence suggests that it provides only short-term shrub control. A long-term perspective is needed to adequately evaluate the response of shrubs and soil surfaces to disturbance. Because many studies have considered only short-term responses (e.g., Robson, 1995), our study adds substantially to society’s understanding of shrub control in semi-arid woodlands. Second, our study combines two elements of

the encroachment problem; removal of the shrubs themselves, and the interactive effect of grazing. Without controlling for the grazing effect, it is difficult to gauge the long-term consequences of shrub removal within a pastoral context.

Grazing is known to reduce the size and number of vegetated patches (e.g., van de Koppel et al., 2002) and thus we predicted a marked decline in measures of landscape function such as soil surface condition and the number and size of resource-accumulating patches with increasing disturbance i.e., from conventional conservation to the actively-managed, pastoral treatment (Table 1). We also predicted that grazing and ploughing would reduce plant diversity and composition by maintaining the dominance by shrubs, consistent with results worldwide (e.g., Bisigato and Bertiller, 1997; Ruthven III et al., 1993). Third, we anticipated shrub species-dependent treatment effects, specifically increases in the densities of grazing- and ploughing-tolerant species such as *E. sturtii* and *Eremophila gilesii* but reductions in grazing- and ploughing-sensitive species such as *Acacia aneura* and *D. viscosa* under the active pastoral treatment. We expected species that are both ploughing-tolerant and grazing-intolerant, such as *Eremophila longifolia*, to be found in the active pastoral treatment while the conventional conservation treatment would be expected to be characterised by a mixture of intolerant species as well as grazing- and ploughing-tolerant species.

Methods

Study area

The study was conducted at ‘Wapweelah’, an extensive grazing property about 35 km west of Enngonia near Bourke in north-western New South Wales, Australia (29° 16’S, 145° 26’E). The site falls within Gumbalie land system (Walker, 1991), which is dominated by mulga (*A. aneura*) woodlands. The landscape is characterised by sandplain with low west–east trending sandy rises and dunes of Quaternary aeolian alluvium. Minor to moderate windsheeting and watersheetings are common. The sandplain unit is level to slightly undulating (slope < 1%) and the soils are dominated by sandy red earths with sandy loam to loam texture. Mean annual rainfall at Wapweelah is

about 312 mm, and about 45% more rain falls during the six warmer months than the cooler months (Robson, 1995).

The sandplain unit of Gumbalie land system is characterised by dense shrubs dominated by turpentine, narrow-leaf hopbush, green turkey bush (*E. gilesii*), budda and wild orange (*Capparis mitchellii*). There are few scattered trees of mulga, ironwood (*Acacia excelsa*), bimbale box (*Eucalyptus populnea*), belah (*Casuarina cristata*), rosewood (*Alectryon oleifolius*), leopardwood (*Flindersia maculosa*), supplejack (*Ventilago viminalis*), wilga (*Geijera parviflora*), gidgee (*Acacia cambagei*) and brigalow (*Acacia harpophylla*). The understorey layer is sparse, and at the time of observation consisted of heavily grazed woollybutt (*Eragrostis eriopoda*), Mitchell grass (*Thyridolepsis mitchelliana*), mulga oats (*Monochather paradoxa*), speargrass (*Austrostipa scabra*), other grasses and forbs. This land system is typical of areas targeted for blade ploughing (Walker, 1991; Robson, 1995). Shrubs do not form a community resembling the ‘brousse tigre’ vegetation of southern Africa but grow in isolated patches, sometimes forming islands. Many shrubs occupy bare area resulting from the loss of perennial grasses through overgrazing (Daly and Hodgkinson, 1996).

Shrub removal design

In 1990, three replicate blocks of 200 m x 400 m were established, and each divided into four equal plots of 100 m wide by 200 m long. The two central plots were then enclosed in a 6 m high, herbivore-proof fence. Half of both the fenced and unfenced plots were then ploughed and the other half unploughed. The grazed plots were subjected to grazing by sheep, goats, cattle, kangaroos, rabbits and camels. The three replicate blocks varied from 1 km to 5 km apart. Shrubs were removed with a single pass of a 4.2 m wide single-tynd ‘Stationmaster’ blade plough pulled by a 90 kW crawler tractor. Only shrubs were targeted. The cutting depth was maintained at 20–30 cm to sever the taproots of *Eremophila* spp. in order to achieve a maximum kill rate (Wiedemann and Kelly, 2001). Examination of fallen shrubs confirmed a satisfactory ploughing effect over most of the treated area (Robson, 1995).

Assessment of landscape units

In August 2008, 18 years after ploughing and fencing, we established a 50 m transect through the centre of each plot in order to measure the composition of different landscape units (i.e., plains, shrub hummocks, and log mounds) in each treatment. Shrub hummocks are the elevated accretions around woody plants and log mounds are accumulations of wind and water eroded material deposited against ploughed shrubs and fallen timber. Along with shrub hummocks, these are sufficient to impede sediment, litter and seed movement. The intervening area between shrub hummocks and/or log mounds, comprised plains, generally bare, but sometimes with a poorly developed cover of cryptogamic crusts.

Landscape-scale functional measures

The same 50 m transect was also used to assess the functional integrity of each plot in terms of the degree to which resources such as runoff water, entrained sediment, seeds, nutrients and organic matter are retained within patches such as grass tussocks, which occur in the interspaces on the plains. Landscape function analysis (LFA) has been shown to be strongly related to empirical measures of soil function (e.g., Ludwig and Tongway, 1995; Maestre and Cortina, 2004). Along this transect we recorded the total length and width of resource-accumulating patches such as grass tussocks, logs, tree and shrub hummocks, and the distances between these units (fetches), which represent resource shedding. A detailed assessment of the LFA technique is given in Ludwig and Tongway (1995).

Soil surface morphology

Detailed measurements of the morphology of the soil surface were made within the landscape units identified on each plot using quadrat-based methods according to the methods of Tongway (1995). Thirteen soil surface features were assessed along the transect within ten 0.5 m² quadrats, stratified according to the relative cover of different landscape units on a plot. These surface features were: 1) surface stability, which measures the ease of soil particles to be removed by wetting and the ability of surface or

projected plant cover to protect them; 2) soil surface roughness, which assesses how rough the soil surface is and the level to which it will act as micro-depression for mobile resources; 3) surface cracking, which measures the proportion of the surface covered with cracks, and the potential for the surface to be dislodged by erosion; 4) cryptogam cover which determines the cover of non-vascular plants on the surface; 5) crust brokenness, which assesses to what extent the surface crust is broken and the degree to which raindrop impact will deform the soil surface; 6) type and severity of erosion, where forms of erosion were used to determine the severity of wind and/or water erosion; 7) litter cover; 8) whether litter is derived from local plants or transported from elsewhere; 9) the degree to which litter is decomposed and incorporated into the soil, 10) perennial vegetation cover, which measures the basal and canopy cover; 11) deposited material which measures the nature and amount of soil and litter transported and deposited on the query zone; 12) surface stability to rapid wetting, using a simple slake test; and 13) soil surface texture, which indicates how good soil infiltration is and its capacity to store water and support plants.

The 13 soil surface attributes described above were used to derive three biogeochemical indices which describe the extent to which the soil: 1) cycles nutrients (nutrients), 2) captures water (infiltration) and 3) resists erosion (stability) (Tongway, 1995). For a particular quadrat the value of each attribute was given a score, usually from 1 to 5, with a larger score equating with a healthier functional surface. Thus for example, the soil surface roughness classes of <5 mm, 5–8 mm, 8–15 mm, 15–25 mm and >25 mm were assigned scores of 1, 2, 3, 4, and 5 respectively such that a rougher surface, which implies a better soil condition, receives a higher score. The overall index for stability for a given quadrat was derived as the sum of the seven scores for surface cracking, surface stability, crust brokenness, degree of erosion, cryptogamic cover, vegetation cover, and litter cover expressed as a percentage of 40, the maximum possible score. In a similar manner, four of the surface attributes described above (surface roughness, cryptogamic cover, vegetation cover, and litter cover) were used to derive a score for the nutrient status of the soil, which is based on the ability of the soil to cycle and retain nutrients. Finally, values for vegetation cover, a combined product of the three litter scores, surface roughness, surface stability and soil texture were used to derive an index of infiltration (Tongway, 1995).

Plant cover and diversity

We recorded separately, the height classes of all dead and live shrubs, by species, along one 50 m x 2 m transect on each plot. Shrubs were measured on a scale of $1 < 0.25$ m, $2 = 0.25\text{--}0.50$ m, and thereafter at 0.50 m increments, to $10 = 3.50\text{--}4.00$ m. Additionally, within a 20 m x 20 m quadrat centrally located along the 50 m transect, we used that quadrat of 100 grid points to estimate the cover of bare ground, plant, litter and cryptogamic crusts and the cover of all groundstorey, midstorey, and upperstorey vascular plant species.

Statistical analyses

We used a mixed-model ANOVA with two strata to examine differences in the three soil surface indices (infiltration, stability, nutrient) in relation to the four treatments and three landscape units. The first stratum considered treatment, and the second stratum landscape unit and its interaction with treatment. To examine differences in shrub density and landscape functions, including the number of resource-accumulating patches, fetch length and patch width, we used a randomized block ANOVA after scaling the data up to the landscape level by adjusting for the relative cover of different landscape units at each plot. Data were checked for normality and homogeneity of variance (Levene's test) using Minitab version 15 prior to analyses. Post-hoc differences in means were tested using Least Significant Difference testing. Differences in shrub height class distributions in relation to the treatments were determined using Ordinal Logistic Regression using Genstat version 12.

Permutational multi-variate analysis of variance (PERMANOVA, Anderson et al., 2008) with the Bray-Curtis similarity coefficients was used to test whether the composition of 1) groundstorey plants and 2) shrubs differed in relation to the four treatments. Values for richness, evenness, abundance (number of individuals) and number of species were determined using the DIVERSE function of PERMANOVA and differences in relation to treatment assessed using the same ANOVA structure described above for the landscape-level study. The SIMPER subroutine of

PERMANOVA was used to determine which species contributed most to the dissimilarity among treatments. The degree of association of different species with the four treatments was assessed with Indicator-Species Analysis using PC-ORD (McCune and Mefford, 1999). Indicator values (IV) are maximal (100%) when all individuals of a given species are restricted, for example, to a given treatment, or all samples from that treatment contain that species.

Results

Landscape-unit level changes

At the scale of landscape units, plains always had the lowest indices of nutrients ($F_{2,16} = 16.9$, $P = 0.003$) and infiltration ($F_{2,16} = 24.5$, $P < 0.001$) compared with shrub hummocks and log mounds, except for the index of stability where the difference was only significant between plains and shrub hummocks ($F_{2,16} = 50.8$, $P = 0.002$; Table 2). We did not find any significant interactions, however, between landscape unit and treatment, indicating consistent effects of landscape unit among the treatments. We only found one significant treatment effect, with active conservation plots having 1.2 times greater values of the nutrient index than active pastoral plots ($F_{2,16} = 7.09$, $P = 0.012$).

Landscape level changes

At the landscape scale, we detected no significant differences in the nutrient ($P = 0.18$), infiltration ($P = 0.16$) or stability ($P = 0.69$) indices among the four treatments (Table 3). However, trends for these indices were similar, with a general decline from the least disturbed to the most disturbed treatments (i.e., from conventional conservation to active pastoral).

There was a significant treatment effect, however, on the number of resource-accumulating patches per 50m of transect, with two- to seven-times more patches in the conventional conservation treatment than the others ($F_{3,8} = 27.0$, $P < 0.001$; Table 3). Mean distance between patches (fetch length) also varied significantly in relation to different combinations of grazing and ploughing, with fourfold larger fetches in the

conventional pastoral plots (mean = 20.72 m) than the conventional conservation plots (4.77 m; $F_{3,8} = 5.91$, $P = 0.02$). There were no treatment effects, however, on patch width ($P = 0.35$; Table 3).

Plant, litter, and cryptogam cover

Plant cover was greatest under the active conservation treatment ($43.3 \pm 4.4\%$; mean \pm SE) compared with the other management scenarios (20.3–27.3%; $F_{3,8} = 6.17$, $P = 0.018$) but there was no difference in cover of bare ground ($P = 0.35$) nor litter cover ($P = 0.56$). Cryptogam cover was about four-times greater under the conventional (unploughed) treatments than the active management (ploughed) treatments ($F_{3,8} = 2.56$, $P = 0.043$; Table 4).

Plant community structure and composition

Averaged over plots, the active conservation treatment had about 60% more species than the active pastoral treatment ($F_{3,8} = 4.92$, $P = 0.032$). The active conservation treatment also supported the greatest number of individuals (18.0 ± 1.15) while the conventional pastoral plots had the least (9.7 ± 1.67 ; $F_{3,8} = 5.76$, $P = 0.021$). There were no significant effects on species richness ($P = 0.16$) nor evenness ($P = 0.71$; Table 4). The composition of understorey plants varied significantly in relation to the different treatments (pseudo $F_{3,8} = 1.73$, P (perm) = 0.027). There was a slight difference in the complement of species between the extreme treatments (active pastoral and conventional conservation: $t = 1.98$, P (perm) = 0.064). Four species, two forbs (*Sclerolaena divaricata*, *Sclerolaena convexula*) and two perennial grasses (*E. eriopoda*, *Monachather paradoxa*) explained more than 50% of the difference between active pastoral and conventional conservation. The two *Sclerolaena* spp. were more abundant in the active pastoral plots while the two grasses were more abundant in the conventional conservation plots. *Maireana appressa* (IV = 84.2, $P = 0.053$) was greatest in conventionally-conserved plot compared to other plots.

Shrub community structure and composition

There were no significant differences in the total densities of either live or total (live \pm dead) shrubs in relation to the four treatments ($P = 0.62$). There were, however, about 2.5–times more shrubs in the active pastoral treatment (5750 ± 3404 shrubs ha^{-1}) than under conventional pastoral (2300 ± 1404 shrubs ha^{-1} ; Table 4). The distribution of shrub sizes on the most disturbed (active pastoral) treatment was skewed towards a large number of small individuals, while the least disturbed treatment (conventional conservation) showed a more hump-shaped size class distribution (Fig. 1). Grazed plots (both under active and conventional pastoral) had a greater proportion of juvenile shrubs than ungrazed (conserved) plots ($F_{3,21} = 13.6$, $P < 0.001$; Fig. 1), which was due principally to the presence of large cohorts of *E. gilesii* seedlings (Fig. 2).

Ploughing and grazing treatments favoured or hampered shrub species to a different degree. *E. sturtii* ($F_{3,8} = 5.26$, $P = 0.027$) was almost 100-times denser under conventional conservation than under active conservation (Table 5, Fig. 2). *E. longifolia* shrubs showed the opposite trend, with 8-times greater density at active conservation plots than conventional conservation plots ($F_{3,8} = 8.20$, $P = 0.008$). *E. longifolia* shrubs were not found at active pastoral plots (Table 5; Fig. 2).

There were no treatment effects on the number of shrub species ($P = 0.18$), the number of individual shrubs ($P = 0.14$), shrub species richness ($P = 0.20$) nor evenness ($P = 0.39$). There were, however, significant differences in shrub composition between treatments (pseudo $F_{3,8} = 2.27$, P (perm) = 0.02). Differences were generally due to a dominance of *A. excelsa* in the conventional conservation plots compared with the active pastoral plots, more *E. sturtii* in the conventional pastoral and conservation plots than the active conservation plots, and more *E. longifolia* in the active conservation plots than the active pastoral plots (Table 5). *E. longifolia* (IV = 94.7, $P = 0.006$) and *A. aneura* (IV = 94.7, $P = 0.006$) were strong indicators of active conservation and conventional conservation plots, respectively (Table 5). SIMPER analyses indicated that ploughed (active pastoral and active conservation) plots supported more small (<0.50 m) *E. gilesii* and more large (>1.50 m) *D. viscosa* than unploughed plots, while the

unploughed plots (conventional conservation and conventional pastoral) supported moderate to large-sized (>1.00 m) *E. sturtii* than ploughed plots (Fig. 2).

Discussion

Treatment effects on landscape units and surface condition

Both the density and size of resource-accumulating patches declined with increased disturbance, consistent with our prediction and with observations worldwide of substantial effects of grazing and disturbance on vegetation patches (Roundy and Jordan, 1988; Allegratti et al., 1997; Eccard et al., 2000; van de Koppel et al., 2002; Golodets and Boeken, 2006). The least disturbed treatment (conventional conservation) had the greatest number of patches (9.3 per 50 m of transect), with average microrelief of 5–10 cm high. Natural rates of patch formation are probably low in the semi-arid woodlands, therefore it is not surprising that we failed to detect a recovery in their density 18 years after ploughing, even under exclosure (active conservation). In a similar landscape, artificial patches created by placing mulga (*A. aneura*) branches on the soil surface accreted at a rate of about $0.5\text{--}0.7\text{ mm yr}^{-1}$ compared with an erosion rate of $0.8\text{--}0.9\text{ mm yr}^{-1}$ in areas devoid of these structures (Tongway and Ludwig, 1996). Based on Tongway and Ludwig (1996) accretion rates, recovery of patches at our study site would take more than a century under exclosure or about 160 years under grazing in the shrubby woodlands. These projections highlight the fact that landscape change in semi-arid woodlands is protracted (Coffin et al., 1996; Valone et al., 2002; Guo, 2004), and that 18 years of recovery is insufficient to restore landscape structure.

Though the density of patches declined, we did not detect significant changes in bare soil nor any treatment effects on the three surface health indices. Cryptogam cover was, however, lower under the active (ploughed) treatments, irrespective of grazing status. Reduced cryptogam cover is a typical responses to increased disturbance in semi-arid environments (Anderson et al., 1982; West, 1990), and while direct physical disturbance by ploughing would have been responsible for the initial crust reduction at our plots, trampling by stock would compromise its recovery (Williams et al., 2008), resulting in persistent soil and nutrient loss for many decades (Neff et al., 2005). Crust cover is

sparse to moderate in the semi-arid wooded rangelands (Eldridge, 2001) and any exacerbation by grazing on an already disturbed surface will likely retard the development of the crust, and could promote a crust dominated by cyanobacteria (Eldridge and Greene, 1994).

Water-repellent crusts enhance the redistribution of water from the interspaces, thereby augmenting water supply to the patches. Breakdown in crust continuity by animal trampling alters runoff–infiltration relationships, leads to greater infiltration in the interspaces, breakdown in patch condition and increases the time period required for the restoration of patches. Removal of the crust is also likely to affect ecosystem processes such as plant germination, establishment, survival and nutrient mineralisation (Eldridge, 2001). The combination of reduced crust cover and low density of patches in both active (ploughed) treatments likely compromises the ability of these landscapes to capture and store essential resources such as water and nutrients, prolonging the recovery process.

Treatment effects on understorey plants and shrubs

Grazing exclusion in grasslands typically leads to a recovery of perennial grass cover (Tiedemann and Klemmedson, 2004; Mata-González et al., 2007), but the time over which this occurs varies widely and is related to the capacity of the landscape to respond to rainfall. Consequently, many studies have failed to detect increased perennial grass density after more than a decade of removal of livestock (West et al., 1984; Valone et al., 2002) or even after physical removal of shrubs and exclosure (active conservation; Roundy and Jordan, 1988). In our study, increased disturbance was associated with significant declines in plant diversity and changes in composition, consistent with our second prediction. Plant cover and diversity were greatest under active conservation (disturbance followed by exclosure) in contrast to grazing post-disturbance (Jauffret and Lavorel, 2003). However, the substantial recovery of perennial grasses at the study site only two years after treatment (Robson, 1995) was not observed in our study 18 years after treatment and can only be attributed to reduced summer rainfall since ploughing. This suggests to us that the greater cover of grazing–sensitive perennial bunch grasses such as *E. eriopoda* and *Monachather paradoxa* that we recorded in the ungrazed–unploughed treatments was due mainly to removal of

grazing rather than to summer rainfall per se. Rainfall records for the 18 year period since treatment confirms our suggestion that rainfall was less effective than grazing (Appendix Fig. 1). Differences in post-treatment rainfall therefore likely account for the wide range of responses to woody shrub removal by ploughing in eastern Australia. This reinforces the importance of managing stocking rates after shrub removal, particularly in areas where the soils are highly erodible and natural rates of surface stability are inherently low.

Treatment effects on shrubs

Studies of shrub density and richness worldwide indicate a range of responses to both the individual and combined effects of grazing and physical shrub removal. In our study shrub densities were two and a half to three-times greater under the active pastoral treatment (ploughing and grazing, 5750 shrubs ha⁻¹) than either the conventional pastoral (grazing only, 2300 shrubs ha⁻¹) or active conservation (3400 shrubs ha⁻¹) treatments. The density of live shrubs on ploughed–grazed plots was two and a half times greater than that on grazed plots that had not been ploughed, even if we take into account shrubs that had died over the past 18 years. There were some highly variable results, particularly in the active pastoral treatment, which could have been due to differences in the initial species composition or soil heterogeneity at the landscape scale. One of the active pastoral plots supported a large number of *E. gilesii* seedlings which were not found at the other two plots. *E. gilesii* are profuse seed producers, unpalatable to stock and able to regenerate by root suckering (Burrows, 1974). It is not surprising that a large number of seedlings can be found in the area that was ploughed and grazed and previously dominated by this species. Our data therefore suggest a trend of greater density of shrubs after ploughing, particularly in the area dominated by species that are able to regenerate by root suckering or epicormic buds. The results suggest a trend of greater density of shrubs after ploughing, even though this difference was not statistically significant because of limited replication at the landscape scale (three landscape-level replicate exclosures). We detected a trend of declining landscape function indices, and probably irreversible structural changes over a period of declining summer rainfall. Given the likely reductions in soil nutrients and depletion of soil seed banks of perennial grasses (Hodgkinson and Harrington, 1985), our study suggests that

shrub-encroached woodlands are unlikely to revert to grassland in the next century (e.g., Jeltsch et al., 1997). Indeed our observations are consistent with widespread reports in the literature of failure of mechanical treatments to provide long-term shrub control. Instead of recovering to grasslands, shrubs continued their domination and left the remaining degraded area bare (Roundy and Jordan, 1988; Ruthven III et al., 1993; Mata-González et al., 2007).

As predicted, the effects of ploughing and grazing on shrub density were highly species specific, with pastoral (grazed) plots supporting fewer *A. aneura*, *Acacia burkitii* and *D. viscosa* subsp. *angustissima* shrubs that are moderately palatable to livestock and macropods (kangaroos), particularly when young (Hodgkinson, 1979; Tiver and Andrew, 1997). There were also fewer *E. longifolia* shrubs under the plough–graze scenario, but not under the plough–ungraze scenario. This result was not surprising given that *E. longifolia* readily reproduces by disturbance-induced root suckering (Chinnock, 2007). *E. longifolia* is also highly palatable to livestock, thus resprouting shrubs would be expected to have been not only more accessible to browsers, but also to have contained higher leaf nitrogen or phosphorus or lower concentrations of grazing suppressing polyterpenes and flavones (Chinnock, 2007), which would discourage vertebrate browsers. Higher concentrations of plant defence substances are known to be present in regrowth leaves in response to heavy browsing (e.g., *Acacia berlandieri*; Forbes et al., 1995).

Ploughing failed to reduce the density of *Dodonaea viscosa*, one of the most abundant shrubs in eastern Australia, and a species regarded as being moderately susceptible to mechanical control (Harland, 1993; Robson, 1995; Eldridge and Robson, 1997). Ploughing did, however, reduce *E. sturtii* densities almost eightfold, with surviving shrubs restricted almost entirely to the two unploughed treatments, and with few shrubs greater than 1.5 m tall. Ploughing would be expected to stimulate regeneration of *E. sturtii* through root suckering or from epicormic buds close to the soil surface (Hodgkinson, 1979; Chinnock, 2007). As subsequent grazing would also favour its regeneration by removing competitors, *E. sturtii* would likely dominate areas with a history of heavy stock grazing (Tiver and Andrew, 1997), unlike its congener *E. longifolia*. Ploughing provides effective control of *E. sturtii* only where the depth of

ploughing is within the range of 20–40 cm (Harland, 1992). The reasons for the different responses of *E. sturtii* and *E. longifolia* to ploughing in our study are unknown and therefore could have resulted from differences in the depth of ploughing as a result of the uneven micro relief of shrub patches. Ploughing at shallow depths, by failing to cover remaining roots with soil, is known to elicit bud formation and resprouting in some shrubs (Wiedemann and Kelly, 2001). Lower levels of re-establishment of *E. sturtii* compared with *E. longifolia* in the ploughed–ungrazed plots could also have been caused by the association of *E. longifolia* with arbuscular mycorrhizal fungi, which is not found in *E. sturtii* (O’Connor et al., 2001).

The distribution of shrub sizes varied substantially in relation to grazing, reinforcing our view that, rather than providing long-term control of shrubs, grazing of ploughed shrubland is likely to skew the distribution of shrubs to one dominated by a larger number of smaller shrubs, in our case, large cohorts of *E. gilesii* seedlings. *E. gilesii* is a prolific seed producer and typically forms dense monospecific stands of up to 12,000 shrubs ha⁻¹ (Burrows, 1974). In the short-term, a larger number of smaller shrubs may be a positive management outcome, as smaller shrubs will likely make access and stock movement easier, and would not suppress understorey plants to the same extent as large mature shrubs with extensive canopies.

Management of shrub-encroached woodlands

The results of this study question the long-term viability of shrub removal using blade ploughing on sandy soils in eastern Australia, and therefore the benefits of investing in mechanical shrub control. There were few clear pastoral benefits of shrub treatment 18 years after treatment, though we acknowledge that some grazing value, in the form of enhanced productivity of pastorally important perennial grasses, may have accrued at various times over the past 18 years (e.g., Robson, 1995). The anticipated recovery of perennial grasses with shrub removal did not occur, and the reasons for this are likely numerous such as prolonged grazing from sheep and feral goats, and below average periods of summer rainfall. Our results indicate that ploughing was not an effective method to control shrubs in this area given that the results are species-specific and likely to depend on post-treatment rainfall (Robson, 1995). In combination with

grazing, ploughing promoted a groundstorey plant community dominated by shortlived, grazing-tolerant species at the expense of perennial grasses. Furthermore, shrub removal by ploughing had generally negative effects on the soil, reduced patches and cryptogamic cover even under exclosure. More importantly, ploughing failed to sustain the increases in grass cover, and resulted in long-term increases rather than reductions in shrub density. In the context of pastoralism, alternative strategies such as adjusting the livestock number, or the use of shrublands for short-term agistment of livestock during productive (La Niña) seasons, a contemporary form of transhumance, or the use of alternative grazing animals such as goats may be more appropriate. An alternative perspective, which is gaining traction worldwide, is to value these encroached shrublands in terms of the ecosystem benefits that they can provide for communities such as fresh water, habitat, fuel wood and sinks for carbon dioxide. We acknowledge, however, that such a shift will likely adversely impact the livelihoods of producers at a time when they are attempting to recoup the costs of these new strategies.

Conclusion

We found that that ploughing was generally an inappropriate method for reducing shrub densities in encroached Australian semi-woodlands. The effects of ploughing (with and without grazing) were largely species-specific. Given that Australian semiarid shrublands are rarely monospecific, broad-scale indiscriminate treatments such as ploughing will provide effective control of only a limited number of species, and could conceivably select for shrubs that resprout after ploughing. The results of our study provide valuable insights into the problems associated with mechanical shrub control in eastern Australia. More studies are needed to assess the efficacy of shrub control with mechanical methods, particularly given the considerable amount of money spent on ‘managing’ shrub-encroached woodlands over the last two decades.

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Table 1. Summary of the four ploughing and grazing treatment scenarios and their extend in eastern Australia

Scenario	Ploughed	Grazed	Extent	Disturbance intensity
Conventional conservation	no	no	Localised (<10% of landholders)	Low
Active conservation	yes	no	Very uncommon (<1% of landholders)	Moderate
Conventional pastoral	no	yes	Widespread (>50% of landholders)	Moderate
Active pastoral	yes	yes	Very common (25–50% of landholders)	High

Table 2. Landscape-unit-level mean (\pm SE) values for measures of soil surface condition for the three landscape units. Letters within a row indicate a significant difference in the attribute at $P < 0.05$.

Soil surface indices	Shrub hummock		Log mound		Plain	
	Mean	SE	Mean	SE	Mean	SE
Nutrient index (%)	24.1 ^a	1.2	22.4 ^a	1.4	16.9 ^b	1.2
Infiltration index (%)	32.7 ^a	1.8	33.2 ^a	2.1	24.5 ^b	1.8
Stability index (%)	58.9 ^a	1.7	54.8 ^b	2.0	50.8 ^b	1.7

Table 3. Mean (\pm SE) values for measures of landscape function for the four grazing and ploughing treatments. Letters within a row indicate a significant difference in the attribute at $P < 0.05$.

Attribute	Conventional conservation		Active conservation		Conventional pastoral		Active pastoral	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Nutrient index (%)	20.1 ^a	1.6	19.7 ^a	0.6	16.9 ^a	2.9	14.7 ^a	1.1
Infiltration index (%)	29.9 ^a	3.9	25.8 ^a	1.1	22.2 ^a	2.3	22.3 ^a	1.5
Stability index (%)	54.6 ^a	1.9	50.3 ^a	5.7	49.5 ^a	6.4	46.9 ^a	2.4
No. of resource accumulating patches	9.3 ^a	0.3	3.3 ^b	0.9	1.3 ^b	0.3	3.3 ^b	0.9
Fetch length (cm)	447.0 ^a	15.2	1240.0 ^{ab}	240.0	2072.0 ^b	414.0	1243.0 ^{ab}	240.0
Patch width (cm)	44.3 ^a	12.0	32.7 ^a	5.6	35.3 ^a	18.7	13.8 ^a	1.6

Table 4. Mean (\pm SE) values of plant, litter, bare ground and cryptogam cover, and measures of community composition for groundstorey and midstorey species for the four treatments. Letters within a row indicate a significant difference in the attribute at $P < 0.05$.

Attribute	Conventional conservation		Active conservation		Conventional pastoral		Active Pastoral	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Plant cover (%)	25.0 ^a	2.9	43.3 ^b	4.4	20.5 ^a	5.0	27.3 ^a	3.4
Litter cover (%)	11.7 ^a	3.3	11.0 ^a	2.1	7.9 ^a	0.3	9.3 ^a	1.3
Bare ground (%)	33.3 ^a	7.3	36.3 ^a	7.9	43.6 ^a	14.7	57.3 ^a	5.8
Cryptogam cover (%)	30.0 ^a	8.7	9.3 ^b	4.3	28.0 ^a	17.4	6.0 ^b	4.5
No. of species	20.3 ^{ab}	1.7	25.0 ^a	2.0	15.3 ^b	1.5	15.0 ^b	3.1
Abundance	13.3 ^{ac}	1.7	18.0 ^{bc}	1.2	9.7 ^a	1.7	12.0 ^{ac}	1.0
Species richness	7.6 ^a	1.0	8.3 ^a	0.7	6.4 ^a	0.4	5.6 ^a	1.0
Species evenness	0.9 ^a	0.01	0.9 ^a	0.01	0.9 ^a	0.03	0.9 ^a	0.02
Dead shrubs (ha ⁻¹)	1516.0 ^a	498.0	1733.0 ^a	833.0	700.0 ^a	150.0	2050.0 ^a	828.0
Live shrubs (ha ⁻¹)	3133.0 ^a	421.0	3400.0 ^a	1505.0	2300.0 ^a	1404.0	5750.0 ^a	3404.0

Table 5. Mean (\pm SE) density of shrubs (ha^{-1}) in relation to the four grazing and ploughing treatments. Differences were significant only for *Eremophila longifolia* and *E. sturtii*. Mean (\pm SE) density of shrubs (ha^{-1}) in relation to the four grazing and ploughing treatments. Differences were significant only for *Eremophila longifolia* and *E. sturtii*.

Species	Conventional conservation		Active conservation		Conventional pastoral		Active pastoral	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Acacia aneura</i>	100	50	50	29	0	0	17	17
<i>Acacia burkittii</i>	100	100	0	0	0	0	0	0
<i>Acacia excelsa</i>	133	33	17	17	167	117	0	0
<i>Acacia tetragonophylla</i>	17	17	0	0	0	0	0	0
<i>Atalaya hemiglauca</i>	0	0	17	17	0	0	0	0
<i>Alectryon oleifolius</i>	0	0	0	0	33	33	0	0
<i>Dodonaea viscosa</i> subsp.								
<i>angustissima</i>	533	324	1317	825	283	192	750	603
<i>Eremophila desertii</i>	67	44	33	33	183	136	133	83
<i>Eremophila gilesii</i>	1733	773	583	192	2800	2800	6083	6008

<i>Eremophila glabra</i>	33	33	67	44	67	67	150	150
<i>Eremophila longifolia</i>	100 ^a	76	817 ^b	262	17 ^c	17	0 ^c	0
<i>Eremophila mitchellii</i>	17	17	0	0	167	167	267	159
<i>Eremophila sturtii</i>	1683 ^a	232	17 ^b	17	1400 ^a	633	383 ^c	169
<i>Grevillea striata</i>	33	33	67	33	0	0	0	0
<i>Pimelea microcephala</i>								
subsp. <i>microcephala</i>	33	33	0	0	17	17	0	0

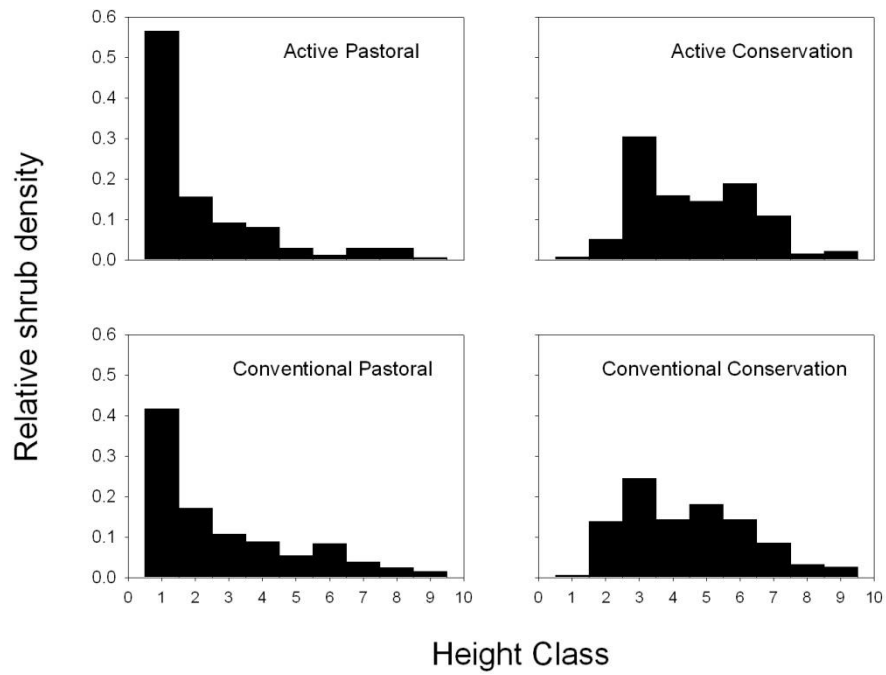


Fig. 1. Distribution of shrub heights for all shrubs in relation to the four grazing and ploughing treatments. Class intervals range from 1 = < 0.25 m to 10 = 3.50–4.00 m (see Methods).

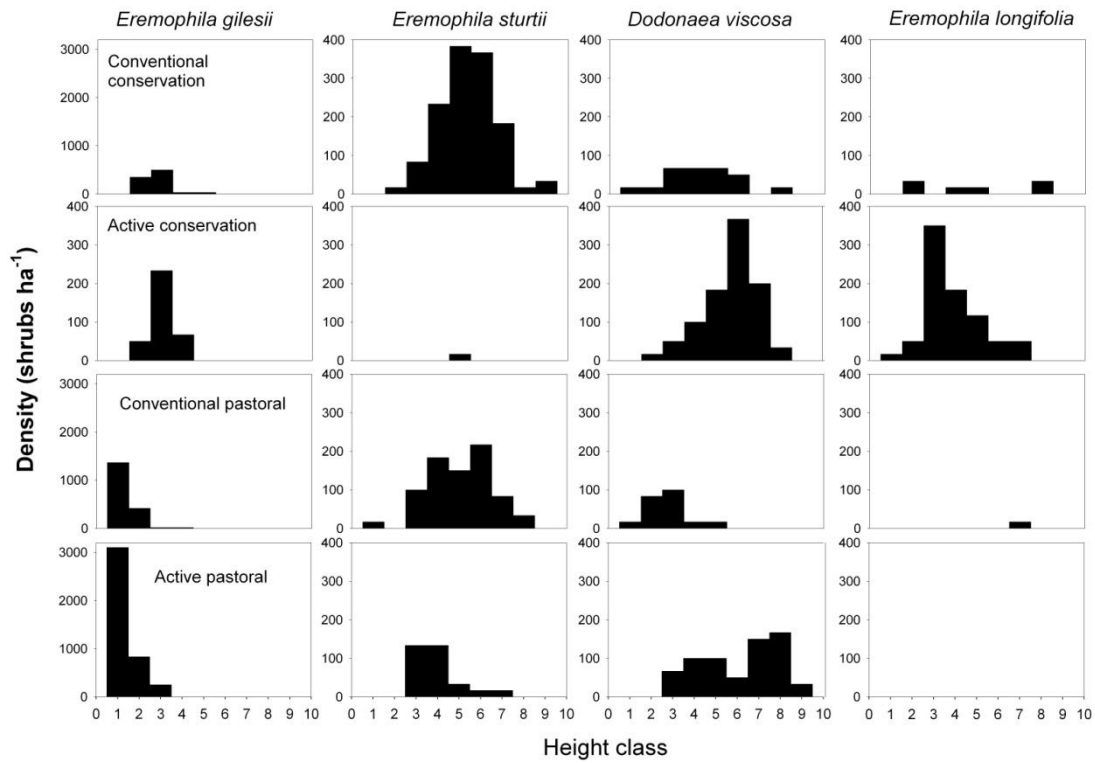
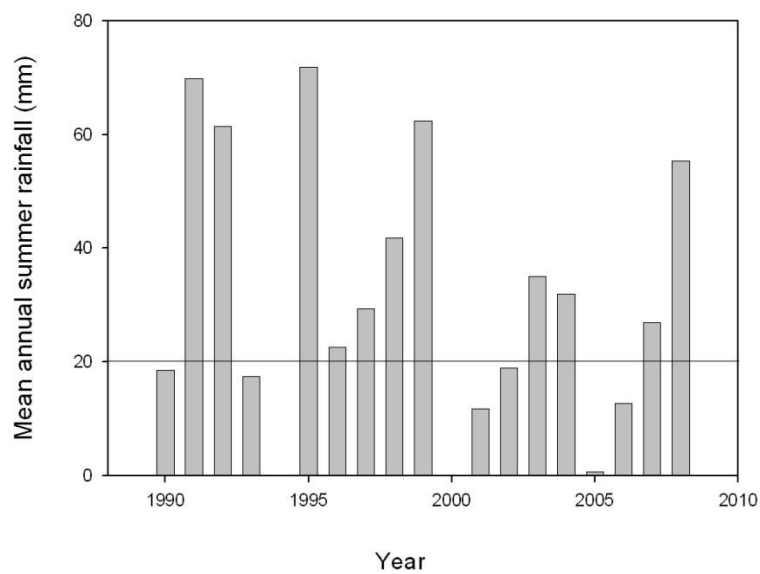


Fig. 2. Distribution of shrub heights for *Eremophila gilesii*, *Eremophila sturtii*, *Dodonaea viscosa* and *Eremophila longifolia* by density (ha^{-1}) for the four grazing and ploughing treatments. Class intervals range from 1 = <0.25 m to 10 = 3.50–4.00 m (see Methods). Note different scale of y-axis for *Eremophila gilesii*.



Appendix Fig. 1. Mean annual summer rainfall (December–February) 1990–2008. The solid line indicates the median rainfall (mm). Source: Australian Bureau of Meteorology (<http://www.bom.gov.au>; accessed 25 May 2010)

Shrub hummocks as foci for small animal disturbances in an encroached shrubland

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Abstract

Resources in semi-arid landscapes are concentrated around woody plants (trees and shrubs), and therefore attract soil-disturbing fauna. Globally the trend has been to remove encroaching shrubs from semi-arid shrublands to increase their value for pastoralism, potentially affecting shrub-resident biota. We examined the distribution of animal disturbances created by a range of organisms (e.g., ants, scorpion, cicada, reptiles, small mammals) under two ploughing treatments, with and without grazing, in a semi-arid shrubland. We hypothesized that 1) animal structures would be clustered around resource-rich shrub patches, and 2) the density and composition of animal structures would differ between undisturbed (ungrazed and unploughed) and disturbed (ploughed and/or grazed) plots. Overall, we found more animal disturbance within shrub patches than in the interspaces irrespective of grazing and/or ploughing treatments, and well-defined increases in density of animal disturbances with increasing shrub cover. Our study highlights the importance of shrub hummocks as habitat patches for animals, and the potential negative feedbacks processes arising from shrub removal.

Keywords: shrubland, foraging, foraging pit, encroachment, thickening, soil processes, bioturbation.

Introduction

The spatial distribution of resource patches is a strong driver of the distribution of faunal assemblages in arid and semi-arid environments (Steward et al., 2000). In semi-arid environments, resources such as nutrients and water are typically concentrated into patches such as shrubs and their hummocks ('islands of fertility' *sensu* Garner and Steinberger, 1989), and to a lesser extent, areas of coarse woody debris (debris mounds). Litter decomposition is generally greater under shrub canopies due to the greater abundance and diversity of soil invertebrates (Doblas-Miranda et al., 2009), and a number of abiotic and biotic attributes such as infiltration and temperature are mediated by the shrubs. Shrubs also act as nurse plants, increasing the diversity, biomass and stability of understorey populations and may protect palatable plant species from herbivory (Soliveres et al., 2011). Further, soil beneath debris mounds have been shown to contain relatively higher concentrations of carbon and nitrogen than interspace soils due to a combination of enhanced decomposition by termites (Tongway et al., 1989), and deposition of surface sediments and aeolian material (Okin et al., 2006).

Over the past century there have been substantial increases in the density, cover and biomass of shrubs over large areas of semi-arid woodland and grassland. This process, known variously as encroachment or woody thickening, has the capacity to alter habitat structure and connectivity (Eldridge et al., 2011) and potentially influence the diversity and abundance of a range of vertebrate and invertebrate taxa (e.g., Simonetti, 1989). Foraging, for example, within shrublands may be associated with a lower risk of predation than foraging in open areas (Brown et al., 1988).

Shrublands are not always viewed positively by land managers because of the perception that they suppress plant biomass and productivity (Eldridge et al., 2011) and exacerbate livestock management problems. Attempts to remove shrubs using a range of techniques including ploughing and destocking have led to mixed success, often stimulating shrub regrowth and leading to the eventual persistence and dominance by

shrubs (Daryanto and Eldridge, 2010). The effects of shrubs on soil and ecological processes are relatively well-known (e.g., Eldridge et al., 2011). Less well-known, however, are their effects on specific biota, including those that disturb the soil surface.

We used long-term vegetation enclosure to examine the effects of ploughing, with and without grazing, on soil disturbance by a range of shrub-resident soil disturbing biota. Our aim was to assess the extent to which soil-disturbing biota use shrub-encroached woodlands and the extent to which patches with different resources (i.e., resource-poor vs. resource-rich) might influence biotic communities. There are many advantages of using disturbances rather than measuring organisms *per se*. Firstly, disturbances such as foraging pits of vertebrates, or nests and emergence holes of invertebrates, indicate surface usage over a longer time period than would be reflected in a one-off assessment of animal activity because surface structures have relatively long half-lives (Borchard and Eldridge, 2011). Secondly, the magnitude of soil disturbances is indicative of the magnitude of ecosystem processes such as nutrient retention and soil removal, which would be influenced by surface-disturbing biota. A number of studies have shown that sites of animal disturbances have enhanced level of nutrients and greater plant germination (e.g., Eldridge and Mensinga, 2007). We predicted that the density of animal disturbances would be greater under resource-rich shrub patches than the relatively resource-poor interspaces and therefore that increasing shrub cover would be associated with higher density of animal disturbance. We expected that the least disturbed site (unploughed and ungrazed) would support the greatest density of animal disturbances, consistent with studies elsewhere (e.g., Eccard et al., 2000).

Materials and methods

Study site

The study was conducted at two semi-arid woodland sites, Wapweelah, 35 km west of Enngonia (29° 16'S, 145° 26'E) and Bloodwood, 120 km north-west of Bourke (29° 30'S, 144° 45'E) in north-western New South Wales, Australia. Wapweelah falls within the Gumbalie Land System and it is characterised by sandy red earths with surface textures of loams to sandy loams. Bloodwood has calcareous red earths and sandy

earths with sandy topsoils and it falls within Goonery Land System (Walker, 1991). Both sites have similar climates characterised by hot summers (mean maximum 36.4°C) and mild winters (mean minimum 17.9°C). Rainfall averages about 300 mm annually at both sites, with 45% more rain during the summer months. The landscape is level to slightly undulating (< 1% slope) and is comprised of sandplains of Quaternary alluvium and aeolian sediment.

Similar shrub species occurred at both sites, though with slightly different composition. Both sites supported narrow-leaved hopbush (*Dodonaea viscosa*), turpentine (*Eremophila sturtii*), green turkey bush (*Eremophila gilesii*) and budda (*Eremophila mitchellii*). However, Bloodwood was dominated by narrow-leaved hopbush while Wapweelah supported denser stands of turpentine and green turkey bush. Scattered mulga (*Acacia aneura*) trees were also found at both sites. The groundstorey vegetation at Bloodwood and Wapweelah 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 200 m x 400 m block was established and divided into four linear plots 200 m long by 100 m wide. The two central plots were enclosed in a 6 m high, herbivore-proof fence, leaving the remaining two unfenced plots grazed. The grazed plots were grazed by camels, sheep, goats, cattle and kangaroos. One of the two central plots and one of the grazed plots was ploughed while the other two plots were unploughed. The ploughing treatment consisted of a single pass with a 4.2 m wide single-tynd 'Stationmaster' blade plough pulled by a 90 kW crawler tractor and only shrubs were removed during ploughing. This design resulted in two different degrees of ploughing (ploughed vs unploughed) and two levels of grazing (grazed vs ungrazed). This experimental setup was repeated at three replicate blocks which were separated by distances of 1–5 km for each site.

Sampling design

In August 2008, 18 years after ploughing and fencing, we established a 100 m² (50 m x 2 m) transect through the centre of each plot in order to measure the density and size of all animal-created soil disturbances such as foraging pits, nests and emergence holes created by a range of vertebrates and invertebrates. Burrows and emergence holes are constructed by ants, ground-foraging spiders such as Lycosids (Main, 2001), scorpions (Hasiotis and Bourke, 2005), cicadas (Moulds, 1990) and skinks in both the shrub hummocks and interspaces. The above-ground cappings of termite (*Drepanotermes perniger*) mounds may also occur in the interspaces where soils clay content is higher (Noble et al., 1989). We also recorded pits excavated by Gould's sand goanna (*Varanus gouldii*) and the Short-beaked echidna (*Tachyglossus aculeatus*). Disturbances vary greatly in their morphology and would be expected therefore to have differential effects on resource capture and retention. Ground-foraging fossorial spiders (e.g., Lycosids) have permanent burrows (Main, 2001), that may sometimes reach 1 cm in diameter and often with an almost invisible trap door. The nests of many ant species have burrows with variable amounts of soil surrounding the entrance (Eldridge and Pickard, 1994). Scorpion burrows are common in sandy soils (Locket et al., 1993) and characterised by a crescent-shaped entrance, angled between 20° and 30° from the surface. The width and height of the burrow range from 5 to 25 mm and from 2 to 10 mm, respectively, and those dimensions are proportional to the size of the occupying scorpion (Rutin, 1996). Skink burrows are characterised by a single opening with a shallow dipping shaft. However, this shaft generally has one or more escape tunnels that switch back on one another to the surface (Hasiotis and Bourke, 2005). Termite pavements, the above-ground cappings of subterranean termites (*D. perniger*), are typically circular, with either concave or convex surfaces, surrounded by termite carton (i.e., a thin surface layer of decomposing soil mixed with organic matters (Noble et al., 1989). The short-beaked echidna constructs shallow nose pokes, deep pits and extensive tracts of bulldozing (Rismiller, 1999) as they forage for macro-invertebrates. Echidna foraging pits tend to be circular-shaped, about 15–25 cm in diameter, 5–15 cm deep, and are surrounded by poorly-aggregated material in sandy soils, but cloddy and highly aggregated material in loamy soils (Eldridge and Mensinga, 2007). Foraging pits constructed by Gould's sand goanna range from narrow, ellipsoid-shaped pits excavated

at an angle of about 40° to the soil surface to wedge-shaped pits characterized by shallow, v-shaped grooves along either side of the base where the soil had been excavated by the reptiles' strong forelimbs (Eldridge and Kwok, 2008).

We recorded the dimensions (length, width, depth or height) of each disturbance found along the transect, as well as the animal that created it (ant, termite, spider, scorpion, cicada, skink, goanna, echidna) and the microsite within which the disturbance was located (shrub hummock, debris mound, interspace). The same transect was used to measure the cover of shrub hummocks, debris mounds, and interspaces. Shrub hummocks are sites under shrubs and their accreting soils and litter, while debris mounds represent sites where shrubs have died and accumulate on the surface. Interspace areas represent the generally sparsely-vegetated areas between the shrubs and log mounds.

Statistical analyses

We used chi-squared tests to examine whether the density of disturbances varied significantly among microsites, given differences in relative proportion of the different microsites. A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used to examine potential differences in the composition of animal disturbances with a split-plot design. The main plot considered block, ploughing and grazing effects, and the second plot microsite effects (i.e., shrub hummock vs debris mound vs interspace) and their interactions with grazing and ploughing. This combination of block, grazing, ploughing and microsite resulted in a dataset of 36 rows for both sites. The data were converted to a similarity matrix using $\log_{(x+1)}$ transformation and Euclidean distance coefficient within the PERMANOVA package. Regression analysis using various linear and non-linear models was used to examine potential relationships among shrub hummock cover and density of disturbances by different animals. The effects of ploughing and grazing were examined using a mixed-models ANOVA of the same structure as that used in the PERMANOVA analyses. Analyses were conducted separately for both sites.

Results

Effects of microsites

At Bloodwood, there was little difference in disturbance density between resource-accumulating (shrub hummocks, debris mounds, 68.7 ± 10.5 disturbances 100m^{-2} ; mean \pm SE) and resource-shedding (interspaces; 62.0 ± 4.6 disturbances 100m^{-2}) microsites. Accounting for the relative proportion of the various microsites however, there were substantially more disturbances in resource-accumulating areas than would be expected by chance (Table 1), a trend that was more apparent at Wapweelah (Fig. 1). Indeed, shrub hummocks and debris mounds at Wapeelah supported more animal disturbances (94.3 ± 25.5 disturbances 100m^{-2}) than the interspaces (35.4 ± 3.3 disturbances 100m^{-2}). At Wapweelah, shrub hummocks consistently supported more ant nests ($\chi^2 = 397.4$, $P < 0.001$, $\text{df} = 2$) and disturbances by either all invertebrates ($\chi^2 = 693.4$, $P < 0.001$, $\text{df} = 2$) or all vertebrates (goannas, skinks, echidnas; $\chi^2 = 87.7$, $P < 0.001$, $\text{df} = 2$) than debris mounds or interspaces. At Bloodwood, we recorded more ant nests ($\chi^2 = 40.71$, $P < 0.001$, $\text{df} = 2$) and disturbances by all invertebrates ($\chi^2 = 32.82$, $P < 0.001$, $\text{df} = 2$) or vertebrates ($\chi^2 = 81.53$, $P < 0.001$, $\text{df} = 2$) in the shrub hummocks (Table 1). We also detected significant differences in composition of animal disturbances (based on density) among microsites at both Bloodwood (Pseudo $F_{2,16} = 8.20$, P (perm) < 0.001) and Wapweelah (Pseudo $F_{2,16} = 5.26$, P (perm) < 0.001). Pair-wise tests for Wapweelah indicated that the composition of disturbances differed between debris mound and either interspace or shrub hummock, but not interspace and shrub hummock (t (perm) = 0.45).

Effects of shrub hummock density

At Bloodwood, the density of all animal disturbances increased with increasing cover of both shrub hummocks ($F_{1,10} = 9.14$, $P = 0.013$) and debris mounds ($F_{1,10} = 47.78$, $P < 0.001$). In particular, the density of cicada emergence holes ($F_{1,10} = 11.93$, $P = 0.006$) and skink burrows ($F_{1,10} = 12.87$, $P = 0.005$) increased with increasing shrub hummock cover (Fig. 2). Similar correlations were apparent when we used data on the area of disturbances. However, we did not find any significant relationship between animal disturbance and the cover of shrubs at Wapweelah.

Effects of grazing and ploughing

We detected some effects of both grazing and ploughing on the cover of shrub hummocks, but only at Bloodwood where the cover of shrub hummocks on the ploughed plots (17.9%) was half that of the unploughed plots (34.9%; $F_{1,6} = 18.24$, $P = 0.005$). Grazing increased the cover of shrub hummocks by 1.5-times from 20.3% to 32.5% ($F_{1,6} = 9.33$, $P = 0.02$). Despite the effects of ploughing and grazing on hummock cover, neither treatment affected the composition of animal disturbances (grazing: Pseudo $F_{1,6} = 2.73$, $P(\text{perm}) = 0.071$; ploughing Pseudo $F_{1,6} = 0.63$, $P(\text{perm}) = 0.639$).

Discussion

Many studies have described the marked differences in abiotic conditions between resource-rich shrub hummocks and their resource-poor interspaces (e.g., Garner and Steinberger, 1989). Because shrubs modify environmental conditions around their hummocks, they are favoured sites for plant germination and establishment (Soliveres et al., 2011), provide nesting, perching and foraging sites for a range of biota (e.g., the ‘perch effect’; Pausas et al., 2006) and act as refugia against predation. Part of the ‘fertile island’ affect associated with shrubs probably results from the activity of hummock-resident biota.

Shrub hummocks in our study were preferred sites of vertebrate and invertebrate disturbances, and increasing cover of hummocks corresponded with increasing densities of cicada emergence holes, skink burrows, and to a lesser extent, ant nests. The hummocks of arid area shrubs provide habitat not only for arthropods (e.g., Whitehouse et al., 2003) but also their reptilian predators (Whitford, 2002). Reptiles use shrubs and their hummocks as refugia from predation (Castellano and Valone, 2006), and sites for foraging and thermal regulation (Diaz, 1992). Soil-disturbing reptiles such as the desert skink (*Egernia inornata*), broad-banded sand swimmer (*Eremiascincus richardsonii*) and the burrowing skink (*Lerista labialis*) inhabit encroached shrubland in our study area (Ayres et al., 2001). Burrowing skinks, in particular, use compacted crusted sand for burrow sites, as sands are easily excavated (Greenville and Dickman, 2009), and the

typically thin biological crust provides a structurally stable burrow entrance (Zaady and Bouskilla, 2002). The close association between skink burrows and shrub hummocks may also provide access to shrub-resident prey such as arboreal invertebrates in the shrub canopies or subterranean termites, which occur in galleries around the roots (Letnic et al., 2004). Surprisingly, debris mounds were not preferred sites of animal disturbance, even though they are substantially resource-rich since only limited number of animals, such as termites, that are able to utilise lignin-rich woody debris (Tongway et al., 1989).

Although the density of ant nests in our study increased with increasing hummock cover, the results were variable and site-specific. Ant biomass is often greater in ecotonal habitats (Dugas, 2001), so one might expect to record more nest entrances at the margins of the shrub hummocks and interspaces. The marked differences in nest size (range: 0.1 to 8 cm diameter) suggest that many taxa inhabited our study sites. Some species such as *Myrmecocystus*, *Melophorus*, and *Monoporum* prefer open habitats (Hoffmann and Andersen, 2003), and their small nest entrance size (< 2 mm) corresponds with the small volumes of soil deposited on the surface. Other species such as *Aphaenogaster barbigula* prefer more vegetated sites, and deposit relatively large volumes of soil (up to 3.4 t ha⁻¹ yr⁻¹) around their large (~ 20 mm diameter) nests (Eldridge and Pickard, 1994). We are unable to determine species-level ant effects because we did not record individual species associated with the burrows and nests. We would expect, however, a stronger relationship between hummock cover and ant nest density if we were able to discriminate between different types of ants.

We failed to detect any differences in scorpion burrow density with changing hummock cover. Scorpions generally prefer coarser-textured soils such as those within hummocks because physically crusted soils restrict their ability to burrow (Bradley, 1986). Lockett (1993) showed that most burrows of the scorpion *Urodacus armatus* occurred at the base of the sand dunes in areas occupied by *Senna* and *Eremophila* spp. shrubs. The concentration of scorpion burrows in sandy soils such as those characterised by shrub hummocks (Shorthouse and Marples, 1980) may be a mechanism for avoiding disturbances in frequently trampled areas since these hummocks often form a dense hemispherical or inverted-cone-shape canopy which are avoided by the herbivores.

Burrowing behaviour may, however, be age-related, and while the burrows of young *Paruroctonus mesaensis* scorpions are associated with sites of dense vegetation cover, those of adults show a more random distribution (Polis et al., 1986), and adults may prefer open microsites. Finally, higher densities of the Desert screamer cicada (*Macrotristria hillier*) in shrub hummocks is related to their preference for the roots of *Acacia cambagei* and *Acacia excelsa*, which are important food plants for the nymphal stage (Moulds, 1990).

The preceding section indicates that there were generally more disturbances associated with shrub hummocks. However, contrary to expectation, we detected no significant differences in either the density or composition of animal disturbances between sites that were ploughed and unploughed, or grazed and ungrazed areas. This result should not be interpreted, however, as the absence of an effect on ecosystem processes. Rather, it suggests a consistent microsite effect across all treatments. The high rates of soil mixing and creation of macropores by ants, and their tendency to alter soil particle size through burrowing (Richards, 2009) suggest that they will likely enhance the infiltration of water (James et al., 2008) in the interspaces. Thus the preponderance of ant nests in the interspaces would be expected to influence the redistribution of water, which is generally localised under the shrubs (Segoli et al., 2008). Ants are also central-place foragers, and are likely to forage in the shrub hummocks. Therefore ant nests may provide a mechanism for reversing flows of water, litter and sediment (which is typically towards the hummocks) to the interspaces. The accumulation of finer material around the nests of ants may improve soil nutrients (James et al., 2008), enhance the diversity of soil microfauna (Zaragoza et al., 2007), and be important for accretion of soil for colonisation by annual plants (Eldridge et al., 2009).

We only detected some grazing effects on the cover of shrub hummocks and no ploughing effects almost two decades after ploughing. However, our results indicate that management practices that reduce hummock cover are likely to have marked effects on the density of some soil disturbances. Removal of shrubs therefore might come at a long-term cost associated with loss of habitat for shrub-resident and shrub-foraging taxa. It could also have potentially large, but unknown effects on ecosystem processes as broad as infiltration and nutrient processes.

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Table 1. Results of χ^2 analyses for different microsites at Bloodwood and Wapweelah. Numbers in brackets represent the percentage cover of the three microsites.

Animal group	Shrub hummock	Debris mound	Interspace	χ^2 value	<i>P</i> -value
Bloodwood	(26.4)	(6.8)	(66.8)		
Ants	397	113	714	40.71	<0.001
All invertebrates	123	14	164	32.82	<0.001
All vertebrates	49	20	22	81.53	<0.001
Wapweelah	(20.8)	(7.2)	(72.0)		
Ants	342	12	302	397.36	<0.001
All invertebrates	232	3	35	693.38	<0.001
All vertebrates	40	9	11	87.73	<0.001

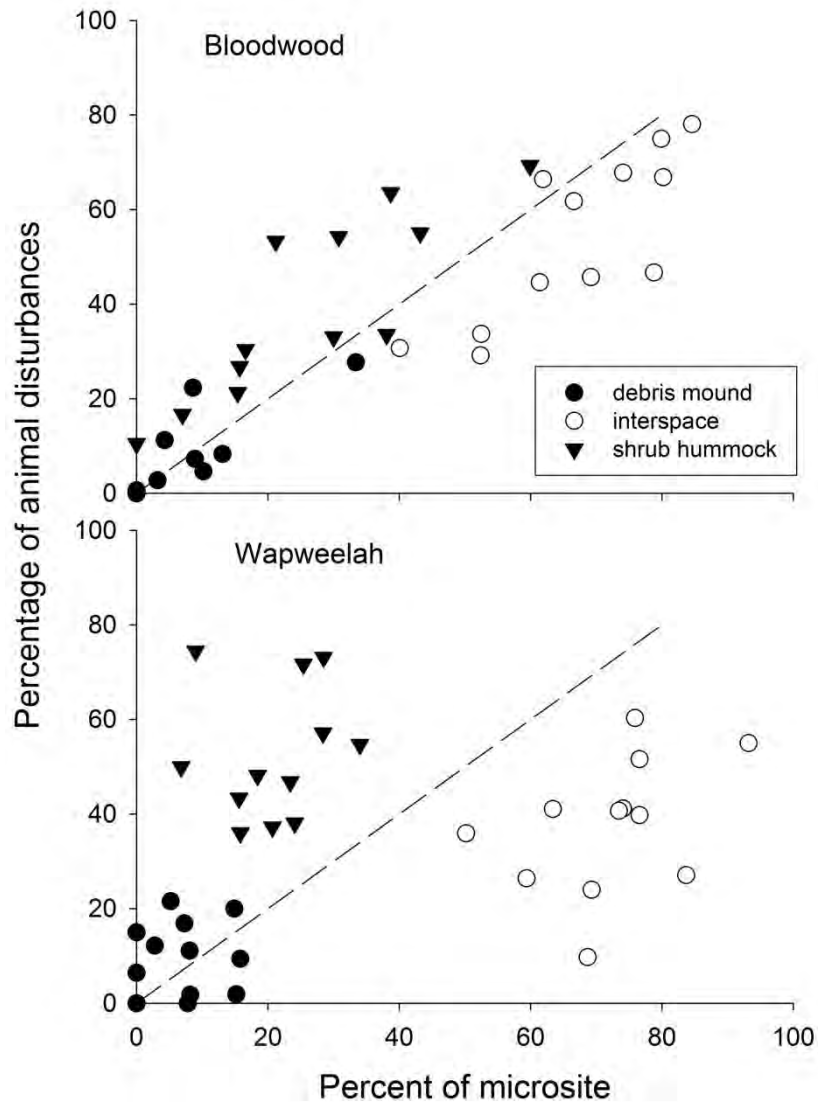


Fig. 1. Relationship between the percentage of animal disturbances found in a given microsite and the percentage of each microsite type available at a site. The broken line represents a 1:1 relationship.

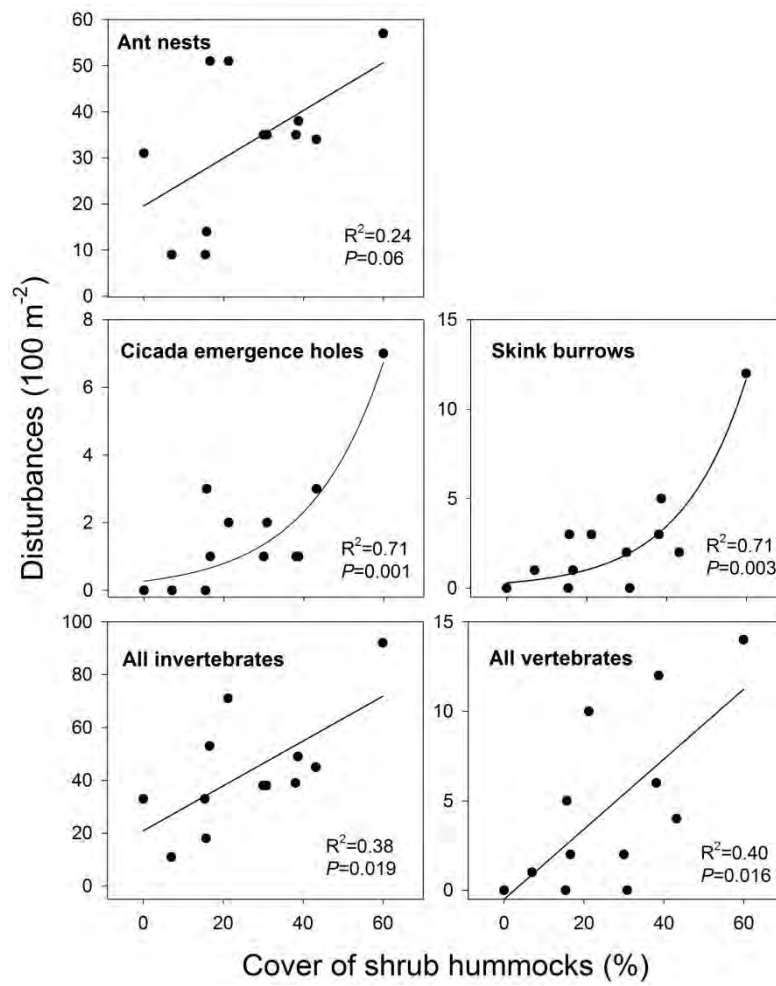


Fig. 2. Relationship between the density of cicada emergence holes, skink burrows and all invertebrates and vertebrates and the cover of shrub hummocks at Bloodwood. Note the different scales of the y-axes.

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

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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.

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 (*but see* Tongway et al., 1989; Tongway and Ludwig, 1996).

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 banded mulga low-open shrubland (log mounds, *sensu* Tongway et al., 1989), they have been poorly studied in encroached woodlands.

We used a long-term exclosure 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).

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, 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 20–30 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 exclosure 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 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 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 (5–10 cm, 15–25 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 $F_{2,22}=3.80$, $P=0.038$ 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 & 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 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 x 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 x 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 x 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 x patch interaction: $F_{2,48}=7.72$, $P=0.002$).

Discussion

Preoccupation with the differences in soil physical and chemical properties between perennial plant 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) because the small cover of resource-accumulating patches is not adequate to subset erosion that continuously happen in the interspace.

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., Schlesinger et al., 1996; Bolling and Walker, 2002). 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 habitats (canopy areas) 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 not only due to greater levels of organic matter (Throop and Archer, 2008) but also concentrated macropores produced by animals (e.g. ants, termites; Tongway et al., 1989), 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., *Eremophila*; 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.

Conclusion

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.

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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 hummocks		Debris mounds		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

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

Component	d.f.	F statistic	P – 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.Old	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.Old	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		

Table 3. Differences in soil physical and chemical properties between different ages and average 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.

Chemical and physical soil properties	Landscape element												Trend among landscape elements
	Shrub hummock				Debris mound				Interspace				
	Mature		Young		Mature		Young		Undisturbed		Recovering		
<i>Bloodwood</i>	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
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
<i>Wapweelah</i>													
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

Table 4. Total C and N pools (g m^{-2}) at Bloodwood and Wapweelah up to a depth of 0.3 m

Site	Attribute	Mature shrub		Young shrub		Mature debris		Young debris		Undisturbed		Recovering	
		hummock		hummock		mound		mound		interspace		interspace	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Total carbon	Bloodwood	2003.17	140.42	2160.07	46.18	1948.98	133.05	2177.05	79.96	1751.68	144.44	2028.49	74.80
	Wapweelah	2840.95	445.62	2199.88	233.71	2930.61	126.38	2886.59	213.16	2180.24	116.97	2229.51	545.90
Total nitrogen	Bloodwood	227.99	11.10	250.56	18.15	262.44	16.75	251.62	12.67	238.15	11.67	252.27	9.66
	Wapweelah	277.73	25.00	201.95	11.95	237.04	17.94	228.40	19.30	206.67	6.92	225.63	39.03

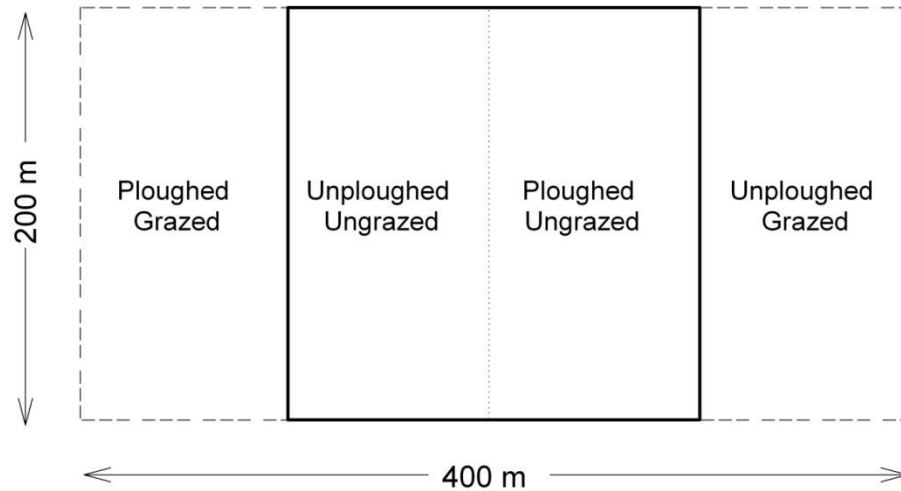


Fig. 1. Layout of the treatments for both sites. The solid line represents a vertebrate-free enclosure and the broken lines outside indicate the extent of the grazed plots.

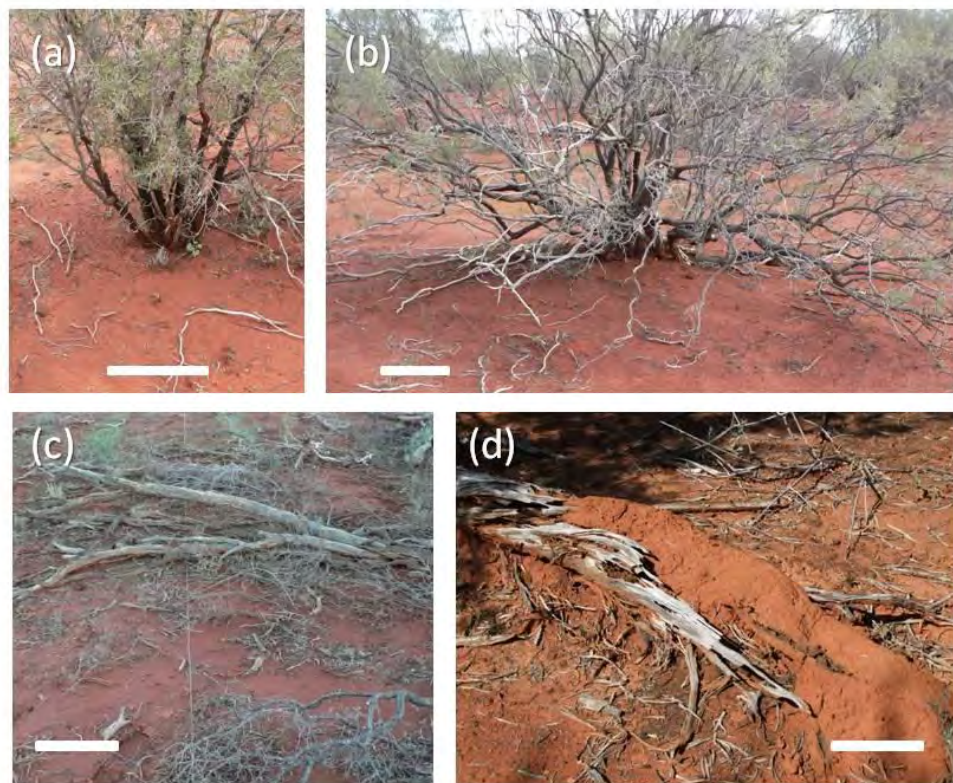


Fig. 2. Images of the shrub hummock and debris mound microsites showing (a) young hummock with *Eremophila sturtii*, (b) mature hummock with *Eremophila sturtii*, (c) young debris mound soon after ploughing and (d) mature debris mound with clear evidence of decomposition by termites. Bars are 30 cm across.

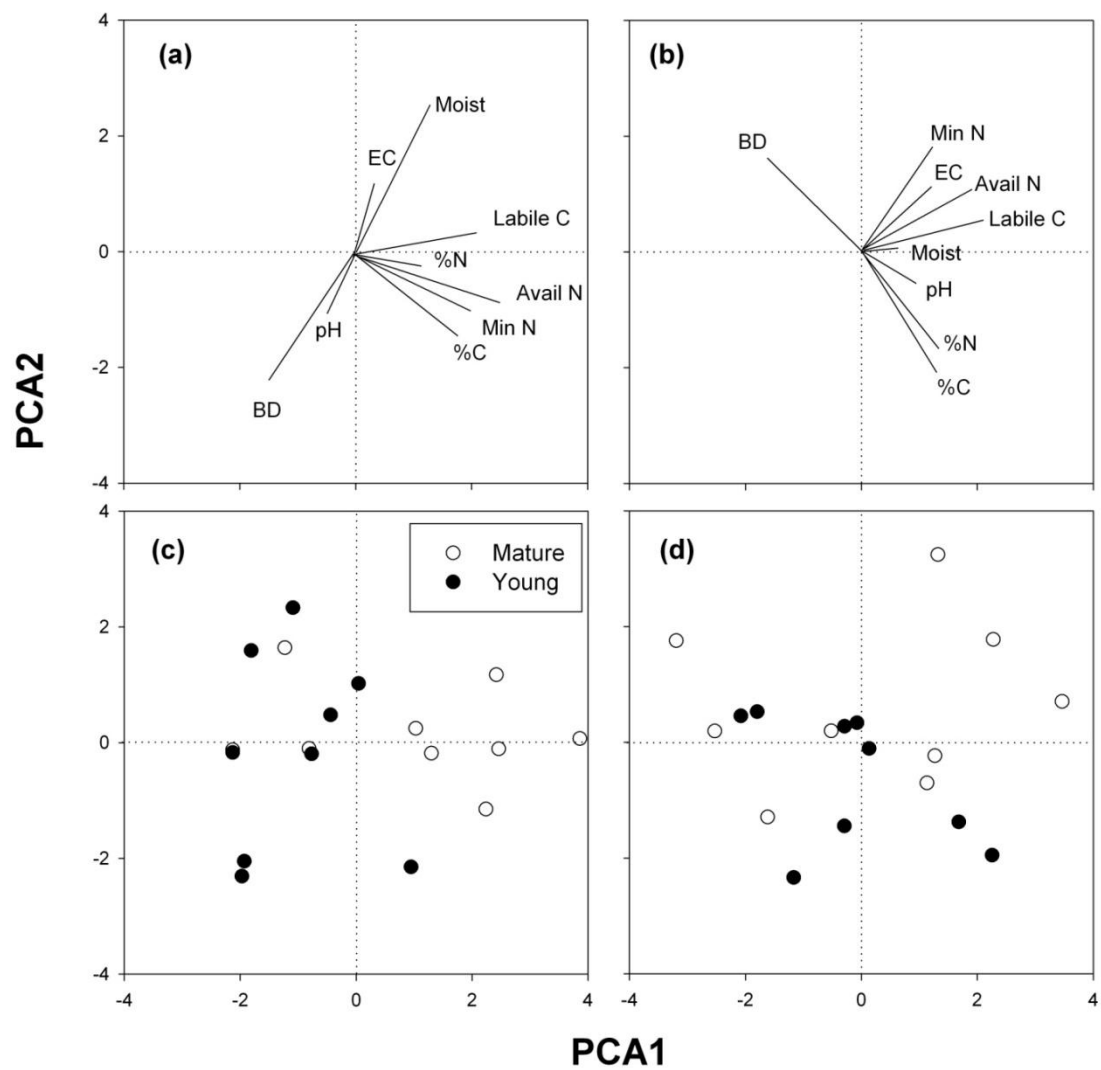


Fig. 3. Principal Component Analysis biplot displaying the first two component axes for sites at Wapweelah (a, c) and Bloodwood (b, d). Interrelationships among soil variables are presented in the top graphics. Sites are coded for age using young shrub hummocks, young mounds and recovering interspaces (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.

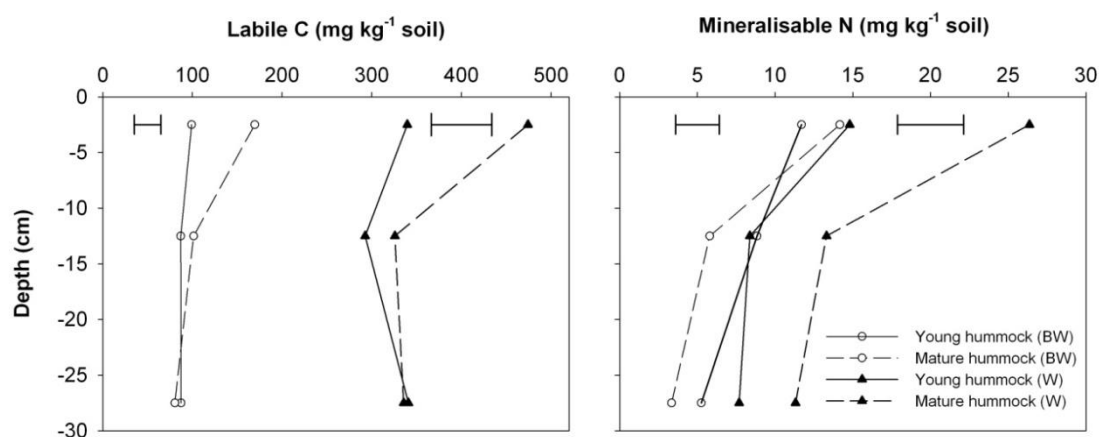


Fig. 4. Depth profiles for labile C and mineralisable N for young and mature hummocks at Bloodwood (BW) and Wapweelah (W). The bars represent the depth by age (young vs mature) LSDs (Least Significant Differences) at $P < 0.05$ for Bloodwood (LHS) and Wapweelah (RHS).

Ploughing and grazing alter the spatial patterning of surface soils in a shrub-encroached woodland

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Abstract

In this study we examined the effects of two land management practices, grazing and ploughing, on the spatial distribution of surface soil resources. At the unploughed–ungrazed site, the connectivity (autocorrelation range) of shrub cover was about 3.9 m and there was a well-defined pattern in soil labile carbon (C) that was related to the distribution of the cover of both shrubs and litter. We also observed a strong pattern of biological crust cover and an autocorrelation range of 2.5 m, similar to that of net nitrogen (N) mineralisation capacity and inorganic N. At the unploughed–grazed site, the autocorrelation range of both shrub and crust cover was reduced to 1.9 m and 1.8 m, respectively, although the range of litter cover increased to 4.4 m. Under a treatment of

grazing without ploughing, the autocorrelation range of soil labile C was less related to litter cover. While ploughing slightly increased the autocorrelation range of both shrub and litter cover at sites that were grazed, it obliterated any spatial pattern in biological soil crusts. We attribute changes in the spatial patterns of soil N under grazing to inputs of animal dung rather than soil crust cover. Our results indicate that grazing alone, or in combination with ploughing, leads to reduced connectivity of shrub and crust cover, reduction in crust patterning, and marked effects on shrub–litter–nutrient spatial relationships. The results reinforce the notion that management of shrublands by grazing and ploughing is likely to have marked effects on the distribution of surface soils.

Keywords: geostatistics, shrubland, encroachment, grazing, krigging, ploughing, semivariogram, spatial distribution

Introduction

A high degree of spatial patterning in vegetation and soil resources is a common feature of water-limited systems (e.g., Borgogno et al., 2009; Wang et al., 2009a). Such patterns can be induced by abiotic factors such as topography, fire, rainfall, wind and water erosion (e.g., Li et al., 2009; Ravi et al., 2009) or by biotic influences due to vegetation (Kefi et al., 2007), particularly the plant canopy (Wang et al., 2009a,b). Plants are strong biotic drivers of the distribution of soil properties, and their effects vary at spatial scales ranging from that of single plants (Jackson and Caldwell, 1993) to entire communities (Gross et al., 1995; Wang et al., 2007a). Individual plants modify their surrounding soils by accumulating nutrients, sediments and essential resources such as water, seed and organic matter around their canopies. Much of these materials are derived from biotic and abiotic processes occurring in the interspaces; the unvegetated areas between plants. The combined effect of these processes is to reinforce the ‘fertile island’ phenomenon around individual plants (e.g., Schlesinger et al., 1996; Wang et al., 2009c). Other biotic factor such as animal activity (i.e., grazing) could also directly, or indirectly, affect the distribution of soil properties. For example, trampling by herbivores alters soil bulk density and infiltration patterns (Stavi et al., 2008). Similarly, herbivores might indirectly affect the spatial distribution of soil properties

either by: 1) removing vegetation or reducing its spatial distribution, thereby altering the capacity of patches to capture resources (Rietkerk et al., 2000), or 2) changing plant community composition and thus the quality (e.g., the C:N ratio) and quantity of litter (Chapin et al., 2002).

Overgrazing has been shown to lead to fragmentation of plant patches (Bisigato and Bertiller, 1997), through the removal of biomass of some palatable shrubs such as *Acacia aneura* (Tiver and Andrew, 1997). Wind erosion further removes fine soil particles and nutrients associated with the presence of grasses, enhancing the movement of resources from the interspaces to the plant patches (Li et al., 2009). In the semi-arid woodlands, this redistribution of resources changes markedly when areas of open grassland are encroached by shrubs. Increases in the density of woody plants alter the scale at which soil nutrients are distributed, from a fine scale, which corresponds to the average distance between former perennial grass tussocks, to one that matches the average spacing of individual shrub hummocks (Schlesinger et al., 1996). While progressive nutrient accumulation under shrubs is associated with grassland degradation (Augustine and Frank, 2001), grazing could further influence the soil nutrient patterning by changing the distribution of litter inputs to the soil, fragmenting the cover of biological soil crusts (Neff et al., 2005) as well as generating inputs of dung (Afzal and Adams, 1992).

Globally, the area of land affected by encroachment of woody plants has increased dramatically over the past half century (Naito and Cairns, 2011). Perceived problems of encroachment in pastoral enterprises have resulted in an intensification of shrub control techniques, particularly mechanical methods (e.g., Herrick et al., 2006). Grazing by domestic livestock is a typical management practice following mechanical shrub removal as managers seek to recoup some of the costs of such treatments. Previous studies in the semi-arid woodlands in eastern Australia have shown that the long-term effects of a single root ploughing treatment tend to increase shrub cover and density without follow up treatment (Daryanto and Eldridge, 2010), potentially increasing the connectedness of shrub canopies and therefore the connectivity of shrub-mediated resources. Although post-ploughing shrubs and their hummocks tend to be smaller than the mature plants and hummocks that they replace, they still act as nutrient-

accumulating patches (Daryanto et al., 2012), suggesting that ploughing might also increase connectivity between soil nutrients. An increase in the connectedness of woody plants (trees and shrubs) would also be mirrored in increases in the continuity of shade, with positive feedback effects on stock movement, potentially altering the distribution of dung. Given that woody plants are often highly preferred areas for animal camping (e.g., Eldridge and Rath, 2002; Milton and Dean, 2001), an increased distribution of both woody patches and dung would likely increase the heterogeneity in soil N (Afzal and Adams, 1992). However, ploughing is known to reduce biological soil crust cover and recovery is slow, even two decades after ploughing (Daryanto and Eldridge, 2010). Destruction of biological crusts increases the risk of erosion because it creates areas of bare soil and destabilises soil aggregates, resulting in the reduction of nutrient accumulation and the size of fertile islands. Because of increased woody cover connectivity and reduced soil crust cover after ploughing, it could be expected, therefore, that the spatial distribution of resources at the ploughed site would be complex, depending on the interactions of multiple factors such as grazing, changes in shrub cover and biological crust cover.

While there have been numerous studies of the effects of grazing on the spatial distribution of vegetation, there are fewer studies of soil- and soil surface-related effects, particularly in response to the physical removal of woody plants by ploughing. To fill this knowledge gap, we aimed to understand how both grazing and ploughing affected the spatial distribution of soil and surface features. In this study, we explore the effects of two land management practices, shrub removal by ploughing, and grazing by domestic herbivores, on the spatial distribution of soil nutrients and the underlying mechanisms forming such spatial patterns in an arid shrubland. First we compared differences in the spatial organisation of soil nutrients between a grazed and ungrazed site, which both had an intact shrub layer (grazing effect). Our second comparison examined potential ploughing effects at two sites, both of which have been grazed for more than 150 years (ploughing effect). Specifically, we expected that grazing would reduce the connectivity of shrub patches, reduce the cover of biological soil crusts, but increase the range of litter, compared with the ungrazed site. This would be expected to occur due to livestock-induced trampling and the effect that grazing animals have on the dispersal of surface litter. As the cover of litter and biological crusts could affect both

soil surface carbon (C) and nitrogen (N) pools, we expected that the spatial pattern (i.e., autocorrelation range) of litter and biological crust cover would change with grazing, and be more closely aligned with the autocorrelation range of C and N, respectively. The increasing density of shrubs at the ploughed sites compared with the unploughed site would increase the connectivity i.e. the autocorrelation range, of shrub and litter cover and thus the connectivity of soil C. Similarly we expected that the autocorrelation range of biological crust cover and thus N would decline with ploughing due to the poor recovery of crusts after ploughing.

Methods

The study area

The study was conducted at 'Wapweelah', an extensive grazing property about 35 km west of Engonia near Bourke in north-western New South Wales, Australia (29° 16'S, 145° 26'E). The site falls within Gumbalie Land System (Walker, 1991), which is dominated by mulga (*A. aneura*) woodlands. The landscape is characterised by sandplains with low west–east trending sandy rises and dunes of Quaternary aeolian alluvium. Minor to moderate windsheeting and watersheetings are common. The sandplain unit is mostly level, with few undulations and the slopes are less than 1%. The soils at Wapweelah are classified as red sodosols with strong texture contrast between the non-strongly acidic A horizons and sodic B horizons. These soils support a wide array of native vegetation communities, including *Acacia* and *Casuarina* shrublands in Queensland and New South Wales (Isbell et al., 1997; Isbell, 2002; NSW Department of Primary Industry, 1998). Mean annual rainfall is about 312 mm, and about 45% more rain falls during summer than winter (Robson, 1995).

The sandplain unit of Gumbalie landsystem is characterised by dense shrubs dominated by turpentine (*Eremophila sturtii*), narrow-leaf hopbush (*Dodonaea viscosa* var. *angutissima*), green turkey bush (*E. gilesii*), budda (*E. mitchellii*) and wild orange (*Capparis mitchellii*). There are few scattered trees of mulga, ironwood (*A. excelsa*), bimbale box (*Eucalyptus populnea*), belah (*Casuarina cristata*), rosewood (*Alectryon oleifolius*), leopardwood (*Flindersia maculosa*), supplejack (*Ventilago viminalis*), wilga (*Geijera parviflora*), gidgee (*A. cambagei*) and brigalow (*A. harpophylla*). The

understorey layer is sparse, and at the time of observation consisted of heavily grazed wollybutt (*Eragrostis eriopoda*), mitchell grass (*Thyridolepsis mitchelliana*), mulga oats (*Monochather paradoxa*), speargrass (*Austrostipa scabra*), other grasses and forbs. This land system is typical of areas targeted for blade ploughing (Walker, 1991; Robson, 1995).

Experimental design

In 1990, one area of 200 m x 400 m was established and divided into four linear plots of 100 m wide by 200 m long. Two of the four plots were then enclosed in herbivore-proof fence 6 m tall, and the unfenced-plots were subject to grazing by sheep, goats, cattle, kangaroos, rabbits and camels. One of both the fenced and unfenced plots was then ploughed and left the remaining unploughed, resulting in four combinations of grazing and ploughing: ploughed–grazed, ploughed–ungrazed, unploughed–grazed and unploughed–ungrazed. Ploughing was conducted with a single pass of a 4.2 m wide single-tynd ‘Stationmaster’ blade plough pulled by a 90 kW crawler tractor. Only shrubs were targeted, and examination of fallen shrubs confirmed a satisfactory ploughing effect over most of the treated area (Robson, 1995). Here we report the spatial heterogeneity of soil in three of these plots. We excluded the ploughed-ungrazed plot because it is unlikely to be applied widely by land managers as a management tool.

Within each plot we established one 10 m x 10 m quadrat and sampled the surface on a coarse 2 m grid ($n=36$) as well as a finer grid of points that were spaced at distances of 25 cm apart ($n=72$) randomly across the quadrat ($n=108$ in total) (Fig. 1). At the 108 points we estimated the cover of litter and biological crust using a small circular quadrat. Litter cover was measured as the percentage of the soil surface within the quadrat covered by debris or detached plant materials. Biological crust cover was measured as the percentage of soil covered by highly-specialised organisms comprising cyanobacteria, lichens, and mosses. We also sampled the topsoil at the 108 points using a soil core of 5.7 cm (radius) x 7 cm (depth). The top 7 cm was sampled because surface soil is the location where most of the biological activity occurs (Schwinning and Sala, 2004). It is also the area in which shrubs are likely to have their greatest effect on soil and therefore where we would expect the greatest effects of grazing and ploughing.

Using this procedure we were able to examine the spatial arrangement of soil nutrients and surface cover at spatial scales ranging from 25 cm up to about 14 m (Fig. 1). We also mapped the location and size of all woody plants at each quadrat in order to derive the spatial distribution of these patches under the different treatments. Soil heterogeneity is highly likely to be affected by the presence of individual shrub since shrubs do not form a community resembling the ‘brousse tigre’ vegetation of southern Africa but grow in isolated patches, sometimes forming islands. Many shrubs occupy bare area resulting from the loss of perennial grasses through overgrazing (Daly and Hodgkinson, 1996).

Laboratory analysis

Each soil sample was analysed for labile C, net N mineralisation capacity and inorganic N. Soil samples were air dried at constant temperature and humidity prior to analyses. Soil labile C was determined using the modified permanganate oxidizable C method (Weil et al., 2003), and inorganic N and net N mineralisation capacity determined using the Salicylate / Dichoroisocyanurate method and the Flow Injection Analysis was conducted using Quikchem 8500 at 660 nm (Gianello and Bremner, 1986).

Geostatistical calculations

Geostatistical analysis was used to estimate the spatial pattern and scale of the examined soil variables (Rossi et al., 1993). Semivariograms were used to explain the semivariance (γ) found in comparison among samples taken at increasing distance from one another (h). The semivariance γ at each h is defined as:

$$\gamma(h) = \sum_{i=1}^{N(h)} [z(i) - z(i+h)]^2 / 2N(h), \quad (1)$$

where $N(h)$ is the number of sample pairs separated by the lag distance h , $z(i)$ is a value measured at location i and $z(i+h)$ is a value measured at location $i+h$.

For randomly distributed data or a pure nugget model, little change in variance is encountered with increasing distance, i.e., the total sample variance is found at all scales of sampling and the semivariogram is essentially flat. For patterned data, the semivariogram first rises from a comparison of neighboring samples that are similar and autocorrelated and then reaches an asymptote, namely the *sill* (C_0+C), suggesting the distance beyond which samples are independent. Nugget variance (C_0) is the variance that occurs at a scale finer than field sampling, and a higher value indicates that more variance occurs over short distances. If a large-scale trend in the distribution of soil properties is found, however, there is no local pattern within the sampling scale, and therefore the semivariogram is linear (Schlesinger et al., 1996).

Parameters derived from the model were used to quantify three key aspects of patchiness in a variable distribution: (i) the magnitude of spatial dependence (i.e., the degree to which patches are differentiated from the surrounding area by their distinct, within-patch homogeneity), (ii) the mean diameter of those patches, and to a lesser extent, (iii) the arrangement of patches across the plot (Augustine and Frank, 2001). The magnitude of spatial structure was obtained using the index of $C/(C_0+C)$. A greater proportion of the total sample is spatially structured if the index approaches 1. The mean diameter of patches and the arrangement of patches across the plot are determined by the distance separating sampling points at which semivariance reaches an asymptote or the autocorrelation range (A_0).

Data analysis

For each plot, descriptive statistics (i.e., mean, median, standard deviation and coefficient of variation) was performed to calculate the overall variability for each observed variable (i.e., litter and crust cover, labile C, inorganic N, and net N mineralisation capacity). Correlation matrix for those variables was also calculated using the modified *t*-test (PASSAGE software; <http://www.passagesoftware.net>), which corrects the degrees of freedom based on the amount of auto-correlation in the data (Wang et al., 2007b). Point biserial correlation was also used to examine potential relationships between shrub cover (i.e. under and at the edge of the canopy vs the open) and those other variables.

In the present study, semivariograms were modeled using GS⁺ software version 9 (Robertson, 2008). There are several commonly used semivariogram models. In most cases however, semivariograms fitted well with spherical models, which has been proven useful in the interpretation of two-dimensional spatial data (e.g., Wang et al., 2007b). We used the spherical model to compare among the observed variables under different treatments. This model was chosen because of its suitable fit with the distribution of those variables based on three criteria: high r^2 , minimal extrapolation of semivariance at spatial scale <25 cm, and fitted model shape (e.g., Wang et al., 2007b). In other cases, where no spatial dependence was detected, a pure nugget model was fitted.

We compared isotropic and corresponding anisotropic semivariograms at 0°, 45°, 90°, and 135° and did not find any significant directional pattern. Therefore, isotropic variograms were used in all analyses. We also ensured that all data had a normal distribution, which is a prerequisite in hypothesis testing using geostatistic theory, by conducting the normal-score transformation prior to analysis (Rossi et al., 1993). To visualize and compare the effect of ploughing on crust distribution, we created inverse distance weighting (IDW) maps at the unploughed–grazed and ploughed–grazed plots. Inverse distance weighting was chosen over krigged maps for both sites because the crust distribution at the ploughed–grazed site was random, and semivariograms cannot therefore be used. Maps were produced with a quadrat size of 10 x 10 m and the data that were transformed prior to semivariogram calculations were back-transformed prior to mapping (Wang et al., 2007b).

Results

In general, we observed higher variability in both litter and biological soil crust cover than labile C, particularly at the ploughed–grazed site, as indicated by the higher standard deviation (SD) and coefficient of variance (CV) for the first two parameters. We also found that inorganic N was more variable than the net N mineralisation capacity at all sites (Table 1). Shrub cover was positively correlated with litter cover, labile C and net N mineralisation capacity, but negatively correlated with soil crust cover at all sites (Table 2). The strongest association between shrub cover and other soil

parameters was found at the ungrazed site, and it became weaker with the presence of grazing and ploughing. For example, we found significant correlation between shrub cover and inorganic N only at the ungrazed site (Table 2). We did not find, however, any significant correlation among the other observed parameters, except a positive correlation between net N mineralisation capacity and inorganic N, at the unploughed–grazed site (Table 3).

Effects of grazing

Consistent with our hypothesis, we found that the connectivity between shrub patches declined with grazing, which was indicated by the shorter autocorrelation range for shrub cover at the grazed (1.9 m; Fig. 2b) than the ungrazed (3.9 m) site (Fig. 2a). These autocorrelations, however, did not correspond to those of litter cover at both grazed and ungrazed sites. The grazed site experienced an increase in the autocorrelation distance of litter cover (4.4 m; Fig. 2d), indicating a spreading of litter, in contrast to the ungrazed site, which was characterised by accumulation of litter under the shrub canopies (autocorrelation range = 2.4 m; Fig. 2c). The autocorrelation range of shrub cover was closer to that of soil labile C (1.4 m) than that of litter cover at the grazed site (Fig. 2f). The autocorrelation range of soil labile C at the ungrazed site (Fig. 2e), however, was closer to that of litter cover than shrub cover.

Grazing also reduced the autocorrelation range of, and therefore the connectivity between, patches of biological crusts, with values of only 1.8 m at the grazed site compared with 2.5 m at the ungrazed site (Figs. 3b & 3a). However, this was not reflected in any decrease in the autocorrelation range of either inorganic N or net N mineralisation capacity at the grazed site (Figs. 3d & 3f). On the contrary, the autocorrelation range of crust cover at the ungrazed site (2.5 m) was very close to that of both net N mineralisation capacity (2.6 m; Fig. 3c) and inorganic N (2.5 m; Fig. 3e).

Effects of ploughing under the scenario of continuous livestock grazing

We found, in general, increases in the autocorrelation range of shrub cover, litter cover and soil labile C with ploughing (Fig. 4). Ploughing resulted in a slight increase in the

autocorrelation range of shrub cover from 1.9 m at the unploughed to 2.2 m at the ploughed site (Figs. 4a & 4b). This increase was mirrored by some increases in the autocorrelation range of litter cover (5.0 m; Fig. 4d) and labile C (6.9 m; Fig. 4f) at the ploughed site. In contrast, at the unploughed site, the autocorrelation range of labile C (1.4 m) was closer to that of shrub cover (1.9 m) than that of litter cover (4.4 m; Figs. 4a, 4c & 4e).

Our observations also indicated that ploughing was associated with a decrease in the $C/(C+C_0)$ ratio for some observed parameters (Figs. 4d & 4f). For example, the $C/(C+C_0)$ ratios of litter cover (0.56) and labile C (0.22) at the ploughed site were lower than the corresponding values at the unploughed sites (litter cover = 0.77; labile C = 0.99). These results indicated that ploughing weakened the spatial structure of litter cover and labile C.

Consistent with our hypothesis, ploughing was also associated with the destruction of spatial patterns in crust cover, indicated by the nugget model of crust cover observed at the ploughed site (Fig. 5b). Our inverse distance map also indicated that islands of high biological soil crust cover were observed at the unploughed site, but not at the ploughed site (Fig. 6). In contrast, we detected stronger spatial structures of both net N mineralisation capacity and inorganic N at the ploughed (Figs. 5d & 5f) than the unploughed site (Figs. 5c & 5e). Neither of these semivariograms had a form resembling that of crust nor litter cover. The autocorrelation range of both inorganic N and net N mineralisation capacity decreased with ploughing from 6.8 to 0.6 m for inorganic N and 12.4 to 1.1 m for net N mineralisation capacity.

Discussion

Soil resource heterogeneity is a common feature of water-limited systems (e.g., Borgogno et al., 2009; Wang et al., 2009a), and in our study, such heterogeneity is likely to be affected more by biotic factors (e.g., individual plant and soil crust typology) than abiotic factors. Although abiotic factors such as topography and rock fragment cover may also play a significant role in modifying the surrounding soils, we consider them less important, as the soil at our study site is highly weathered and the slope was negligible (< 1%).

Shrub effects

Consistent with the shrub concentration effect, we found that shrub cover was highly correlated with litter cover, soil labile C, net N mineralisation capacity and inorganic N, particularly at the ungrazed site (Table 2). In addition, the autocorrelation range of those soil properties, as well as litter cover, did not exceed that of shrub cover, but only at the ungrazed site (Figs. 2a, 2c, 2e, 3c & 3e). Increases in surface soil nutrients around the canopies of woody plants have been widely reported in the semi-arid literature (e.g., Wang et al., 2009a). Water, sediment and airborne nutrients tend to accumulate under shrub canopies through processes of litter fall, wind and water erosion. Canopy areas tend to experience lower surface temperatures and evapotranspiration, increased organic matter incorporation, nitrification, ammonification, and reduced erosion than the unvegetated interspaces (Schlesinger et al., 1996). Shrubs are also known to act as ion pumps, and shrub litter has been shown to be a source of soil nutrients (Facelli and Pickett, 1991). The cellular products of comminuted plant litter, particularly carbohydrates, amino acids and sugars, peptides and lipids, are a readily available source of labile C to the soil (Loginow et al., 1987). Shrub concentration effects have been observed for soil C (Wang et al., 2009a), soil N (Wang et al., 2007b) and soil mineral nutrients (Schlesinger et al., 1996; Wang et al., 2009b).

A significant positive association between inorganic N and shrub cover was also detected, but only at the ungrazed site. We attribute this to the presence of palatable, N-fixing shrubs such as *A. aneura* mostly at the ungrazed sites (Daryanto and Eldridge, 2010). Shrub concentration effects, combined with the absence of stock movement under exclosure, would likely result in greater litter accumulation under the shrubs, moderating soil temperature, promoting decomposition, and increasing surface stability against rainfall (Geddes and Dunkerley, 1999). As the mechanism underlying the shrub effects on soil nutrients is likely mediated through plant litter cycling beneath the canopy, any nutrient concentration effects will likely diminish with increasing disturbance. Thus in our study, both grazing and ploughing weakened the association between shrub cover and litter cover, and therefore soil C and soil N (Table 2).

Consistent with earlier observations, we found that grazing reduced shrub patch size (*sensu* van de Koppel et al., 2002), which is apparent from the lower values for the shrub autocorrelation range under grazing (Fig. 2b) than inside enclosure (Fig. 2a). At the grazed site, we found a stronger effect of shrubs than litter in explaining the distribution of soil C (Fig. 2), due most likely to dispersion by livestock and movement of litter towards the interspace by wind or water erosion (Li et al., 2008). Our results show a strong relationship between shrub cover and labile C (Table 2) and an increase in the autocorrelation range of litter cover at the grazed compared with the ungrazed site (Figs. 2c & 2d). The ecosystem effect of litter scattering and redistribution would be to reduce the depth of litter cover and diminish its capacity to absorb energy of gravity drops from shrub foliage (Geddes and Dunkerley, 1999) or its ability to function as a resource-attenuating litter dam (Eddy et al., 1999; Lechmere-Oertel et al., 2005) and therefore restrict infiltration rates (Dunkerley, 2000). Thus while decomposition might occur more readily in the shrub interspaces due to high UV exposure (Throop and Archer, 2007), decomposed material in the interspaces would be more mobile than the material under the shrubs, reinforcing the resource concentration under shrubs.

Both grazing and ploughing had marked effects on soil crusts. Grazing reduced the connectivity between patches of biological soil crust, though the effect was less than expected, with a decrease in the separation distance from 2.5 to 1.8 m (Figs. 3a & 3b). Ploughing altered crusts from a separation distance of about 1.8 m to a complete destruction of spatial pattern, which is apparent in the inverse distance map (Fig. 6). Indeed the adverse effects of mechanical disturbance by ploughing on soil crusts was still evident at our sites almost two decades after ploughing, even under enclosure (Daryanto and Eldridge, 2010). In functional, undisturbed woodland, biological soil crusts are common components of the interspaces between shrubs where they protect the soil against wind and water erosion and are important drivers of the nutrient economy of semi-arid soils. Reduced biological crust cover is, however, a typical response to increased disturbance in semi-arid environments. Crust destruction would be expected to reduce their capacity to fix nitrogen, as evidenced by the low correlation coefficients between biological soil crust cover and N at grazed sites (Table 3). More

subtle changes in crusts including a reduction in cover or richness by trampling, even in small patches, would be expected to reduce the activity of enzymes in the crust and therefore impair nutrient cycling (Maestre et al., 2011).

Our results imply that inputs of dung from sheep and goats, the main vertebrate grazers at our study site, play an important role in determining the distribution of soil resources, particularly N. Grazing is known to promote fine-scale (< 25 cm) heterogeneity in soil N (Augustine and Frank, 2001) as a result of scattered dung and urine inputs (Afzal and Adams, 1992). The effects of dung and urine appeared to be more pronounced than expected, given the increased autocorrelation range of both inorganic N and net N mineralisation capacity under grazing (Figs. 3d & 3f). Although inputs of N from dung and urine might partially counteract the negative effects of grazing, their distribution would be expected to be highly localized (Bardgett and Wardle, 2003), resulting in limited response of primary productivity to such inputs at the landscape scale. We found a pronounced effect of animal dung (and presumably nitrates in urine) in determining the spatial dependence of both inorganic N and net N mineralisation capacity at the ploughed-grazed site (Figs. 5d & 5f), which would seem to correspond more to potential movement by grazing animals than to the presence or size of patches of shrub or soil crust. Increasing connectivity between shrub patches suggests a suitable environment for livestock sheltering, given the tendency of animals to use woody cover for camping and resting (Eldridge and Rath, 2002; Milton and Dean, 2001).

In contrast to the unploughed site, the autocorrelation range of soil labile C under ploughing was more closely related to litter cover than shrub cover (Fig. 4). Indeed, shrub cover was only weakly correlated with labile C at the ploughed site (Table 2). This trend would be expected given the marked difference in shrub age between ploughed and unploughed plots. Most shrubs at the ploughed site would have been about 17 years old at the time of our study (Daryanto et al., 2012), having germinated about two years after the initial shrub removal program. We found no evidence of differences in shrub canopy area at the ploughed compared with the unploughed plot at either the level of the entire plot ($F_{1,107} = 0.03$, $P = 0.89$) nor at the scale of our 100 m² quadrats (S. Daryanto, unpublished data). However, notwithstanding these results, nutrient concentration tended to be less under younger than older shrubs (Daryanto et

al., 2012) due to a number of mechanisms. Firstly, small shrubs have smaller, more open canopies (Pugnaire et al., 1996; Wezel et al., 2000) that would capture fewer soil particles (Okin et al., 2006). Secondly, less sediment adhering to the foliage reduces the potential pool of sediment for transport by stem-flow (Whitford et al., 1997). In addition, smaller shrubs would not act as strong nutrient pumps and would support lower levels of biological activities than their mature counterparts. We argue therefore that the influence of decomposed litter on soil C would be greater than any shrub accumulation effects due to weaker-functioning shrubs (Daryanto et al., 2012). Greater shrub density at the ploughed site also resulted in fewer differences between shrub canopy and open sites. Indeed, Bolling and Walker (2002) reported a greater spatial autocorrelation range for undisturbed shrublands than post-disturbance recovering shrubs due to changes in soil hydrology such as the formation of erosional gullies.

The combination of fewer nutrient ‘sinks’ from smaller shrubs and reduced nutrient ‘source’ from biological crust cover might be responsible to some persistent soil and nutrient loss (Neff et al., 2005), as well as a decline to essential ecosystem processes, such as nutrient mineralisation (Barger et al., 2006). Given the key roles they play in maintaining ecosystem functions as well as prolonging recovery time, management of grazing should consider the maintenance of shrub and soil crust patches as they may contribute toward the re-establishment of a more highly functional ecosystem.

Conclusions

In this study, grazing and ploughing affect the spatial patterning of surface soils through biologically-mediated processes such as the removal of plant biomass and deposition of dung. Based on both conventional and geostatistical analyses of spatial patterns of soil and vegetation in a typically managed, semi-arid Australian woodland we found that soils with a long history of grazing by domestic livestock has experienced degradation, indicated by the following: (i) reduction in the autocorrelation range of shrub cover, and (ii) reduction in the shrub concentration effects by diminishing the patch size, resulting in a decrease in the spatial range of soil labile C. Similarly, ploughing caused: (i) the disappearance in the spatial pattern of soil biological crusts, but (ii) some increases in the spatial range of litter cover and labile C due to litter scattering by the grazing

animals. Our study emphasizes the importance of vegetation and soil crust cover in maintaining the functioning of arid ecosystem in Australia. Given the indiscriminate nature of ploughing (e.g., reducing overall shrub diversity) and the lack of sustained control, we suggest that ploughing is an inappropriate form of land management in this semi-arid landscape. Management of grazing is therefore crucial in determining the existence of resource-accumulating patches (i.e., shrubs and crusts) and long-term consequences of their loss.

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Table 1. Summary of statistical parameters of litter and biological soil crust cover, labile C, net N mineralisation capacity, and inorganic N at the unploughed–ungrazed, unploughed–grazed and ploughed–grazed sites; $n = 108$ for all parameters; CV = coefficient of variation, SD = standard deviation.

Treatment	Parameter	Mean	Median	SD	CV (%)
Unploughed– ungrazed	Litter cover (%)	40.9	10.0	43.7	106.8
	Labile C (mg kg ⁻¹ soil)	197.8	197.4	81.8	41.4
	Biological crust cover (%)	51.3	65.5	45.3	88.3
	Net N mineralisation capacity (mg kg ⁻¹ soil)	8.8	7.5	5.3	59.6
	Inorganic N (mg kg ⁻¹ soil)	1.9	1.1	1.7	92.3
Unploughed– grazed	Litter cover	50.7	50.0	40.4	79.6
	Labile C	392.4	377.6	105.5	26.9
	Biological crust	23.5	0.0	33.6	142.7
	Net N mineralisation capacity	23.3	19.3	13.9	59.8
	Inorganic N	3.2	1.9	5.1	159.6
Ploughed– grazed	Litter cover	19.1	7.5	27.6	144.6
	Labile C	182.2	178.2	81.7	44.8
	Biological crust	7.1	0.0	19.8	280.0
	Net N mineralisation capacity	10.6	7.8	6.1	58.0
	Inorganic N	3.1	1.4	8.4	267.8

Table 2. Point biserial correlation coefficients between shrub cover and the five continuous parameters such as litter cover, biological crust cover, labile C, net N mineralisation capacity, and inorganic N. [#] $P>0.05$

Attributes	Litter cover	Biological crust cover	Labile C	Net N mineralisation capacity	Inorganic N
Unploughed– ungrazed	0.72	–0.79	0.49	0.59	0.36
Unploughed– grazed	0.27	–0.31	0.37	0.44	0.09 [#]
Ploughed–grazed	0.36	–0.32	0.57	0.57	0.13 [#]

Table 3. Correlations of litter cover, labile C, biological crust cover, net N mineralisation capacity, and inorganic N at the unploughed–ungrazed, unploughed–grazed and ploughed–grazed sites. The correlations were calculated using a modified t–test that corrects the degrees of freedom based on the amount of auto–correlation in the data * $P<0.05$, ** $P<0.01$.

Attributes	Litter cover	Biological crust cover	Labile C	Net N mineralisation capacity
Unploughed– ungrazed				
Biological crust cover	–0.90			
Labile C	0.53	–0.54		
Net N mineralisation capacity	0.62	–0.61	0.50	
Inorganic N	0.49	–0.42	0.24	0.33
Unploughed–grazed				
Biological crust cover	–0.72*			
Labile C	0.47	–0.45		
Net N mineralisation capacity	0.50	–0.44	0.67	
Inorganic N	0.05	–0.19	0.32	0.33**
Ploughed–grazed				
Biological crust cover	–0.17			
Labile C	0.25	–0.05		
Net N mineralisation capacity	0.23	–0.21	0.42	
Inorganic N	–0.04	–0.09	0.08	0.09

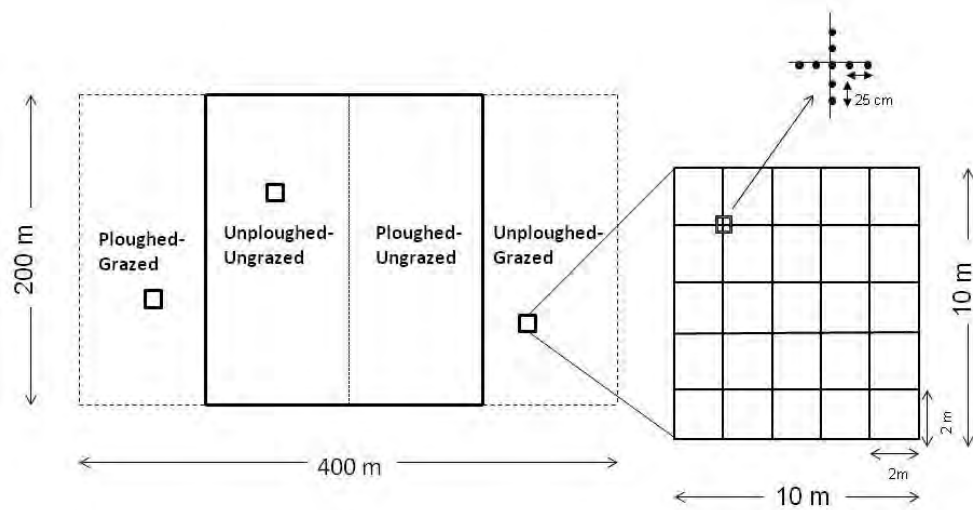


Fig. 1. Sampling design for measuring surface soil condition and soil nutrient heterogeneity. A 10x10 m grid was placed in each plot and samples were taken at the 36 intersections (coarse grid, minimum sampling interval = 2 m). An additional 72 points were located randomly along the grid (minimum sampling interval = 25 cm)

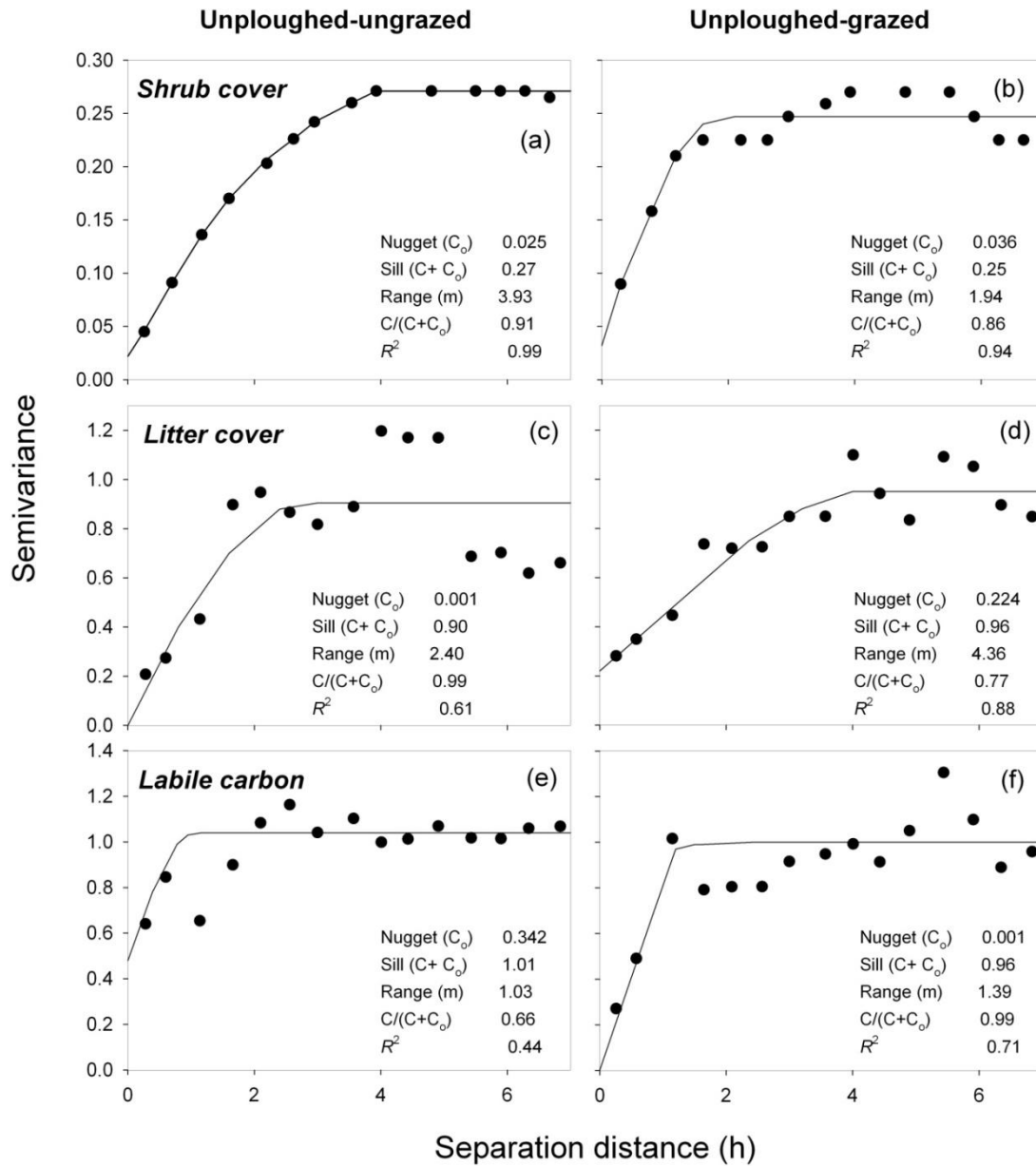


Fig. 2. Semivariograms for shrub cover, litter cover, and labile C at the unploughed–ungrazed (a, c, e) and unploughed–grazed sites (b, d, f). All semivariograms used spherical models.

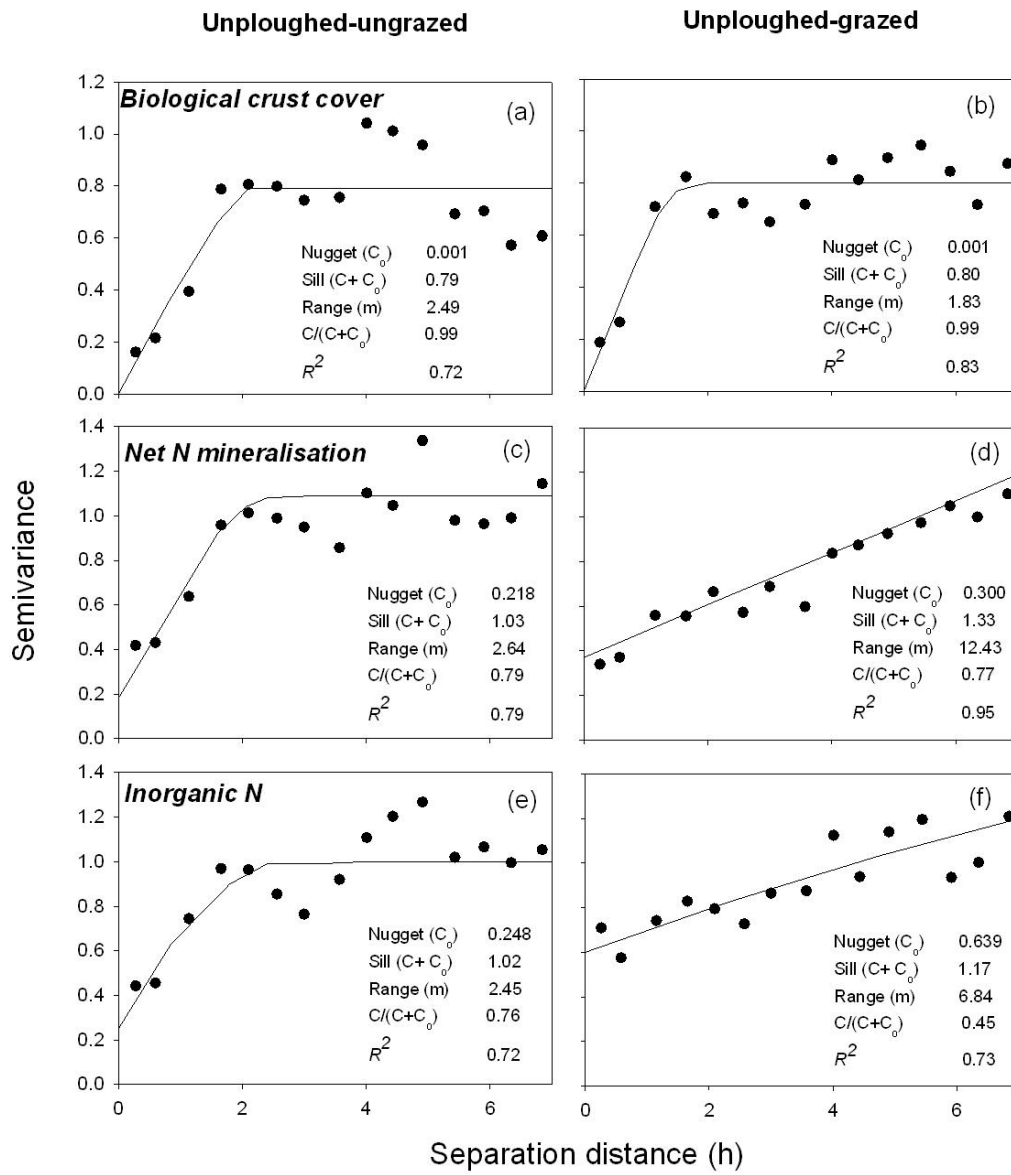


Fig. 3. Semivariograms for biological crust cover, net N mineralisation capacity, and inorganic N at unploughed–ungrazed (a, c, e) and unploughed–grazed sites (b, d, f).

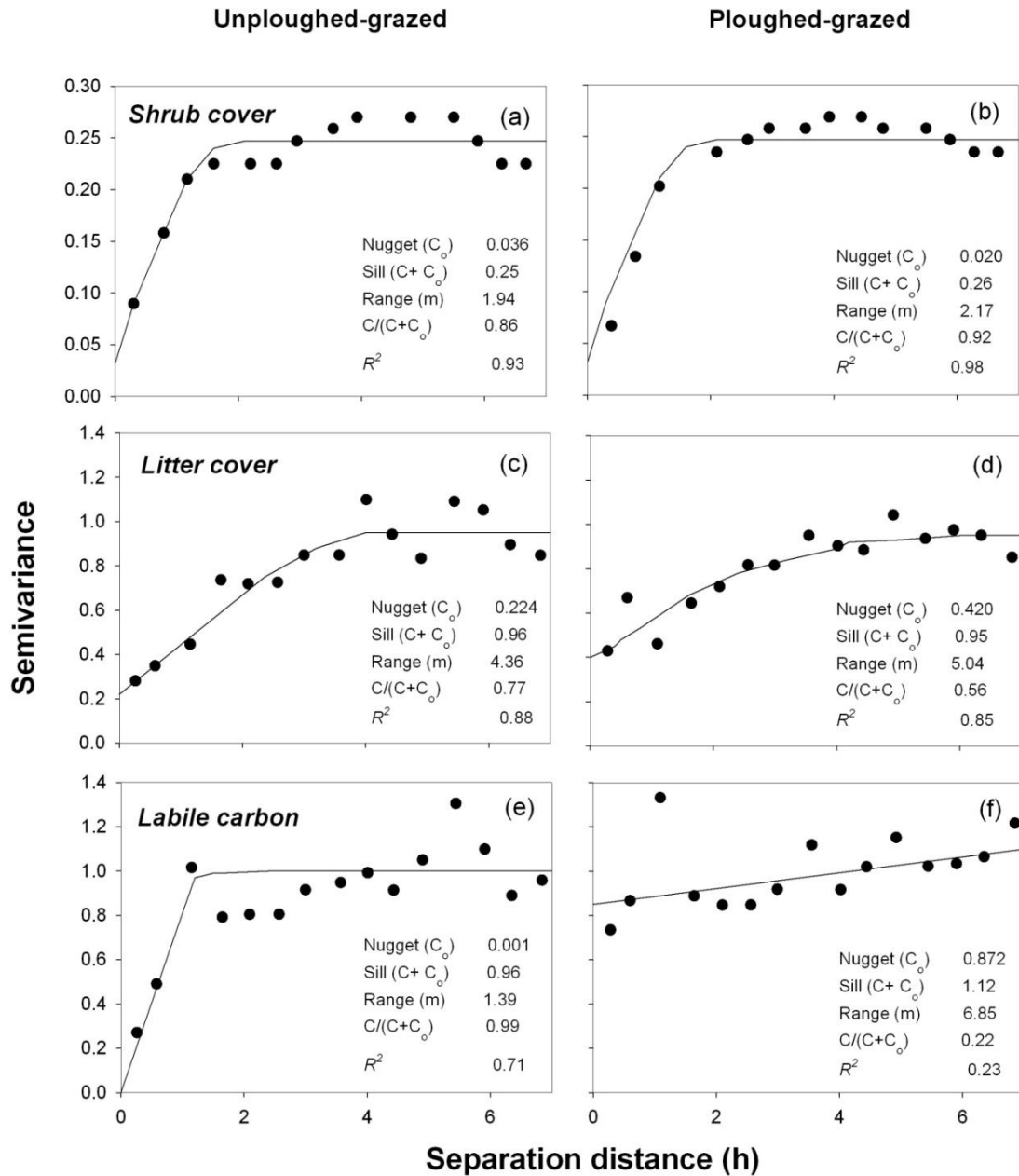


Fig. 4. Semivariograms for shrub cover, litter cover, and labile C at the unploughed-grazed (a, c, e) and the ploughed-grazed sites (b, d, f).

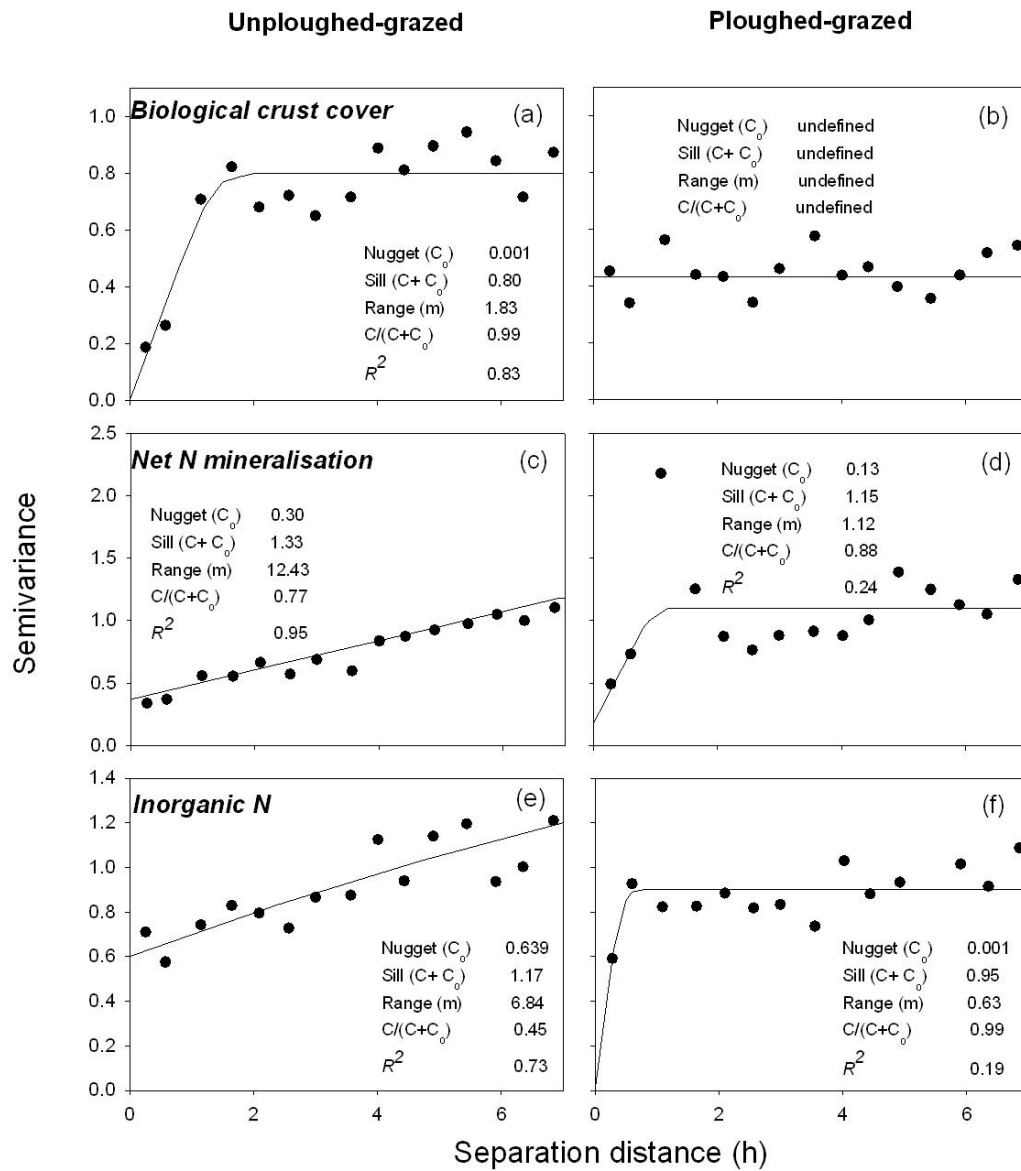


Fig. 5. Semivariograms for biological crust cover, net N mineralisation capacity, and inorganic N at the unploughed-grazed (a, c, e) and ploughed-grazed sites (b, d, f).

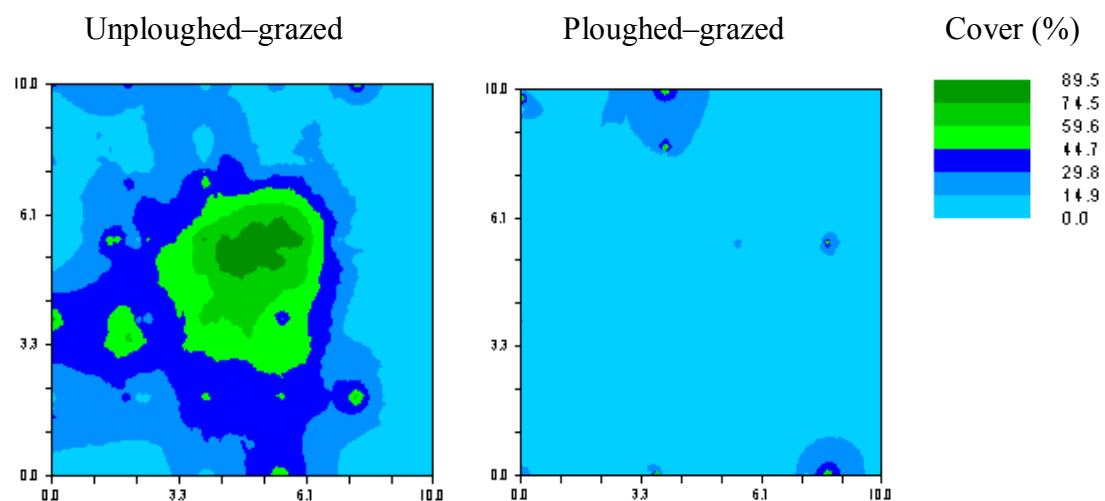


Fig. 6. Interpolated map of biological crust cover using the inverse distance weighting (IDW) method at unploughed-grazed and ploughed-grazed sites. Cover ranges from < 15% (light blue) to 75–90% (dark green).

Infiltration of water varies with disturbance in a shrub-encroached woodland

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Abstract

Woody plant encroachment is known to have substantial effects on a range of ecosystem processes. Research worldwide indicates that the area around shrubs and trees has higher levels of infiltration than the interspaces. Little is known, however, about the hydrological consequences of shrub removal on infiltration, and how this might be influenced by grazing. We examined the spatial patterns of infiltration across three treatments relating to shrub removal and grazing: (i) undisturbed (ungrazed and unploughed), (ii) grazed but unploughed, and (iii) grazed and ploughed. In general we found that disturbance was associated with a greater cover of bare soil but lower infiltrability, our laboratory-based measure of infiltration. At the undisturbed site, bare soil was patchy and localized, with an autocorrelation range or connectivity of 1.4 m.

The autocorrelation range of infiltrability at this site ($A_0 = 3$ m) was larger than would be predicted from the size of the shrub canopy, and this was attributed to the presence of a well-developed understorey layer and biological soil crust community. At both grazed sites, infiltration was confined to the immediate canopy area of the remaining shrubs ($A_0 = 1.2$ m in the unploughed–grazed site). Additionally, there was increasing connectivity of bare soil with disturbance, up to 6.8 m at the ploughed–grazed site. With increasing disturbance, resource-rich shrub patches are likely to become more developed, further reinforcing their growth and persistence at the expense of the bare interspaces. Our results indicate the importance of shrubs for maintaining landscape connectivity, and the long-term unsustainable practice of removal by ploughing, which is likely to promote shrub dominance rather than suppression.

Keywords: grazing, infiltration, encroachment, semi-arid, woodland shrubs, spatial pattern

Introduction

The proliferation of woody plants (encroachment or thickening) has been widely documented across many of the world's drylands (Ravi et al., 2009; Naito and Cairns, 2011). Encroachment has substantial effects on ecosystem properties and functions including soil hydrological properties and water balance (Nie et al., 2012). The commonly accepted view is that encroachment leads to higher levels of evapotranspiration compared with grasslands and open woodlands (Scott et al., 2006) and reduced volumes of runoff (Huxman et al., 2005; Nie et al., 2012). As water is a key determinant of productivity in semi-arid systems (Le Houerou et al., 1988; Wang et al., 2012), dryland managers are particularly interested in the long-term effects of different land management practices, including woody plant removal and grazing, on the spatial distribution of soil water, particularly infiltration, as it is the major pathway for the entry of water into the soil. Control of woody plants, therefore, has the potential to yield higher volumes of runoff and therefore enhance water capture for urban and rural land uses (Saleh et al., 2009).

Woody plants are known to have a strong modifying influence on the physical environment around their canopies through their effects on biotic and abiotic processes (Shachak et al., 2008). The soil around woody plant canopies typically has greater levels of carbon (e.g., Wang et al., 2009), improved physical structure and stability, and greater macroporosity than the surrounding soil matrix (Elkins et al., 1986; Dunkerley, 2000). The infiltration of water is generally greater within patches of woody plants than in the interspaces (e.g., Reid et al., 1999; Bhark and Small, 2003) due to greater litter production and cycling beneath the canopy. Litter moderates evaporative loss of soil moisture and reduces the formation of physical soil crusts by reducing raindrop impact on the surface (Stavi et al., 2009). Enhanced soil moisture and greater litter production beneath woody canopies lead to greater microbial activity and the accumulation of organic matter (Gutiérrez and Jones, 2006).

Apart from their effects on decomposition processes, the cover and distribution of woody plants also have a strong influence on the spatial patterning of soil properties, including infiltration rates, in shrublands and encroached woodlands. Management of these shrublands has the potential, therefore, to alter the spatial distribution of runoff and infiltration and eventually the spatial distribution of soil moisture. For example, removal of woody plants by chaining or cutting can enhance soil moisture (Bates et al., 2000) and may even enhance soil water recharge (e.g., Weltz and Blackburn, 1995). Studies of the effects of woody plant removal in encroached Australian shrublands indicate that physical removal of woody plants and their hummocks by root ploughing leads to a reduction in the number of resource-accumulating patches and an increase in inter-patch distance (Daryanto and Eldridge, 2010). Grazing-induced disturbance is known to fragment soil biological cover that occurs in the interspaces and lead to destabilization of surface soil aggregates (Daryanto and Eldridge, 2010). Grazing-induced trampling has been shown to reduce infiltration rates through surface compaction (Castellano and Valone, 2007), but little is known of the joint effects of grazing and soil disturbance associated with the physical shrub removal, on soil surface condition and infiltration processes.

The aim of the study reported here is to examine the spatial arrangement of soil infiltration in relation to physical shrub removal, with and without grazing-induced

disturbance, based on data from a semi-arid, shrub-encroached woodland in eastern Australia. We hypothesized that grazing and shrub removal by ploughing would alter the spatial distribution of infiltration, cover of bare soil and bulk density, and that with increased disturbance, infiltration would be concentrated more strongly in the area around the shrubs. Specifically, we expected that grazing and/or ploughing would increase the connectivity of patches of bare soil, but create localized patches of more porous soil around shrubs, resulting in reduced connectivity of infiltrability. We also expected that infiltrability would decline with increasing distance from shrub canopies, particularly at disturbed sites, in response to a reduction in cover of litter and biological soil crusts and increases in bare soil cover and bulk density.

Methods

Study site

The study was conducted at Wapweelah, an extensive grazing property near Bourke in north-western New South Wales, Australia (29° 16'S, 145° 26'E) which experienced shrub encroachment. The site falls within Gumbalie Land System (Walker, 1991), which is characterized by sparse perennial grasses but dense native shrubs such as turpentine (*Eremophila sturtii*), narrow-leaf hopbush (*Dodonaea viscosa* var. *angustissima*), green turkey bush (*Eremophila gilesii*), and budda (*Eremophila mitchellii*) with scattered trees of mulga (*Acacia aneura*), ironwood (*Acacia excelsa*), bimbale box (*Eucalyptus populnea*) and wilga (*Geijera parviflora*). The sandplain unit is mostly level, undulations are scant and if any, the slopes are less than 1%. The soils are sandy red earths with sandy loam to loamy texture. Annual rainfall is approximately 312 mm with 45% more rain falls during six warmer months than the cooler months (Robson, 1995).

Experimental design

In 1990, one area (200 m x 400 m) was established and divided into four blocks of 200 wide long by 100 m wide. Two of the four blocks were then enclosed in a 6 m high, herbivore-proof fence while the unfenced blocks were subject to grazing by domestic

stock and other herbivores (e.g., kangaroos, camels, goats, and rabbits). One of both the fenced and unfenced blocks was then ploughed with a single pass of a 4.2 m wide single-tined 'Stationmaster' blade plough pulled by a 90 kW crawler tractor (Robson, 1995), while the remaining blocks were left unploughed. This design resulted in four grazing by ploughing treatments: ploughed and grazed, ploughed and ungrazed, unploughed and grazed, and, unploughed and ungrazed. We did not undertake any measurements in the ploughed–ungrazed treatment as we were interested in potential effects on shrublands more broadly, and the ploughed–ungrazed strategy is, to our knowledge, unlikely to be adopted by land managers. The treatments represented a gradient in disturbance from most disturbed (ploughed–grazed) to least disturbed (unploughed–ungrazed).

Within each of the three treatments, we established a 10 m x 10 m plot and sampled the surface on a coarse 2 m grid ($n=36$) as well as a finer grid of points that were spaced at distances of 25 cm apart ($n=72$) across the plot ($n=108$ in total). For each sampling point, we recorded its distance to the canopy of the nearest shrub or tree, which enable us to determine whether each sampling point was located under the canopy or in the open. We also estimated the surface coverage of bare ground using a small quadrat of 25 grid points at each of those sampling points. Soil, sampled using an intact soil corer of 5.7 cm diameter x 7 cm depth, was collected at each of the 108 points and air dried at constant temperature and humidity before the bulk density and infiltration measurements were made. We used as our measure of infiltration a laboratory-derived index of infiltrability which is based on a syringe method (Mills et al., 2006).

Calculation and data analysis

For each plot, descriptive statistics (i.e., mean, median, standard deviation, and coefficient of variance) were performed to indicate the overall variability for each observed variables (i.e., bare ground, bulk density and infiltrability). Kruskal–Wallis and *post-hoc* tests were performed to indicate if significant difference occurred among the treatments. A correlation matrix for those variables was calculated using a modified *t*-test (PASSAGE software; <http://www.passagesoftware.net>), which corrects the degrees of freedom based on the amount of auto–correlation in the data (e.g., Wang et

al., 2007). Point biserial correlation was also performed to examine potential relationships between shrub cover (i.e. under the canopy vs the open) and those observed variables.

Spatial patterns in the infiltrability index in relation to the disturbance gradient were examined using semivariograms with the GS⁺ geostatistical package (Gamma Design Software, Michigan, USA). We compared isotropic and corresponding anisotropic semivariograms at 0°, 45°, 90°, and 135° and did not find any significant directional pattern. We therefore used isotropic variograms in all analyses. We also ensured that all data were normally distributed, which is a prerequisite in geostatistical theory, by conducting the normal–score transformation prior to analyses (Rossi et al., 1993). Parameters derived from the semivariograms were used to quantify three key aspects of patchiness in the distribution of each of the variables: (i) variability that occurs at a scale less than the sampling scale and the magnitude of spatial dependence (i.e., the degree to which patches are differentiated from the surrounding area by their distinct, within–patch homogeneity), (ii) the mean diameter of those patches (e.g., Rodríguez et al., 2009; Li et al., 2010), and to a lesser extent, (iii) the arrangement of patches across the plot (Augustine and Frank, 2001). The variability less than the sampling scale was obtained using the nugget variance (C_0) while the magnitude of spatial structure calculated using the index of $C/(C_0+C)$. A greater proportion of the total sample is spatially structured if the index approaches unity.

The mean diameter of patches and the arrangement of patches across the plot were determined by the distance separating sampling points at which semivariance reaches an asymptote or the autocorrelation range (A_0). There are several commonly used semivariogram models and spherical model is often used in ecological studies (Schlesinger et al., 1996; Wang et al., 2009). This model was used to facilitate the comparison between the observed variables under different treatments, and was chosen because it is consistent with the distribution of those variables based on three criteria: high r^2 , minimal extrapolation of semivariance at spatial scale <25 cm (our smallest sampling scale), and the fitted model shape (Wang et al., 2007).

To test the relationship between the distance to canopy and the observed soil properties, the segmented quantile regression was performed. An envelope that includes the extreme responses of a variable to a single factor could therefore be the only meaningful feature to explain the relationship between distance to canopy and soil properties. However, modelling the envelope by 99% quantile, for example, may lead to ‘biased results as potential errors in the response variable have different influence depending on the direction of deviation’ (Schröder et al., 2005). We therefore used the 95% quantiles to obtain a compromise between the envelope and the influence of measurement error (Schröder et al., 2005). Segmented quantile regression involved the subdivision of data into segments to ensure that there was sufficient number of segments and data points within each segment to reflect the distribution of the response variable (i.e., bare ground cover, bulk density and infiltrability) over the particular range of independent variable (i.e., distance to canopy; Koenker and Hallock, 2001). We applied the segmented quantile regression because it is less affected by the presence of outliers than the common non-linear quantile regressions (e.g., Mills et al., 2006). We divided our data into nine classes of equal size ($n=12$), which were then sorted in ascending order, and parametric regression used to fit a line or curve through the 95% quantiles of each class. The regression line with the greatest r^2 value was selected from first and second order polynomial, logarithmic, exponential and power relationship. Segmented quantile regression analyses were performed using Sigmaplot version 11.0 and the 95% quantiles were determined using Microsoft Excel 2003. Details of the segmented quantile method are given in Mills et al. (2006) and Medinski et al. (2010).

Results

Univariate analysis

We detected significant difference in the cover of bare ground (Kruskal–Wallis; $H_2 = 166.42$, $P < 0.01$, $n = 108$), bulk density ($H_2 = 66.78$, $P < 0.01$), and infiltrability ($H_2 = 32.34$, $P < 0.01$) among the three treatments varying in levels of disturbance. The mean and median values of bare ground increased with increasing disturbance from 7.8% and 0% at the least disturbed (unploughed–ungrazed) to 74.4% and 87.5% at the most disturbed (ploughed–grazed) site. The variability of bare ground, however, showed an

opposite trend. The highest coefficient of variability (CV) was observed at the unploughed–ungrazed site (252.3%) while the lowest CV was at the ploughed–grazed site (41.4%). Mean infiltrability was greatest at the unploughed–ungrazed site, with the lowest variability. Bulk density was greatest at the ploughed–grazed site, and variability was lower at the two unploughed sites, which had similar values (Table 1). We also recorded, but only at the unploughed–grazed site, positive correlation between bare ground and bulk density as well as negative correlation between bulk density and infiltrability (Table 2).

Spatial analysis of bare soil, bulk density and infiltrability

Consistent with our hypothesis, bare ground was highly patchy and localized ($A_0 = 1.4$ m) at the unploughed–ungrazed site, in contrast to that at the disturbed sites (Figs. 1a–1c). The connectivity between patches of bare ground increased with either grazing or ploughing. This was indicated by the longer autocorrelation range at the unploughed–grazed (3.0 m) and the ploughed–grazed site (6.9 m). We also found higher nugget variances at these disturbed sites (Figs. 1b & 1c) than that at the undisturbed site (Fig. 1a), indicating higher small-scale variability occurred with grazing and ploughing. There was a decreasing trend of bare ground cover with increasing distance from shrub or tree canopy at the unploughed–ungrazed site, but consistent increase beyond the shrub canopy at both grazed sites (Figs. 1d–1f). The presence of shrubs, however, was correlated with the presence of bare ground only at the unploughed–ungrazed site (Table 3).

Unlike bare ground ($C/(C+C_0) = 0.92$; Fig. 1a), we did not find strong spatial structure in bulk density ($C/(C+C_0) = 0.50$; Fig. 2a) at the unploughed–ungrazed site. Instead, there was evidence of high connectivity and high small-scale variability in bulk density, indicated by the long autocorrelation range (2.5 m) and high C_0 (0.40; Fig. 2a). The trend, however, was different at the unploughed–grazed site, where bulk density exhibited a stronger spatial structure ($C/(C+C_0) = 0.75$) but a decline in its autocorrelation range ($A_0 = 1.8$ m; Fig. 2b), similar to the autocorrelation range of shrub cover (1.9 m; S. Daryanto, unpublished data). The autocorrelation range of bulk density at the ploughed–grazed site was even shorter than that at the unploughed–grazed site

(1.2 m), with high small-scale variability ($C_0 = 0.42$; Fig. 2c). There was only slight increase in bulk density beyond plant canopy at the unploughed–ungrazed site (Fig. 2d), but higher increases at both grazed sites (Figs. 2e & 2f). Overall, a high shrub cover was associated with a low bulk density (Table 3).

The importance of shrubs in determining infiltration, by creating patches of low density soil, was reflected at the autocorrelation range of infiltrability. The autocorrelation range of infiltrability changed in relation to ploughing and grazing (Figs. 3a–3c). The semivariogram of infiltrability at the undisturbed site (unploughed–ungrazed) had a high autocorrelation range (3 m) and high small-scale variability, indicated by nugget variance of 0.45 (Fig. 3a). In contrast, infiltrability under the unploughed–grazed treatment was highly spatially structured ($C/(C+C_0) = 0.83$) and was autocorrelated at distances of about 1.2 m (Fig. 3b), which corresponded to the zone of maximum biological activity of the shrubs. Under the same treatment, there was a relatively rapid decline in infiltrability with distance from the canopy, with the sharpest decline close to (< 0.5 m) shrub canopies (Fig. 3e). Conversely, there was only a slight decline in infiltrability with increasing distance from the canopy at the ungrazed site (Fig. 3d). This trend, supported by our correlation results (Table 3), indicated that under grazing, infiltration was restricted to the area in the immediate vicinity of the canopy. Both connectivity and small-scale variability in infiltrability were higher under the ploughed–grazed than the unploughed–grazed treatment (Figs. 3b & 3c). We also noted rapid decline in infiltrability with increasing distance from canopy under the ploughed–grazed treatment (Fig. 3f).

Discussion

Biologically-mediated processes are known to affect the spatial patterning of soil properties, including water flow, and worldwide research in semi-arid systems has shown that infiltration is generally greater under the canopies of perennial plants than in their interspaces (Bhark and Small, 2003; Stavi et al., 2008; Muñoz-Robles et al., 2011). Our research showed that the pattern of infiltrability, our surrogate for infiltration, changed with disturbance. Infiltrability at the undisturbed site remained high beyond shrub canopy, but this was not the case at the disturbed sites. This pattern indicated that

there was an abrupt change in properties between soils beneath the canopy and in the interspaces at the disturbed sites, but only gradual changes at the undisturbed site. The dichotomy between shrubs and their interspaces thus seemed to be more intense with disturbance due to the absence of understorey plants and biological crust cover. Consequently, the importance of shrubs as loci for infiltration increases with increasing disturbance.

Hydrological processes in the undisturbed site

Consistent with our hypothesis, the undisturbed site (i.e., unploughed–ungrazed) had the longest autocorrelation range of infiltrability (Fig. 3a), corresponding to that of bulk density (Fig. 2a). We observed that surfaces beneath shrub canopies in the least-disturbed area were generally well-vegetated with perennial grasses and forbs, which would have led to a reduction in bulk density out from the shrub canopies (Muñoz-Robles et al., 2011), resulting in zones of higher infiltration beyond the canopy (Fig. 3d). Enhanced soil porosity would be expected in the absence of livestock trampling, which has been shown to lead to distinct patterns of areas with high bulk density and low infiltration (Andrew and Lange, 1986; Stavi et al., 2008), and could also contribute to the weak decline in infiltrability up to 150 cm away from the shrub canopy (Fig. 3d). Such a trend was not observed at both grazed sites, which exhibited a rapid decline in infiltrability within 25 cm of the edge of the canopy (Figs. 3e & 3f).

About half of the variation in bulk density and infiltrability at the undisturbed site occurred at a scale < 25 cm, which corresponded to our highest sampling resolution. Such variation might occur due to small-scale variability in: (i) rainfall interception by shrubs, (ii) litter cover and depth, and (iii) biological crust cover. Bare soils exposed to direct raindrops are susceptible to raindrop impact from the foliage, which results in effects ranging from dislodgement of soil particles to widespread compaction (Geddes and Dunkerley, 1999). Rainfall interception by shrubs might moderate those effects, though some raindrops will penetrate the canopy. Variability in interception is likely affected by shrub morphology, with densely-arranged canopies able to intercept more rainfall than those with a sparsely-arranged canopy (Bochet et al., 1998; Cowling and Mills, 2011; Archer et al., 2012). Variation in morphology also determines the ability of

shrubs to retain litter (Bochet et al., 1998), likely creating small-scale, uneven distribution of litter under and around their canopy. Sub-canopy litter has been shown to alter the effect of raindrops by dissipating raindrop energy, thereby minimizing rainsplash that would lead to soil crusting (Geddes and Dunkerley, 1999). By increasing organic material, localized deposits of litter could also lead to reductions in bulk density and therefore increased infiltration (Shukla et al., 2006). A thick cover of litter could also serve as a microterrace or litter dam, retaining water and reducing the likelihood of runoff (Eddy et al., 1999). Indeed, our data indicated that there was a close association between the autocorrelation range of litter cover (~ 2.4 m; S. Daryanto, unpublished data) and infiltrability (~ 3 m; Fig. 3a) at this site.

Finally, the presence of a well-developed matrix of cryptogamic crusts in the shrub interspaces at this undisturbed site (Daryanto and Eldridge, 2010) and small patches of bare soil (Fig. 1a) would have created microsites of enhanced water ponding and reduced the time to initiation of runoff (Eldridge et al., 2010), eventually leading to an increase in infiltration in the zone immediately surrounding the canopy. Although some types of cryptogamic crusts (e.g., thin and smooth crusts) have been known to generate run-off due to their water-repellency properties (Yair, 1990), some others could actually increase water retention by forming micro-catchments (Yair et al., 2011), analogous to litter dams. Increasing structural development of biological crust cover, generally characterized by thicker and darker-colored crusts, has been recorded to improve soil water-absorbing capacity (Madsen et al., 2008). Their composition, however, might be random, likely generating high infiltration variability at small scale.

Changes of hydrological processes with grazing and ploughing

Although grazing and ploughing both increased the autocorrelation range of bare ground (Figs. 1b & 1c) and lowered that of bulk density (Figs. 2b & 2c), the spatial patterning of infiltrability differed between the unploughed-grazed and ploughed-grazed sites. At the unploughed-grazed site, we detected a strong spatial dependence, but short autocorrelation range, of soil infiltrability (Fig. 3b), indicating that infiltration was restricted to the area around the margins of the shrubs. Indeed, at the unploughed-grazed site, the autocorrelation range for bulk density (~ 1.8 m) and infiltrability (~ 1.2

m) was similar to that of shrub cover (~ 1.9 m; S. Daryanto, unpublished data). At the more disturbed ploughed–grazed site, however, the spatial dependence of infiltrability was weak, but it had a long autocorrelation range (Fig. 3c), suggesting that small cohort of shrubs, rather than single, mature shrubs, might be responsible for the variability in infiltrability. This is consistent with our data indicating a distribution of shrub sizes tending to younger smaller shrubs of higher density at the ploughed–grazed compared with the unploughed–grazed site (Daryanto and Eldridge, 2010).

We also observed a more gradual decline in infiltrability beyond the canopy at the ploughed–grazed than the unploughed–grazed site (Figs. 3e & 3f). Elevated levels of infiltrability just beyond the canopy comparable with levels under the canopy suggest that plant roots were responsible, to some extent for the increased infiltration (Segoli et al., 2008). Differences in infiltrability could also be due to differences in the size or age of individual shrubs. Given that the ploughed–grazed site was dominated by young, shorter shrubs (Daryanto and Eldridge, 2010), they are likely to have more lateral, surface-feeding roots than the larger, older shrubs, thus extending the area over which they are likely to scavenge for water to areas beyond their canopy. Since the development of plant roots would adjust to the availability of limiting resources such as water and nitrogen (February et al., 2011), we would expect that newly–regenerating plant roots in the ploughed–grazed area would be closer to the soil surface due to limited soil nutrients and most probably infiltration depth in the interspace (Daryanto et al., 2012).

While there was close association between the autocorrelation range for litter cover and infiltrability at the undisturbed site, we found that at both grazed sites the autocorrelation range of litter cover (~ 4.5 m; S. Daryanto, unpublished data) did not correspond with that of infiltrability. The weak litter effect might be due to dispersion by livestock, and/or scattering of litter into the interspaces by wind or water (Li et al., 2008). This scattering greatly diminishes the ecosystem effects of litter such as its capacity to reduce the energy of gravity drops (Geddes and Dunkerley, 1999), form resource–attenuating litter dams (Eddy et al., 1999; Lechmere-Oertel et al., 2005) or improve infiltration rates (Dunkerley, 2000). Infiltrability on the two disturbed treatments instead was autocorrelated at distances of 1.2 to 3.5 m, closer to that of shrub cover (1.9 m; S.

Daryanto, unpublished data). This is also supported by the high positive correlation between infiltration and shrub cover at the disturbed sites (Table 3). In heavily grazed area, trampling generally leads to increased soil compaction and bulk density, except for areas around the shrubs (Stavi et al., 2008) and therefore restricting infiltration only to under-canopy areas. Similarly, both ploughing and grazing limited infiltrability in the interspaces by reducing biological soil crust cover, which has been shown to improve soil infiltrability (Eldridge et al., 2010). Clearly grazing- and ploughing-induced disturbances have substantial impacts on soil surface cover types, altering their distribution, and ultimately affecting the infiltration of water in the interspaces beyond the shrub canopies.

Our results showed that the autocorrelation range of bulk density was slightly smaller, but that of bare areas was much larger, at the ploughed-grazed than the unploughed-grazed site (Figs. 1b, 1c, 2b & 2c). These results were unsurprising, given that the ploughed-grazed site was dominated by small shrubs, and the area beyond the canopy was typically bare and unvegetated, often due to ploughing. The greater distances between patches in the ploughed area was apparent, even two decades after ploughing (Daryanto and Eldridge, 2010). Shrub-free (bare) interspaces experience higher surface temperatures and evapotranspiration, reduced organic matter incorporation, denitrification, ammonia volatilization, and increased erosion (Schlesinger et al., 1990). The formation of physical soil crusts due to direct raindrop impacts reduces water availability in the interspaces, further decreased possible plant establishment (Holmgren, 2009). Grazing-induced disturbances reinforce the differences between shrubs and their interspaces, with eroded sediment and airborne nutrients accumulating under shrub canopies due to wind and water processes (Li et al., 2009). In addition, increased infiltration beneath shrub canopies, enhanced micro- and macroarthropod activity (Doblas-Miranda et al., 2009) and therefore decomposition processes promote a new set of positive feedbacks between shrubs and the remaining bare ground (Holmgren, 2009), where shrub growth is promoted at the expense of plants in the interspaces.

Conclusions

Our findings demonstrate the marked changes in our measure of soil infiltration and soil physical properties in relation to woody canopies under different levels of disturbance. While the effect of shrubs on infiltration extended beyond the canopy at the undisturbed site, it was concentrated close to the canopy at sites that were disturbed. Similarly, the rate of change in soil physical properties out from woody plant canopies increased markedly with increasing disturbance. Increasing disturbance therefore reinforces the difference between shrubs and their interspaces by restricting the effects of shrubs on soil processes to the immediate vicinity of their canopies. The effect of this disturbance is therefore to reinforce the shrub-dominant state by preventing the movement of resources to the interspaces. Maintaining existing patches of perennial woody vegetation is therefore critical for preserving high levels of connectivity between shrubs and their interspaces and for increasing landscape-level values of infiltration. When applicable, the use of contour banks might further enhance infiltration in hillslope areas (Muñoz-Robles et al., 2013). Our results highlight the importance of shrubs for maintaining hydrological processes in drylands. Severe disturbances such as shrub removal and overgrazing will result in reduced areas of high infiltration, potentially leading to greater runoff and resource loss.

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Table 1. Summary of statistical parameters of bare ground, bulk density and infiltrability at the unploughed–ungrazed, unploughed–grazed and ploughed–grazed sites. The different letters indicate different means at $\alpha = 0.05$.

Attribute	Unploughed– ungrazed	Unploughed– grazed	Ploughed– Grazed
Bare ground cover (%)			
Mean	7.81	25.71	74.41
Median	0.00 ^a	15.00 ^b	87.50 ^c
SD	19.69	28.45	30.80
CV	252.31	110.65	41.40
Soil bulk density (Mg m⁻³)			
Mean	1.46	1.40	1.58
Median	1.46 ^a	1.42 ^b	1.55 ^c
SD	0.13	0.16	0.15
CV	8.88	11.20	9.23
Infiltrability (mm h⁻¹)			
Mean	352.52	277.12	345.43
Median	344.80 ^a	255.19 ^b	324.34 ^c
SD	104.37	126.86	131.61
CV	29.61	45.78	38.10

Table 2. Correlations of bare ground, bulk density and infiltrability at the unploughed–ungrazed, unploughed–grazed and ploughed–grazed sites. The correlations were calculated using a modified t–test that corrects the degrees of freedom based on the amount of auto–correlation in the data * $P<0.05$

Treatment and attributes	Bare ground	Bulk density
Unploughed–ungrazed		
Bulk density	0.05	
Infiltrability	0.06	0.09
Unploughed–grazed		
Bulk density	0.24*	
Infiltrability	–0.02	–0.45*
Ploughed–grazed		
Bulk density	–0.01	
Infiltrability	–0.20	–0.13

Table 3. Point biserial correlations between shrub cover versus bare ground cover, bulk density and infiltrability at the unploughed–ungrazed, unploughed–grazed and ploughed–grazed sites. * $P<0.05$

Treatments	Bare ground cover	Bulk density	Infiltrability
Unploughed–ungrazed	0.20*	–0.18*	0.38*
Unploughed–grazed	–0.14	–0.48*	0.30*
Ploughed–grazed	–0.07	–0.12	0.40*

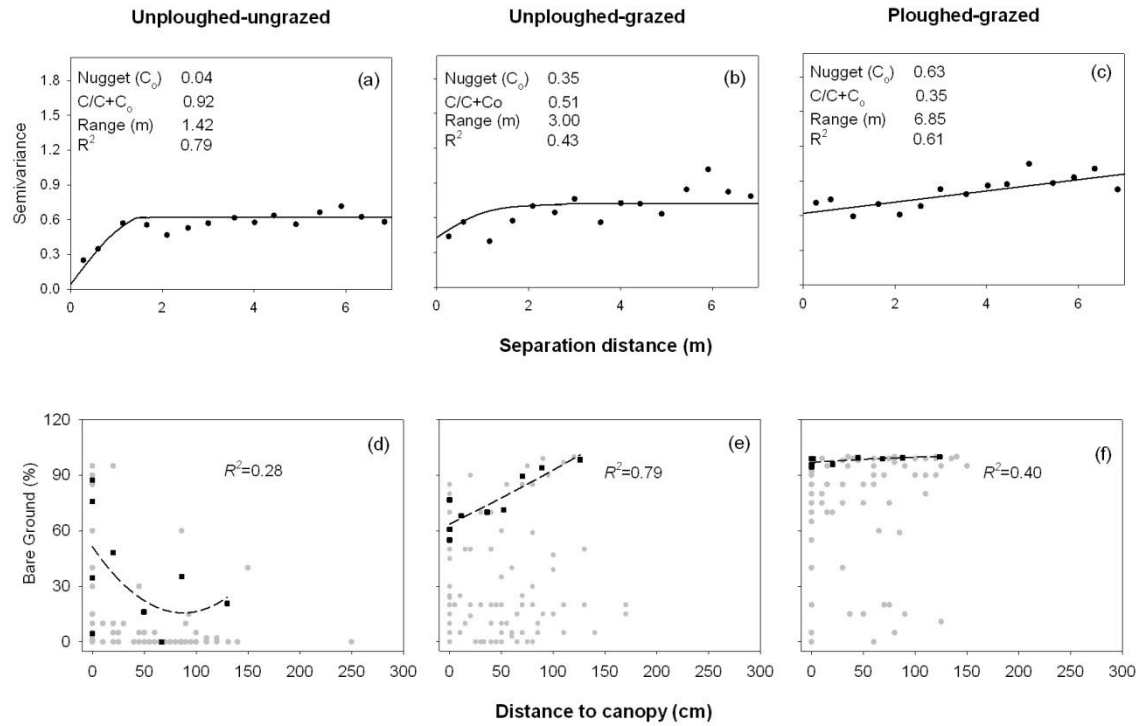


Fig. 1. Semivariograms of bare ground (a–c) and segmented quantile regressions between bare ground and distance to canopy (d–f) at unploughed–ungrazed, unploughed–grazed and ploughed grazed sites. Black squares in graph d, e, and f depict the 95th quantiles of each class ($n = 12$) and segmented quantile regression lines (dashed) were delineated through those values.

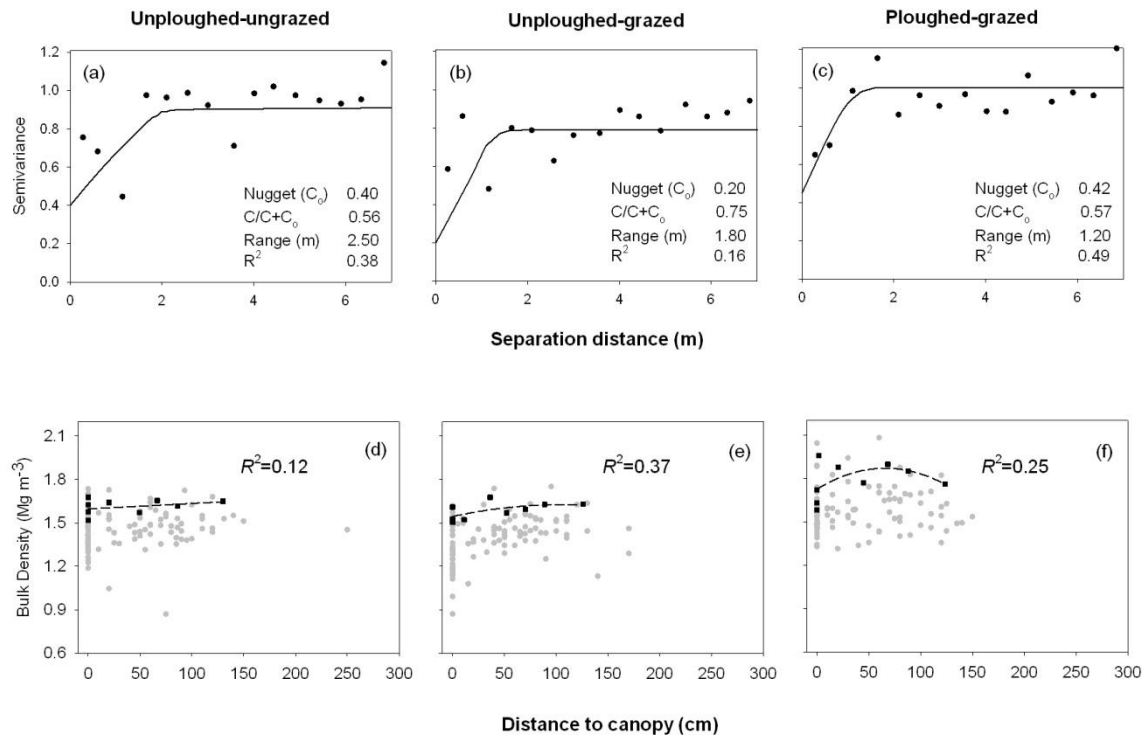


Fig. 2. Semivariograms of bulk density (a–c) and segmented quantile regressions between bulk density and distance to canopy (d–f) at unploughed–ungrazed, unploughed–grazed and ploughed grazed sites. Black squares in graph d, e, and f depict the 95th quantiles of each class ($n = 12$) and segmented quantile regression lines (dashed) were delineated through those values.

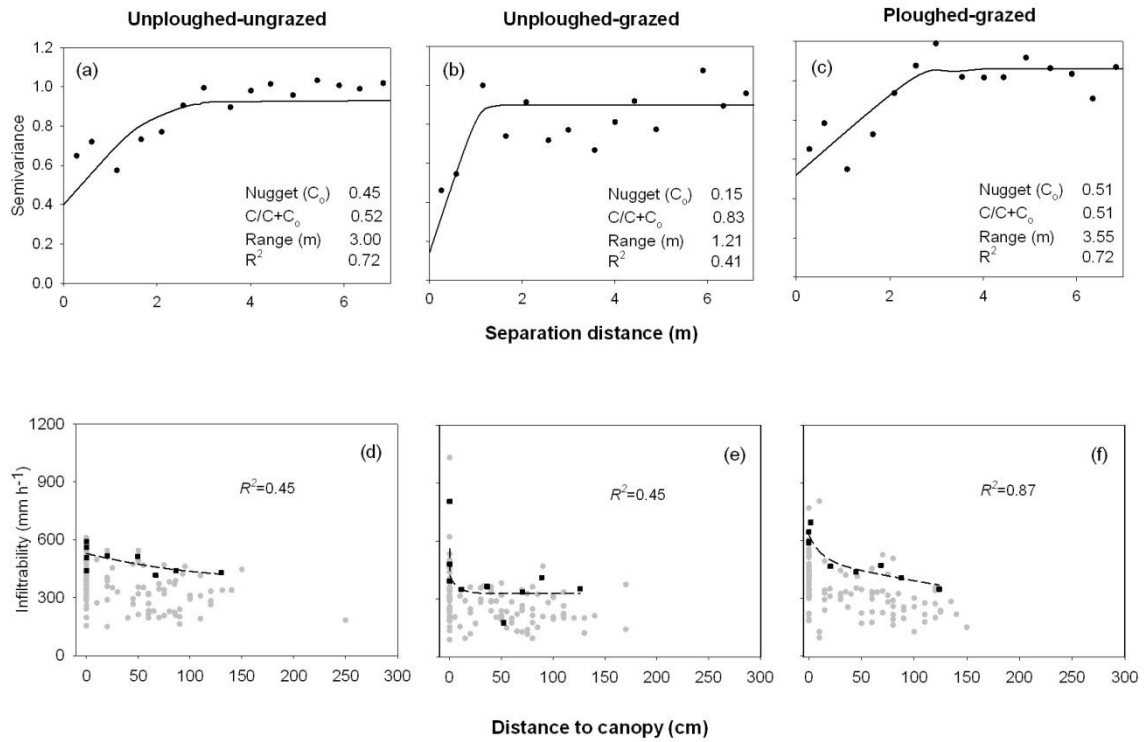


Fig. 3. Semivariograms of infiltrability (a–c) and segmented quantile regressions between infiltrability and distance to canopy (d–f) at unploughed–ungrazed, unploughed–grazed and ploughed grazed sites. Black squares in graph d, e, and f depict the 95th quantiles of each class ($n = 12$) and segmented quantile regression lines (dashed) were delineated through those values.

Managing semi–arid woodlands for carbon storage: grazing and shrub effects on above– and belowground carbon

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Abstract

Shrub cover has increased in semi-arid regions worldwide. This change has generally been viewed as land degradation, due to shrub-induced declines in pastoral productivity. As a consequence, widespread management treatments to reduce shrub density have been applied in many pastoral areas. These treatments, however, often do not have long-term positive benefits for forage production. Alternative uses for shrub-encroached lands have received little consideration, but a recent move toward economic incentives for carbon (C) storage could lead to financially viable alternative land management strategies. We examined changes in above- and belowground C storage following 20 years of factorial land management treatments (grazing/no grazing and shrub removal/no removal) in an Australian semi-arid woodland. Disturbance by shrub

removal (root ploughing) and/or livestock grazing significantly reduced the amount of soil organic carbon (SOC). The most disturbed treatment (grazed and ploughed) contained the least SOC ($15.30 \text{ t C ha}^{-1}$) while protection from grazing and shrub removal led to the greatest SOC ($28.49 \text{ t C ha}^{-1}$). Declines in SOC in shrub removal treatments (with and without grazing) were compensated, in part, by enhanced aboveground C accumulation, derived mainly from woody plants. Destocking currently grazed shrublands for two decades resulted in a net C accretion, over 20 years, in the order of 6.5 t ha^{-1} , almost entirely through increasing belowground C. At the current price for C in Australia, the economic benefit for C accumulation from removing livestock grazing would be similar to the economic benefit of grazing. The results suggest that C farming in this semi-arid woodland system may offer an economically viable alternative management strategy to grazing, although uncertainties in future climate, C credit value, and assessment protocols present hurdles for implementing alternative management aimed at C farming.

Keywords: carbon farming, carbon sequestration, dryland, grazing, shrub removal, shrubland

Introduction

Humans have had a substantial impact on the physical and biological features of Earth, with approximately 83% of all terrestrial environments experiencing some kind of direct human influence, including urban settlement, agricultural or pastoral land use, and transport networks (Sanderson et al., 2002), resulting in various degrees of ecosystem degradation. One of the most severely impacted ecosystems is arid and semi-arid environments ('drylands'), which cover about 40% of the globe and support 40% of its human population (Maestre et al., 2012). Although disturbance (e.g., fire) has been a natural part of many dryland systems, these systems are still prone to human-induced disturbance processes, largely brought about by the introduction of domestic livestock grazing, agricultural practices, and changes to natural fire regimes (Van Auken, 2009).

One globally widespread form of land cover change in drylands is the increase in the density of woody plants, which leads to dramatic declines in pastoral productivity in

many systems (e.g., Oba et al., 2000; Van Auken, 2009). The apparent mechanisms behind woody encroachment range in spatial scale from local-to-regional (e.g., increases in grazing and reductions in fire frequency) and regional-to-global (e.g., changes in N deposition, atmospheric CO₂ concentration, and climate; Sankaran and Anderson, 2009). Long periods of heavy grazing suppress grass production, and the resulting decline in grass fuel loads can alter the frequency and severity of wildfire, which exerts a controlling feedback effect on shrubs (D'Odorico et al., 2011). Increasing atmospheric CO₂ may favour the establishment of C₃ shrubs at the expense of C₄ grasses (Polley et al., 1997), and deep-rooted C₃ shrubs may be more physiologically active in dry conditions than shallow-rooted C₄ grasses (Throop et al., 2012b). Furthermore, biological feedbacks may promote the dominance of shrubs following their establishment. Enhanced soil faunal activity and deposition of nutrients beneath shrubs leads to positive plant–soil feedbacks whereby shrub growth is promoted in the interspaces at the expense of herbaceous plants (Holmgren, 2009). With generally greater levels of erosion in the interspaces and the collapse of facilitatory mechanisms due to excessive herbivory (Pugnaire et al., 2011), grass seedling establishment is infrequent. These ‘novel systems’ (Bridgewater et al., 2011), characterised by a greater cover and density of woody plants, are more strongly resistant to human-induced disturbances than the original systems from which they were derived (Standish et al., 2009).

The structure and composition of Australian vegetation has changed substantially in the two short centuries since European settlement. Large areas of Australia's grassland and woodland matrix have become encroached by shrubs, resulting in substantial reductions in pastoral productivity (Noble, 1997), and encouraging many pastoralists to control shrubs chemically and mechanically (Harland, 1993). One popular mechanical method is blade-ploughing (*aka* root ploughing), which has been widely promoted by government agencies to control a range of woody species (e.g., *Dodonaea*, *Senna* and *Eremophila* spp.; Robson, 1995). However, this method has been largely unsuccessful for long-term shrub eradication, and the failure of small-scale shrub removal has been blamed on regional-to-global factors such as highly variable regional rainfall (Brown et al., 1997) and rising atmospheric CO₂ concentrations (Morgan et al., 2007). As an alternative to mechanical removal, attempts to convert shrublands to their original open

woodlands structure by destocking have produced inconsistent results (Trodd and Dougill, 1998; Angassa and Oba, 2007).

While the encroachment of woody plants is regarded by many as symptomatic of a degraded ecosystem (Grover and Musick, 1990), this view is mainly perpetuated in the grazing context. Considerable attention has been paid to the consequences of short- and long-term shrub removal on primary productivity (e.g., Robson, 1995; Daryanto and Eldridge, 2010). The ecological and economic consequences of shrub encroachment have received little research emphasis beyond pastoral impacts, despite evidence suggesting that encroachment can have positive impacts on multiple ecosystem functions (Maestre et al., 2009; Eldridge et al., 2011) or ecosystem ‘multifunctionality’ (Maestre et al., 2012). An emerging view is that encroaching shrubs, whether occurring in isolated patches or as extensive shrublands, can cause a state transition from historical grass dominance to an alternative, but stable, state (Standish et al., 2009). However, ecosystem multifunctionality in this altered stable state may still remain high (D’Odorico et al., 2011), even where herbaceous productivity is sparse or patchy. For example, shrubs may moderate surface micro-climate, reduce nutrient loss from erosional processes, enhance nutrient inputs via N fixation (Lajtha and Schlesinger, 1986), increase soil structure, stability, and the infiltration of water (Howard et al., 2012), and provide essential habitat for a range of shrub-obligate taxa (Maestre et al., 2009; Eldridge et al., 2011; Daryanto and Eldridge, 2012; Howard et al., 2012). Shrubs can also hasten the recovery of degraded systems by facilitating seedling establishment (Padilla and Pugnaire, 2006) due to their ability to moderate the effects of drought, and extremes of fire, salinity and frost (Richmond and Chinnock, 1994; Booth et al., 1996).

Carbon (C) uptake and storage may be substantially enhanced by shrub encroachment (Barger et al., 2011), and the potential ecological, economic, and atmospheric consequences of substantial shrub C uptake make this a key response variable. In North America, woody encroachment has been identified as one of the largest, albeit highly uncertain, components of the terrestrial C sink (Pacala et al., 2001; Houghton, 2003). This accumulation of C appears to be a function of enhanced below- and aboveground net primary productivity (NPP), low decomposition rates below shrubs, biochemical recalcitrance of woody litter, and organic matter stabilization in protected soil

aggregates (e.g., Liao et al., 2006; Throop and Archer, 2007; Knapp et al., 2008). Recent modelling using remote sensing data and measurements of C flux and vegetation growth as a function of climatic and soil data has identified a similar potential for C sequestration by shrubs in semi-arid system in Australian (e.g., Dean, 2011; Fensham and Guymmer, 2009; Harper et al., 2007; Howden et al., 2001; Witt et al., 2011) and Mediterranean woodlands (e.g., Ruiz-Peinando et al., 2013). The magnitude of this C sink, however, is largely unknown. Also critical, but unknown, is the potential efflux of C that arises when existing shrubs are removed through management practices. This lack of information is surprising, given the large financial investment by regional and local governments in Australia in supporting the removal of shrubs from encroached woodlands on the expectation of enhanced pastoral (grazing) productivity (Robson, 1995). With recent legislation on a C price in Australia, financial incentives for landholders to sell or to lease their land for long-term C-sequestration schemes are likely (Prowse and Brook, 2011). Although shrublands typically sequester less C and are therefore less profitable than monocultural C plantations, a price on C should increase the development of ‘biodiversity planting’ (Prowse and Brook, 2011) or ‘ecological carbon planting’ through market-driven processes (Crossman et al., 2011). For Australian drylands, this ecological C planting may also provide a biodiversity and conservation co-benefit (Watson et al., 2011) and provide other ecosystem functions such as reduced salinisation and erosion (Scanlan et al., 1992).

Here we report on a study aimed at evaluating the long-term impact of different land management practices on above- and belowground C pools. In doing so, we re-evaluate the current paradigm that shrub encroached woodlands have low ecological and economic values. We do this by quantitatively assessing changes in plant and soil C stocks at different microsites in a shrub-encroached semi-arid woodland in eastern Australia subjected to varying combinations of grazing and mechanical shrub removal by blade-ploughing. We anticipated that the unploughed site from which grazing has been excluded for almost two decades would have greater total C than sites that were either ploughed or grazed, as both types of disturbance would decrease landscape-level pools of soil C. We expected therefore that the least-disturbed site would be valued more highly in terms of the ecosystem service of storing C; a service that has until recently not garnered much economic value.

Methods

Study area

The study was conducted at 'Wapweelah', an extensive grazing property about 35 km west of Enngonia near Bourke in north-western New South Wales, Australia (29° 16'S, 145° 26'E). The site falls within Gumbalie Land System (Walker, 1991), and is characterised by sandplain with low west-east trending sandy rises and dunes of Quaternary aeolian alluvium, and subject to moderate windsheeting and watersheeting. The slope is < 1%, soil texture is sandy loam to loamy and the mean annual rainfall is about 312 mm, with 45% more rain falling during summer than winter (Robson, 1995).

The vegetation in the area is typical of areas in eastern Australia targeted for shrub removal by blade-ploughing (Harland, 1993). The community is characterised by an open to dense woodland of mulga (*Acacia aneura*), which has a structure ranging from discrete islands within large patches free of woody cover to continuous groves (Tongway and Ludwig, 1990). Additionally, our site contained scattered ironwood (*Acacia excelsa*), rosewood (*Alectryon oleifolius*), leopardwood (*Flindersia maculosa*), supplejack (*Ventilago viminalis*), wilga (*Geijera parviflora*), gidgee (*Acacia cambagei*) and brigalow (*Acacia harpophylla*). The understorey layer was sparse at the time of soil sample collection and consisted of woollybutt (*Eragrostis eriopoda*), mitchell grass (*Thyridolepis mitchelliana*), mulga oats (*Monochather paradoxa*), rough speargrass (*Austrostipa scabra*) and other grasses and forbs. This community supports dense stands of shrubs of inverted-cone morphology (Y-shaped) such as turpentine (*Eremophila sturtii*), narrow-leaf hopbush (*Dodonaea viscosa* var. *angutissima*), budda (*Eremophila mitchellii*) and hemispherical shrubs such as green turkey bush (*Eremophila gilesii*) and silver cassia (*Senna artemisioides*; Walker, 1991; Robson, 1995). Shrub morphology is known to affect the capacity of shrubs to retain litter beneath their canopies, with hemispherical-shaped shrubs retaining a greater amount of litter beneath their canopies than shrubs with an inverted-cone morphology (*aka* inverted-cone shrubs; De Soyza et al., 1997). This morphological difference could influence soil C and nitrogen (N) pools.

Shrub removal treatments

In 1990, three replicate blocks (1 to 5 km apart) of 400 m x 200 m were established and each was divided into four plots of 100 m wide by 200 m long. The two central plots were fenced in a 6 m high, herbivore-proof fence while the two outer plots were subject to grazing by sheep and cattle, with typical stocking rates ranging from 0.07 sheep ha⁻¹ (i.e., a non-lactating ewe) during dry periods to 0.5 sheep ha⁻¹ during wet periods (Robson, 1995). Kangaroos, feral goats, and feral European rabbits also grazed the outer plots, but at unknown densities. One of the two central plots was left unploughed and the other one was ploughed. Similarly, one of the outer (grazed) plots was ploughed and the other one left unploughed, which resulted in four treatments based on all possible grazing by ploughing combinations (Table 1). These four treatments represent different land management scenarios reflecting the range of land management practices in shrub-encroached woodlands in eastern Australia. The ‘conventional pastoral’ treatment represents the most common land management scenario in eastern Australia and is based on set stocking with no shrub removal, while ‘active pastoral’ indicates shrub removal combined with various levels of set stocking in order to recoup some of the costs associated with shrub removal. ‘Conventional conservation’ is a strategy practiced within national parks and conservation reserves whereby livestock are removed but shrubs are not controlled. The ‘active conservation’ strategy, however, is rarely used, and represents an experimental treatment (Robson, 1995) that may have some management value within a conservation context such as the removal of isolated shrubs around fences or other infrastructure, or shrub removal in the absence of grazing to meet specific conservation objectives such as creating habitat for key plant or animal species (Table 1).

Shrubs were removed with a single pass of a 4.2 m wide single-tynd ‘Stationmaster’ blade-plough pulled by a 90 kW crawler tractor. Only shrubs were targeted during ploughing and cutting depth was maintained at 20–30 cm to sever the taproots of most shrubs, particularly *Eremophila* spp., to prevent resprouting (Wiedemann and Kelly, 2001). Examination of fallen shrubs confirmed a satisfactory ploughing effect over most of the treated area (Robson, 1995). The remains of shrubs, either those pushed over by ploughing or those that died naturally were thus considered as coarse woody debris

(CWD; log mounds; Tongway et al., 1989). They act as a barrier against the movement of runoff and sediment and become sites of soil and organic matter accumulation. They often form fertile mounds (up to 10 m² area) with higher available nutrients and small animal activity (Daryanto and Eldridge, 2012; Daryanto et al., 2012).

Field sampling and laboratory analyses

In September 2010, two decades after ploughing and fencing, three 50 m long by 2 m wide belt transects were established through the centre of each of the 12 plots to measure the cover of different landscape elements. We identified six landscape elements across the study site: 1) N-fixing trees (i.e., *Acacia* spp.), 2) non N-fixing trees (e.g., *Geijera parviflora*), 3) inverted-cone shaped shrubs (e.g., *Eremophila sturtii*), 4) hemispherical shrubs (e.g., *Senna artemisioides*), 5) mounds of CWD, and 6) interspaces. For each landscape element on each plot, we collected between two and five intact soil cores (4.2 cm diameter, 30 cm depth); the number of cores increased with the relative cover of each landscape element. Cores were separated into four depth increments (0–5, 5–10, 10–20, and 20–30 cm). For each of the 12 plots, we combined all depth increments obtained from within each of the six landscape elements in order to obtain one bulked sample for each landscape element per plot for each depth. Soil samples for shrubs and trees were taken at mid-canopy positions, while interspace soils were sampled on bare soil surfaces at least 5 m from any other landscape elements. For CWD mounds, samples were taken about 10 cm from the mounds in an upslope position. Soil cores were air dried, passed through a 2 mm sieve to remove any roots or organic debris, ground, and subjected to combustion analysis (LECO CNS–2000; LECO Corporation, St. Joseph, MI, USA) in order to quantify soil organic C (SOC; i.e., without carbonates) and N concentrations on a per mass basis (i.e., %SOC and soil %N, respectively). Additional cores for each soil depth by landscape element combination were collected to determine bulk density and to allow us to convert %SOC and %N to area-based pools. Bulk density was calculated as the mass of the fine earth (< 2 mm) fraction, divided by the volume of the entire core to avoid overestimating the mass of fine earth when stones are present (Throop et al., 2012a).

Landscape element and plot-level carbon estimates

Stocks of SOC and soil N were calculated as a product of C or N concentration (%SOC or soil %N), bulk density and soil depth. This was done firstly by calculating the segment delimited by polynomial equations ($R^2 > 0.999$; $n = 72$) that specifically describe the relationship between %SOC or soil %N of each landscape element in each of the 12 plot and its corresponding depths using Matlab R2010b. Depth-specific bulk density was then used to convert the %SOC and soil %N to g SOC m⁻² or soil N m⁻² for each depth, enabling comparison of SOC or soil N across landscape elements on an areal basis (hereafter ‘landscape element SOC’ or ‘landscape element soil N’; Harms et al., 2005). Mass of SOC or soil N for all landscape elements within a management treatment plot (hereafter ‘plot-level SOC’ or ‘plot-level soil N’) was calculated by multiplying landscape element SOC or landscape element soil N by the percent cover of the corresponding landscape element.

We estimated the mass of woody plant tissue in each landscape element based on allometric equations and area-adjusted cover of woody plants and CWD in each plot. Cover data were obtained from belt transects (see section 2.3); plants were included if their stem was rooted within the belt transect. For the upperstorey, we measured the height and canopy width of all trees and shrubs, except for tall (> 2 m high) *Acacia aneura*, for which we used diameter at breast height (DBH). Biomass of individual woody plants was calculated using species-specific algorithms for *Acacia aneura* woodlands (Suganuma et al., 2006) based on plant width and height or DBH. Root biomass was estimated as 27.14% of aboveground biomass, except for *Acacia aneura* (40.2%), based on previously established relationships (Suganuma et al., 2006). Total mass of CWD was estimated using a ‘standard log’ (Andrew et al., 1979) whose weight and dimensions were used as a comparison against all CWD found in all plots. A further 12 logs were estimated and their mass assessed across the 12 sites to derive predictive equations similar to the groundstorey biomass. We included all CWD where 50% or more of the material was within the belt transect. Mass of C was estimated from all aboveground (upperstorey and understorey), root, and CWD biomass by assuming 50% C content (Snowdon et al., 2000).

Total aboveground herbaceous biomass was estimated at the plot level within ten to twenty five 0.25 m² (0.5 × 0.5 m) quadrats per plot by an experienced observer (David Eldridge). A greater number of quadrats were sampled in plots with more herbaceous cover. Biomass was estimated using a portfolio of photographic standards of known weight, which are used widely in rangeland assessment (Eldridge and Koen, 2003). At the completion of measurements we estimated the biomass within an additional five quadrats for each plot, where all aboveground material was removed, dried at 60°C for 72 hours and weighed. We then established relationships between actual mass of clipped material and estimates based on the photographic standards in order to correct our field-based estimates. The predictive power of these regressions was relatively strong ($R^2 = 0.74-0.89$; $P < 0.001$, $n = 60$).

Total C pools were estimated for each of the 12 management treatment plots (Fig. 1). Plot-level belowground C was the sum of plot-level SOC and plot-level root C while plot-level aboveground C was the sum of plot-level aboveground woody C (shrub aboveground C, tree aboveground C, and CWD) and plot-level aboveground herbaceous C. The sum of plot-level aboveground and belowground C was defined as plot-level total C.

Statistical analyses

Univariate analysis using a randomized-block ANOVA was used to determine the effect of treatments on the percentage cover of different landscape elements while differences in %SOC, soil %N, C:N ratio, and bulk density in relation to treatment and landscape elements were analysed using a mixed-models ANOVA. The main plot of the mixed-model ANOVA considered block ($n=3$) and treatment ($n=4$) effects, and the sub-plot landscape element effects (i.e., interspace, CWD mound, inverted-cone shrub, hemispherical shrub, N-fixing tree, non N-fixing tree) and their interactions with treatment. Univariate analyses for assessing differences in plot-level soil N, aboveground, belowground and total C among treatments were tested using randomized-block ANOVA after scaling the data up to the plot level by adjusting for the percent cover of different landscape units at each plot. Data were checked for normality and homogeneity of variance (Levene's test) using Minitab 15 prior to

analyses. *Post-hoc* differences in means were tested using Least Significant Difference testing.

Results

Distribution of landscape elements in management treatment plots

Averaged across all management treatments, interspaces occupied $67 \pm 0.6\%$ (mean \pm SE) of the surface area, inverted cone-shaped shrubs $13 \pm 0.9\%$, and the other landscape elements each occupied 3 to 6% of the area (Table 2). With the exception of N-fixing trees, there were no differences in the cover of landscape elements among the four management types. The cover of N-fixing trees (e.g., *Acacia aneura* and *Acacia excelsa*) was significantly greater in the active conservation plots compared with those under active pastoral and conventional pastoral treatment ($F_{3,6} = 12.32$, $P = 0.013$; Table 2).

Carbon and nitrogen in landscape elements

Averaged across all depths and management treatments, soils in the interspaces had the highest bulk density ($F_{5,40} = 3.39$, $P = 0.012$), but a consistently lower %SOC ($F_{5,40} = 13.09$, $P < 0.001$), soil %N ($F_{5,40} = 11.62$, $P < 0.001$), and C:N ratio ($F_{5,40} = 8.16$, $P < 0.001$; Table 3) than the other landscape elements. There were also significant treatment by landscape element interactions for %SOC ($F_{15,40} = 3.17$, $P = 0.002$) and soil %N ($F_{15,40} = 3.15$, $P = 0.002$), with levels of both %SOC and soil %N similar under all elements for all treatments, except for the conventional pastoral treatment where values under non N-fixing trees were substantially greater (Appendix Fig. 1). When analysed by depth, the same trends for %SOC and soil %N were also observed for the three topmost layers (0–5, 5–10, and 10–20 cm) but not in the deepest soil layer (20–30 cm; $P=0.093$ and $P=0.089$ for %SOC and soil %N, respectively). In contrast, bulk density patterns were driven by changes in the surface soils, as surface soil (0–5 cm) drove the pattern of greatest bulk density in interspace soils compared to other landscape elements ($F_{5,40} = 3.60$, $P = 0.009$). This pattern was consistent across treatments (Table 4 and Table 5).

Carbon and nitrogen pools at the plot level

At the plot level, grazing and ploughing caused significant declines in belowground C (soil + root C; $F_{3,6} = 11.39$, $P = 0.007$). The mass of plot-level belowground C on the least disturbed treatment (conventional conservation; 30.1 t ha^{-1}) was almost 50% greater than that at sites under the most disturbed treatment (active pastoral; 19.1 t ha^{-1} ; Fig. 2a). Most of this difference was due to storage in the uppermost layer (0–5 cm) of the soil profile ($F_{3,6} = 45.70$, $P < 0.001$; Table 4), with an almost five-fold greater SOC at 0–5 cm in the conventional conservation (16.3 t ha^{-1}) than the active pastoral (3.3 t ha^{-1}) plots. The interspaces contributed most to the SOC in the 0–5 cm soil layer (Table 4), largely due to their areal (Table 2) and bulk density extent (Table 3). We also detected some significant differences in the SOC in deeper soil layers, with soils under active conservation consistently having the highest SOC in the 5–10 cm layer (4.9 t ha^{-1} ; $F_{3,6} = 5.83$, $P = 0.03$) and 10–20 cm layer (6.2 t ha^{-1} ; $F_{3,6} = 9.05$, $P = 0.01$) compared with the other treatments. These substantial differences in SOC storage in the upper layers, however, attenuated strongly with depth (20–30 cm; $P = 0.07$). We did not detect any differences, however, in soil N with different treatments within each corresponding soil depth (Table 5).

In contrast to belowground C, there was a trend toward increased aboveground biomass in the ploughed treatments, although this pattern was not significant ($P = 0.13$; Table 6). Total C was generally lowest in the conventional pastoral treatment. However, there were no significant differences among management treatments ($P = 0.18$; Fig. 2a), reflecting the combination of disturbance-induced declines in belowground C and positive aboveground responses to ploughing. The contribution of aboveground C to total C was greater for treatments that were ploughed (active conservation = 32.6%; active pastoral = 41.6%) than for unploughed (conventional conservation = 16.6%; conventional pastoral = 20.1%; Fig. 2a & 2b).

Discussion

Large areas of semi-arid woodland in eastern Australia have been encroached by woody plants (Noble, 1997), presenting substantial problems for land managers whose primary

enterprise has been the grazing of sheep and cattle on native pastures. Many pastoral managers have considered few alternative land uses for shrub-affected woodlands apart from opportunistic harvesting of feral goats and, in some cases, ecotourism (Prowse and Brook, 2011). Our study sought to test whether C farming could be an alternative (i.e., profitable) land use option for shrub-affected woodlands. Increasing disturbance resulted in a 37% decline (from 30 to 19 t ha⁻¹) in belowground C from the least disturbed (conventional conservation) to the most disturbed (active pastoral) treatments. These values are remarkably close to those from studies conducted by Harms et al. (2005) on the clearing of mulga country in Queensland using similar methods. This drop in SOC was driven by the top 5 cm of soil, where SOC was five-times greater under the least disturbed treatment (16.3 t ha⁻¹) than under the most disturbed treatment (3.3 t ha⁻¹; Table 4). While %SOC and soil %N were least in the unvegetated interspaces (Table 3), the extensive cover of interspaces across all treatments (Table 2) resulted in them supporting the largest pools of both SOC (Table 4) and soil N (Table 5). In contrast to belowground C, there was a trend toward increasing aboveground C in the ploughed treatments. Overall, our results indicate that surface disturbances such as grazing, and physical removal of shrubs by ploughing, lead to reductions in SOC, but encroachment, by increasing the cover and biomass of woody plants, partially compensates for this reduction. The importance of shrubs thus increases with disturbance since SOC after land clearing was also associated with vegetation type (i.e., root distribution; Harms et al., 2005). *Acacia* spp., in particular, have denser roots in the surface soils than other species (Burrows 1976; Suganuma et al., 2006) which may explain why maintaining native vegetation is important if C sequestration is a management objective.

Depth effects on carbon and nitrogen

Observed declines in SOC with depth are consistent with global observations of soil C and nutrient accumulation in the topsoil and their rapid attenuation with depth (e.g., Jobbágy and Jackson, 2001). Responses to disturbance also attenuated with depth, such that a reduction in SOC pools was not apparent at depths > 5 cm even though the depth of ploughing was substantially greater (~30 cm deep; Robson, 1995). While the relative contribution of SOC in the 0–5 cm layer declined from conventional to active

conservation, i.e., with only the imposition of ploughing, further disturbances by grazing did not lead to additional declines in SOC pools (Table 4).

Trends in N pools, however, did not reflect those for C, with no apparent difference in N pool distribution with depth among treatments or landscape elements (Table 5). Part of the increased %SOC but not soil %N could have been due to the difference in the composition of biological soil crusts; complex associations between the surface soil layers and microphytic organisms (e.g., cyanobacteria, lichens, mosses; Kidron et al., 2010). Crusts are known to fix C and N as well as moderating their loss from the ecosystem (Barger et al., 2006). They differ, however, in their N fixing capability with darker (i.e., increased chlorophyll, protein and carbohydrates) crusts able to fix more N than the light-coloured ones (Kidron et al., 2010). The former type of crusts, however, only occurred in stable, undisturbed soils (Kidron et al., 2009). Because of the strong suppressive effect of disturbance on biological soil crust cover (e.g., trampling and ploughing) and their long time to recovery (e.g., Daryanto and Eldridge, 2010), it was likely that the dominant biological crusts at our sites were those that had less capability to fix N.

Soil and aboveground carbon among different landscape elements

While interspaces contained the largest SOC pools (due to large area and high bulk density), this large pool of SOC was highly responsive to disturbance by grazing or ploughing. In contrast, differences in %SOC and soil %N increased markedly from the interspaces, through coarse woody debris and shrubs, to trees, with concentrations under large, non N-fixing trees twice that in the interspaces (Table 3). Our results are consistent with the large body of empirical evidence indicating the accumulation of essential resources (nutrients, water, litter) under shrubs and coarse woody debris (e.g., Tongway and Ludwig, 1996; Wang et al., 2007; Daryanto et al., 2012). Examination of C pools in relation to landscape elements showed that inverted cone-shaped shrubs contributed relatively large amounts of C at the undisturbed sites ($\sim 6 \text{ t ha}^{-1}$; Table 4). We attribute this to increased %SOC under shrubs, as the cover of these cone-shaped shrubs was consistent across treatments (11–16%; Table 2) and soil bulk density was generally lower around these shrub hummocks (Table 3).

Our results suggest that the importance of vegetation patches relative to interspaces as pool of C increases as sites become degraded. Much of this shift is driven, however, by C in aboveground biomass. While ploughing generated SOC loss, it tended to increase aboveground C due to vegetation shift to a younger, more productive age state, similar to patterns reported by Hughes et al. (2006). Therefore, unlike belowground C pools, aboveground pools were lowest on the interspaces (i.e., herbaceous cover) and for hemispherical-shaped shrubs, and greatest for N-fixing or inverted cone-shaped shrubs (Table 4). Ploughing is known to stimulate shrub (e.g., *Eremophila* spp.) regrowth, either from seed or belowground woody structures such as root suckering or epicormic buds (Wiedeman and Kelly, 2001; Chinnock, 2007). Our previous studies at this site show that ploughing increased the overall densities of woody plants (Daryanto and Eldridge, 2010), hence the high C on these ploughed plots. Both ploughed treatments (Active Conservation and Pastoral) had a substantial density of shrubs (mainly *Dodonaea viscosa* and some *Eremophila* spp.) as well as some N-fixing trees (mainly *Acacia aneura*) that made up a substantial percentage (~82%) of the total aboveground C pool. As subsequent grazing would also favour shrub regeneration by removing competitors (e.g., grasses), the unpalatable *Eremophila* spp. would tend to dominate areas with a history of heavy stock grazing (Tiver and Andrew, 1997), likely compensating in aboveground C for the loss of SOC.

Managing shrubland for ecosystem carbon stocks

These results indicate that the consequences of even one disturbance event can persist for decades in this system, including the lasting effect of grazing that 18 years of exclusion was not sufficient to create ecosystem recovery. In most low productivity systems, such as semi-arid rangelands, plants recover slowly after disturbance (Lunt et al., 2007). It is likely that the decline in surface soil C was due to the combination of enhanced heterotrophic respiration following the disturbance (Schulze, 2006) and limited nutrient and C input due to lack of vegetative cover. Expanding shrub biomass in the decades since ploughing suggest that the depressed soil C may decline with time, and it is likely that it has recovered, at least in part, from surface disturbance. While the active conservation scenario might yield approximately the same amount of plot-level C, with cost \pm A\$ 45 ha⁻¹ in 2009 (NSW Department of Primary Industry, 2010), the

economics of ploughing will depend on many things such as the opportunity cost of not grazing (i.e., the foregone grazing value of land that is left to thicken with shrubs) and the cost of treatment (e.g., labour, machinery, and fuel). This cost, however, may vary depending on soil texture, soil type, soil moisture, plough model, tractor type, shrub size, and density (Harland, 1993). Our one-off treatments were conservative; under more active pastoral management, follow-up treatment such as spot spraying with herbicide, active grazing with goats or burning with a hand-held burner would be applied a few years after any signs of shrub regrowth following ploughing (Vitelli and Madigan, 2004; Noble et al., 2005). Ploughed treatments such as ours might have even been re-ploughed, depending on the success of the original treatment, resulting in further surface destabilisation and removal of C.

Removal of domestic and feral herbivores for two decades coupled with no soil disturbance produced the greatest C accumulation benefits, consistent with observations from other exclosure studies in eastern Australian woodlands (Witt et al., 2011). Our results suggests a net C accretion in the order of 6.5 Mg ha^{-1} of total C when management changes from a conventional pastoral system to one based on conservation with no active soil disturbance (Conventional Conservation), almost entirely through increasing belowground C (Figure 2A). While we have no data on annual changes over the past two decades, this potentially greater C pool represents a net financial benefit of about $\$A 548 \text{ ha}^{-1}$ over that time ($\$A 27.40 \text{ ha}^{-1} \text{ yr}^{-1}$), based on the Australian Government's current price for carbon of $\$A 23 \text{ Mg}^{-1}$ of CO_2 equivalents ($=\$A 84.27 \text{ Mg}^{-1}$ of C; Australian Government, 2012; Dean, 2011). Thus, land-based C sequestration may become a profitable alternative to offset emissions from pastoral and agricultural areas as the price of C increases and there is greater participation in the C trading market (Cowie et al., 2012). Methods to maintain long-term SOC may vary in different pastoral or agricultural settings (e.g., afforestation and reforestation, management of crop residues, grazing land management, forest management, and revegetation; Harper et al. 2007). However, the value of woody encroachment as a revegetation technique and for enhancing C is more viable as it is less likely to be affected by drought than changes in the more ephemeral vegetative that might be altered by grazing.

In contrast, pastoralists would earn about \$A 66 to \$A 470 ha⁻¹ over a period of 20 years from livestock grazing alone. This assumes a carrying capacity of between 0.07 sheep ha⁻¹ (in dry seasons) to 0.50 sheep ha⁻¹ (in wet seasons; Robson, 1995) and gross margins of \$A 47 sheep⁻¹ year⁻¹ (in 2010 Khairo and Hacker, 2011). In addition to sheep grazing, pastoralists could earn an additional benefit, as much as \$A 38 ha⁻¹ over the same period of time, from running cattle (assuming an average carrying capacity of 0.004 cows ha⁻¹), whose gross margin is higher than that of sheep (\$A 454 cow⁻¹ year⁻¹ in 2010; Khairo and Hacker, 2011). However, the likelihood of experiencing wet seasons is likely to decline given current projections of increasing numbers of low-rainfall years (Appendix Fig. 2) and an increase in the frequency of droughts (Dai, 2011). Thus, the pastoral value of any increases in herbaceous biomass following ploughing is also likely to decline.

Conclusions

Our data suggest that the profits derived from C farming (\$A 27.40 ha⁻¹ yr⁻¹) are comparable to those from grazing (\$A 23.50 ha⁻¹ yr⁻¹; assuming a run of wet seasons). However, our study is based on the first two decades after ploughing when the greatest increase in aboveground C is expected due to re-sprouting and germinating shrubs. Responses in the following decades are likely to be substantially less, as increases in above- and belowground C stabilise. Similarly, the extent to which C farming is more profitable than grazing will depend on many things, including the relative distribution of wet and dry periods. For example, while the best possible scenario is two decades of above-average rainfall (\$A 23.50 ha⁻¹ yr⁻¹), a more typical scenario involving an even distribution of wet and dry periods would result in profits from grazing of only \$A 13.40 ha⁻¹ yr⁻¹.

Notwithstanding the apparent favourability of C farming over grazing, many uncertainties are likely to influence profitability, and therefore the uptake of C farming by the pastoral community. These include a changing price on C, the costs associated with destocking (e.g., fencing or control of feral animals), obligations for long-term C stock maintenance (Parliament of the Commonwealth of Australia, 2011) and

development of more precise methods for assessing C, particularly belowground C, which take into account its spatial and temporal variability.

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Table 1. Summary of the four grazing by ploughing combinations and their relative extent in eastern Australia (derived from Daryanto and Eldridge, 2010).

Scenario	Description	Extent	Disturbance intensity
Conventional conservation	Historically grazed, then ungrazed for 20 years prior to sampling	Localized (<10% of landholders)	Low
Active conservation	Historically grazed, one-off ploughing, then ungrazed for 20 years prior to sampling	Very uncommon (<1% of landholders)	Moderate
Conventional pastoral	Historically and continuously grazed for 20 years prior to sampling	Widespread (>50% of landholders)	Moderate
Active pastoral	Historically grazed, followed by a one-off ploughing, then continued to be grazed for 20 years prior to sampling	Very common (25–50% of landholders)	High

Table 2. Mean (\pm SE) of cover (%) of the six landscape elements under the four different management treatments. Significant differences in cover of landscape elements among treatments at $P < 0.05$ are denoted by different letter superscripts. Significant differences were apparent only for N-fixing trees.

Landscape element	Conventional conservation		Active conservation		Conventional pastoral		Active pastoral	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Interspace	65.2	5.0	62.9	2.1	69.4	3.2	72.2	3.2
Coarse woody debris	6.0	2.2	4.6	1.7	6.7	3.0	5.0	1.6
Inverted-cone shrub	12.0	4.6	15.5	4.0	13.4	6.9	11.0	2.8
Hemispherical shrub	8.0	2.9	4.4	1.5	6.5	5.0	6.0	3.7
N-fixing tree	6.6 ^{ab}	1.4	8.9 ^b	3.2	1.5 ^a	0.3	2.8 ^a	1.6
Non N-fixing tree	2.3	0.3	3.7	0.7	3.0	1.2	1.2	0.4

Table 3. Mean (\pm SE) of %SOC, soil %N, C:N ratio, and bulk density averaged across soil depth and the four land management treatments for soil under different landscape elements. SE = standard error of the mean. Different superscripts indicate a significant difference in values among different landscape elements at $P < 0.05$.

Attribute	Interspace		CWD mound		Inverted cone-shaped shrub		Hemispherical shrub		N-fixing tree		Non N-fixing tree	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Soil organic C (%)	0.32 ^a	0.03	0.59 ^b	0.06	0.52 ^b	0.32	0.52 ^b	0.05	0.63 ^b	0.06	0.78 ^c	0.96
Soil N (%)	0.038 ^a	0.002	0.049 ^b	0.004	0.050 ^b	0.002	0.050 ^b	0.003	0.057 ^c	0.005	0.066 ^d	0.007
C:N ratio	8.38 ^a	0.50	12.04 ^c	0.66	10.22 ^b	0.38	10.19 ^b	0.73	10.63 ^b	0.55	11.33 ^{bc}	0.45
Bulk density (Mg m ⁻³)	1.77 ^a	0.04	1.68 ^{ab}	0.06	1.69 ^{ab}	0.05	1.64 ^b	0.04	1.63 ^b	0.04	1.60 ^b	0.06

Table 4. Mean (\pm SE) of bulk density, %SOC and SOC across the four land management treatments for soil under different landscape elements.

SE = standard error of the mean, I = interspaces, CW = coarse woody debris, SY = inverted-cone shrubs, SH = hemispherical shrubs, TN = N-fixing tree, TO = non N-fixing tree

Land- scape ele- ment	Conventional conservation						Active conservation						Conventional pastoral						Active pastoral					
	Bulk density		SOC (%)		SOC (Mg ha ⁻¹)		Bulk density		SOC (%)		SOC (Mg ha ⁻¹)		Bulk density		SOC (%)		SOC (Mg ha ⁻¹)		Bulk density		SOC (%)		SOC (Mg ha ⁻¹)	
	(Mg m ⁻³)						(Mg m ⁻³)						(Mg m ⁻³)						(Mg m ⁻³)					
	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE
0–5 cm																								
I	1.90	0.103	0.32	0.027	8.13	0.353	1.49	0.126	0.56	0.118	2.66	0.679	1.66	0.168	0.53	0.174	2.95	0.703	1.63	0.038	0.41	0.117	2.32	0.508
CW	1.85	0.077	0.73	0.113	1.44	0.444	1.34	0.117	0.85	0.127	0.26	0.099	1.26	0.193	1.17	0.143	0.44	0.138	1.65	0.214	0.85	0.221	0.30	0.066
SY	1.46	0.063	0.84	0.122	3.33	1.293	1.48	0.036	0.69	0.104	0.83	0.309	1.43	0.092	0.90	0.151	0.88	0.434	1.50	0.099	0.75	0.138	0.64	0.205
SH	1.70	0.199	0.65	0.063	1.64	0.574	1.50	0.078	0.63	0.033	0.20	0.054	1.46	0.168	1.19	0.261	0.41	0.275	1.34	0.188	0.71	0.097	0.26	0.162
TN	1.53	0.008	0.56	0.055	1.16	0.302	1.44	0.152	1.05	0.157	0.63	0.203	1.48	0.090	1.17	0.257	0.13	0.029	1.51	0.133	1.23	0.149	0.25	0.123
TO	1.48	0.050	0.99	0.110	0.64	0.110	1.23	0.304	0.81	0.051	0.19	0.065	1.25	0.074	2.15	0.134	0.41	0.163	1.47	0.059	1.27	0.267	0.10	0.030
5–10 cm																								
I	1.94	0.025	0.27	0.030	1.67	0.094	1.98	0.284	0.52	0.090	3.11	0.751	1.82	0.207	0.33	0.056	2.12	0.307	1.79	0.010	0.30	0.066	1.86	0.230
CW	1.93	0.133	0.49	0.051	0.30	0.096	1.97	0.168	0.59	0.118	0.28	0.127	1.44	0.089	0.89	0.188	0.40	0.183	1.72	0.076	0.58	0.161	0.21	0.031
SY	1.89	0.119	0.68	0.089	0.80	0.365	1.94	0.147	0.49	0.042	0.76	0.240	1.82	0.210	0.60	0.079	0.73	0.357	1.68	0.152	0.47	0.047	0.43	0.113

SH	1.75	0.119	0.41	0.064	0.34	0.130	1.64	0.117	0.48	0.013	0.17	0.046	1.95	0.198	0.63	0.106	0.35	0.143	1.71	0.038	0.46	0.106	0.22	0.105
TN	1.92	0.101	0.35	0.039	0.25	0.057	1.50	0.222	0.83	0.165	0.46	0.127	1.63	0.060	0.66	0.145	0.08	0.020	1.66	0.219	0.79	0.056	0.17	0.087
TO	1.73	0.079	0.67	0.058	0.13	0.024	1.53	0.342	0.56	0.059	0.16	0.044	1.61	0.105	1.16	0.177	0.31	0.120	1.78	0.034	0.79	0.182	0.08	0.027
10–20 cm																								
I	1.83	0.069	0.20	0.010	2.48	0.184	1.73	0.066	0.31	0.058	3.57	0.644	1.71	0.097	0.30	0.032	3.46	0.304	1.73	0.142	0.25	0.035	2.94	0.198
CW	1.93	0.100	0.41	0.066	0.44	0.143	1.71	0.170	0.45	0.106	0.67	0.168	1.60	0.227	0.59	0.106	0.53	0.201	1.52	0.144	0.39	0.028	0.28	0.077
SY	1.74	0.177	0.47	0.045	1.01	0.449	1.65	0.175	0.36	0.018	1.03	0.417	1.64	0.165	0.42	0.087	0.92	0.461	1.64	0.076	0.32	0.021	0.60	0.153
SH	1.64	0.047	0.29	0.024	0.45	0.154	1.65	0.164	0.33	0.034	0.24	0.078	1.72	0.077	0.42	0.074	0.38	0.258	1.53	0.107	0.35	0.047	0.28	0.151
TN	1.72	0.083	0.32	0.018	0.34	0.101	1.60	0.057	0.52	0.113	0.76	0.317	1.58	0.054	0.46	0.121	0.11	0.030	1.62	0.113	0.52	0.048	0.25	0.160
TO	1.95	0.167	0.42	0.029	0.20	0.032	1.41	0.334	0.37	0.031	0.19	0.059	1.71	0.076	0.86	0.177	0.41	0.131	1.59	0.081	0.46	0.102	0.08	0.023
20–30 cm																								
I	1.68	0.064	0.18	0.011	1.98	0.146	1.74	0.044	0.25	0.049	2.70	0.475	1.77	0.060	0.29	0.027	3.67	0.574	1.98	0.293	0.25	0.021	3.27	0.325
CW	1.74	0.139	0.32	0.039	0.32	0.104	1.68	0.022	0.38	0.084	0.30	0.138	1.87	0.182	0.51	0.096	0.67	0.363	1.68	0.085	0.32	0.021	0.26	0.082
SY	1.81	0.225	0.38	0.012	0.74	0.189	1.66	0.063	0.33	0.018	0.88	0.291	1.92	0.160	0.38	0.029	0.87	0.384	1.74	0.173	0.27	0.027	0.53	0.176
SH	1.43	0.121	0.56	0.288	0.30	0.076	1.68	0.070	0.27	0.034	0.20	0.083	1.68	0.051	0.42	0.070	0.34	0.201	1.90	0.237	0.52	0.282	0.27	0.133
TN	1.67	0.064	0.24	0.020	0.27	0.063	1.70	0.070	0.43	0.100	0.62	0.268	1.63	0.070	0.42	0.092	0.10	0.021	1.88	0.301	0.43	0.020	0.19	0.092
TO	1.57	0.048	0.36	0.029	0.13	0.026	1.77	0.035	0.29	0.007	0.19	0.026	1.81	0.076	0.87	0.115	0.40	0.117	1.75	0.197	0.39	0.065	0.07	0.019

Table 5. Mean (\pm SE) of soil %N and soil N across the four land management treatments for soil under different landscape elements. SE = standard error of the mean, I = interspaces, CW = coarse woody debris, SY = inverted-cone shrubs, SH = hemispherical shrubs, TN = N-fixing tree, TO = non N-fixing tree

Land– scape element	Conventional conservation				Active conservation				Conventional pastoral				Active pastoral			
	Soil N (%)		Soil N (kg ha ⁻¹)		Soil N (%)		Soil N (kg ha ⁻¹)		Soil N (%)		Soil N (kg ha ⁻¹)		Soil N (%)		Soil N (kg ha ⁻¹)	
	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE	χ	SE
0–5 cm																
I	0.04	0.002	257.48	16.070	0.05	0.007	247.41	31.208	0.06	0.010	324.46	68.890	0.04	0.009	247.52	30.903
CW	0.06	0.006	29.53	8.519	0.07	0.006	21.52	7.628	0.09	0.014	39.77	17.724	0.06	0.004	23.00	7.510
SY	0.08	0.012	73.45	29.174	0.06	0.009	72.19	26.867	0.08	0.011	76.64	33.406	0.06	0.010	47.45	14.648
SH	0.06	0.003	41.28	14.631	0.06	0.006	18.62	4.993	0.10	0.013	47.94	37.163	0.06	0.008	23.14	15.611
TN	0.05	0.005	25.68	4.900	0.08	0.011	50.48	16.395	0.10	0.016	10.93	1.342	0.10	0.009	20.39	10.609
TO	0.08	0.012	14.47	2.252	0.07	0.003	15.97	5.464	0.16	0.016	33.53	14.965	0.10	0.020	7.65	2.070
5–10 cm																
I	0.03	0.002	227.80	8.377	0.04	0.004	266.55	43.809	0.04	0.006	312.86	128.435	0.04	0.005	227.22	5.400

CW	0.05	0.004	28.31	9.209	0.04	0.006	21.80	9.328	0.08	0.025	34.90	19.942	0.04	0.002	17.95	2.274
SY	0.06	0.007	70.44	32.210	0.05	0.006	72.96	26.496	0.06	0.003	62.25	29.266	0.04	0.003	36.21	8.234
SH	0.05	0.004	29.51	9.008	0.04	0.020	15.21	4.441	0.06	0.005	48.38	40.295	0.04	0.004	22.67	10.165
TN	0.04	0.003	25.60	5.142	0.06	0.016	35.07	9.064	0.06	0.007	7.54	0.940	0.07	0.006	16.48	8.959
TO	0.06	0.005	11.37	0.841	0.05	0.002	13.80	4.073	0.09	0.017	26.60	10.713	0.07	0.011	6.33	1.968

10–20 cm

I	0.03	0.003	401.79	22.162	0.03	0.001	380.63	14.569	0.03	0.003	397.54	67.657	0.03	0.004	420.90	20.871
CW	0.04	0.003	51.40	19.461	0.04	0.006	41.36	20.948	0.06	0.012	50.24	17.549	0.03	0.001	24.36	9.061
SY	0.05	0.002	97.69	38.801	0.04	0.006	96.96	36.663	0.05	0.006	88.36	40.417	0.03	0.001	59.26	14.233
SH	0.04	0.001	43.61	17.752	0.04	0.004	27.32	9.112	0.05	0.003	67.49	25.515	0.04	0.002	33.94	21.816
TN	0.04	0.001	39.43	9.891	0.05	0.009	66.69	26.171	0.05	0.010	9.98	2.240	0.05	0.003	25.07	16.080
TO	0.04	0.003	19.00	0.416	0.04	0.002	19.87	6.534	0.07	0.002	40.73	16.213	0.04	0.005	7.28	1.786

20–30 cm

I	0.03	0.002	376.41	20.871	0.04	0.003	399.14	33.332	0.04	0.008	501.19	151.734	0.04	0.001	531.04	111.445
CW	0.04	0.002	42.01	15.328	0.04	0.004	37.82	20.789	0.04	0.010	55.70	23.641	0.03	0.001	25.53	7.666

SY	0.04	0.004	80.33	23.410	0.04	0.002	96.08	28.366	0.06	0.008	87.65	35.298	0.03	0.001	59.92	15.506
SH	0.04	0.003	34.14	8.593	0.03	0.005	27.42	10.624	0.05	0.006	69.38	58.681	0.05	0.020	20.92	20.920
TN	0.03	0.004	37.28	7.080	0.04	0.006	60.86	23.224	0.05	0.010	11.90	0.791	0.05	0.002	20.27	9.083
TO	0.04	0.005	13.60	1.709	0.04	0.003	22.40	1.609	0.07	0.005	42.67	17.477	0.04	0.005	6.90	1.916

Table 6. Mean (\pm SE) of aboveground C (t ha^{-1}) of the landscape elements under the four different management treatments. Interspaces were not included as all biomass was herbaceous and assessed at the plot level. There were no differences in mass of C of any landscape element among treatments at $P < 0.05$.

Landscape element	Conventional conservation		Active conservation		Conventional pastoral		Active pastoral	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coarse woody debris	0.82	0.154	0.56	0.071	0.97	0.361	1.21	0.213
Inverted cone shrub	2.67	0.291	7.60	2.440	3.17	1.360	10.06	8.050
Hemispherical shrub	0.30	0.022	0.14	0.099	0.26	0.142	0.28	0.117
N-fixing tree	3.31	1.500	6.07	2.780	0.68	0.157	4.68	4.030
Non N-fixing tree	0.31	0.004	0.66	0.004	1.45	0.800	0.84	0.197

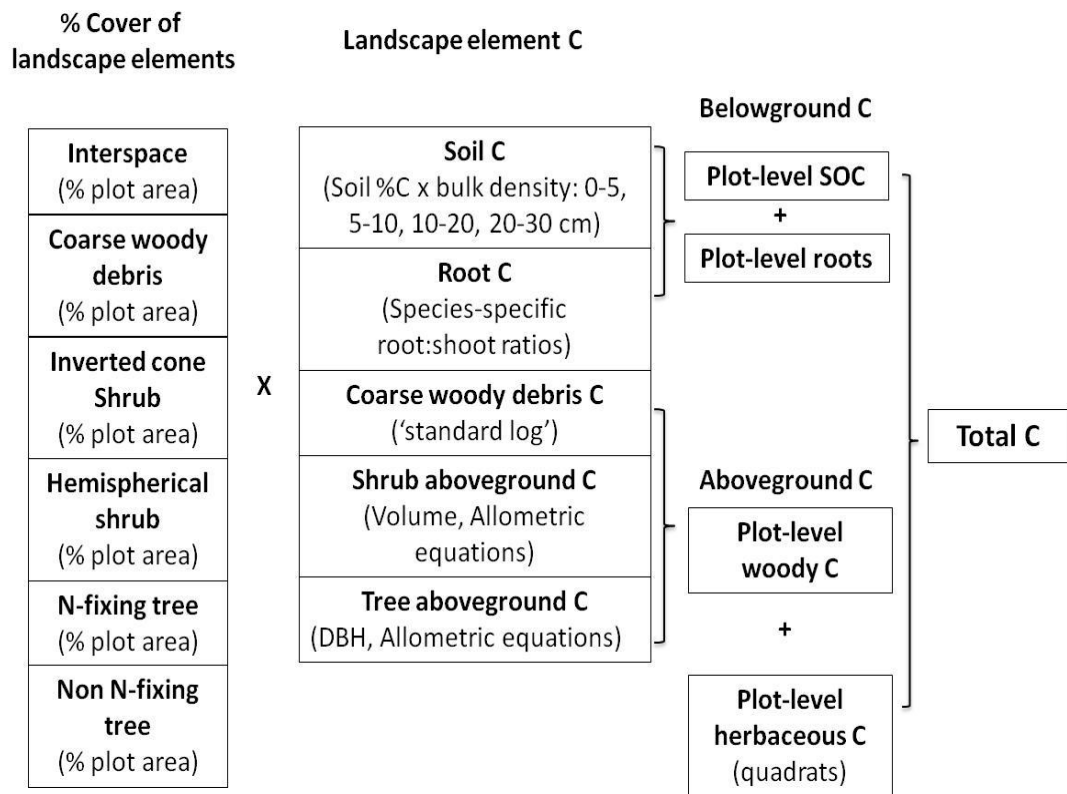


Fig. 1. Summary of the components and methods used for constructing C pools. Plot-level C pools were calculated as the sum of all measured aboveground and belowground components. Except for herbaceous aboveground C, landscape element C pools were multiplied by the corresponding percent area of each landscape element to obtain plot-level C pools for each management treatment.

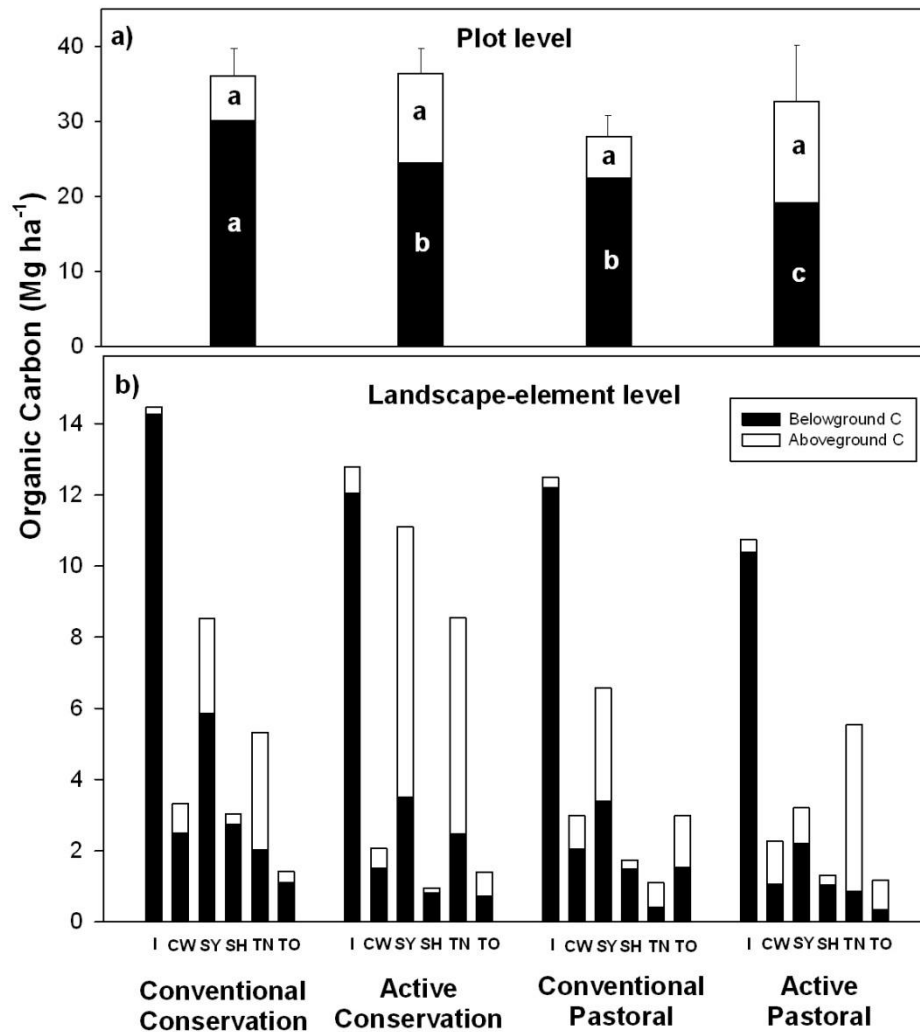
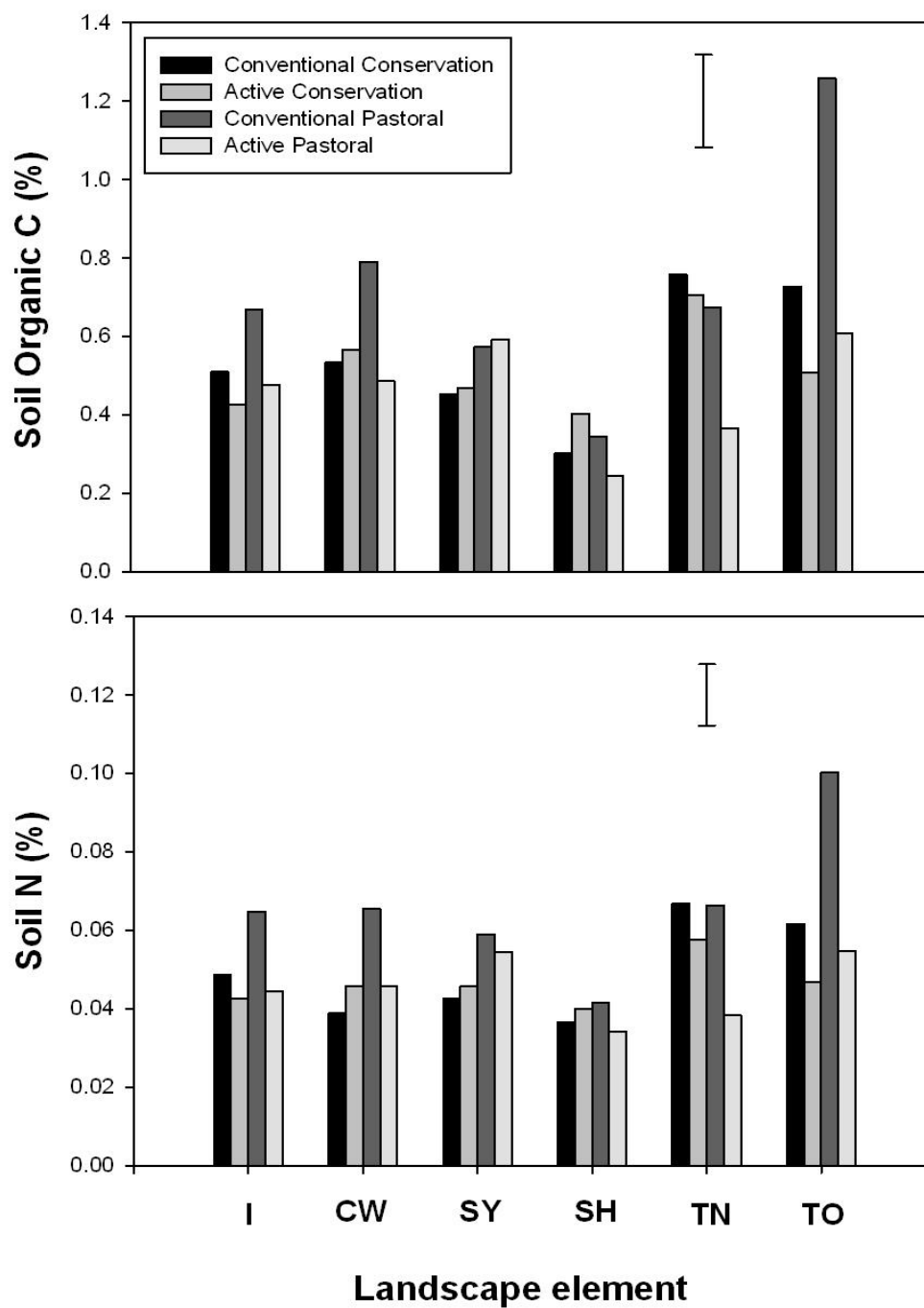
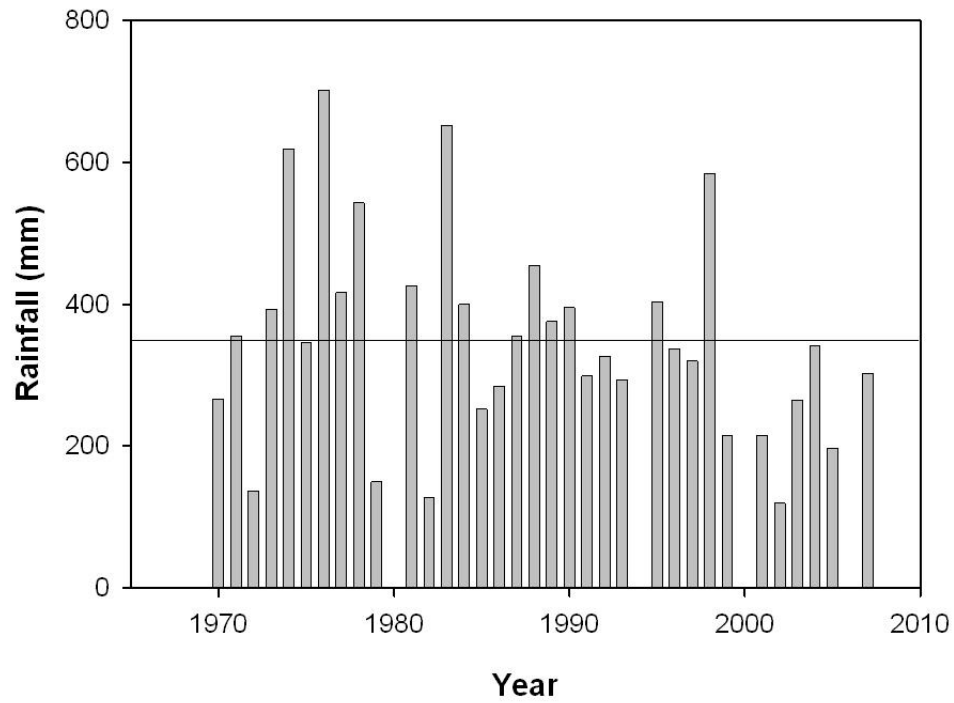


Fig. 2. (a) Mean mass of aboveground, belowground (soil + root), and mean mass (\pm SE) of total (aboveground + belowground) C (t ha^{-1}) for different land management treatments and (b) Mean mass of belowground and aboveground C, subdivided into landscape elements within management treatments. Values represent the product of aerial cover of each landscape element and the area-based C concentration. Landscape elements are abbreviated as I = interspace, CW = coarse woody debris, SY = inverted-cone shrub, SH = hemispherical shrub, TN = N-fixing tree, TO = Non N-fixing tree. Different letters indicate a significant difference at $P < 0.05$. Letters in Fig.1A indicate that difference is only significant for belowground C, but not aboveground and total C.



Appendix Fig. 1. Response of %SOC and soil %N to land management treatments in the different landscape elements. Error bars indicate the 5% LSD for the landscape element by management treatment interaction. Data are the integrated by depth and represent the mean 0–30 cm values. I = interspace, CW = coarse woody debris mound, SY = inverted-cone shrub, SH = hemispherical shrub, TN = N-fixing tree, TO = Non N-fixing tree. Note different scale on y-axis.



Appendix Fig. 2. Annual Rainfall at Fords Bridge ($29^{\circ}75'S$, $145^{\circ}43'E$), the closest weather station (approximately 50 km) to Wapweelah ($29^{\circ}16'S$, $145^{\circ}26'E$), over the period of 1970 to 2010. Solid line indicates mean annual rainfall.

Conclusion

This thesis has examined the ecological values of shrubland, and the consequences of shrub removal by mechanical methods (i.e., ploughing) on ecosystem properties such as vegetation, the composition of disturbances created by small animals, soil nutrient accumulation, water infiltration, and soil carbon (C) and nitrogen (N) in the presence and absence of grazing. In contrast to the commonly held perspective that shrublands are analogous to unproductive systems, this shrub-encroached Australian woodland does not represent a degraded landscape with dysfunctional ecosystem processes. Rather, the presence of shrubs has altered soil chemical (e.g., increasing labile C and soil N) and physical properties (e.g., increasing soil infiltrability and reducing bulk density), and provided habitat for plants and animals. Ploughing, which aims to remove these shrubs, has failed to reduce long-term shrub density (i.e., 20 years after ploughing). Rather, it resulted in substantial soil disturbance, particularly when under grazing, leading to insufficient time for the surface to recover. Consequently, I maintain that mechanical shrub removal is an inappropriate land management strategy to apply to this semi-arid system dominated by shrubs.

Key findings from this thesis

This study has shown that the responses of vegetation and soil surfaces to ploughing were generally negative, particularly under continuous grazing regime. More importantly, ploughing failed to control shrub encroachment as there was no significant difference in shrub density between areas where shrubs were treated and the control sites 20 years after shrub removal. The application of a one-off shrub removal to a diverse shrub community with different regenerative strategies resulted in a range of responses to ploughing so that species regenerating from root suckers were advantaged and increased in density. Similarly, continuous grazing selected for unpalatable species over more palatable ones, and thus the effects of ploughing and grazing were species-specific (Chapter 2).

Ploughed sites also had significantly fewer resource-accumulating patches and less biological soil crust cover, indicating the slow response of both patches and crusts to recovery even in the absence of grazing (Chapter 2). This results implied that there were

potential negative feedback processes arising from shrub removal as positive association occurred between shrub cover and the density of disturbances created by small animals (Chapter 3). While a dense and diverse shrubland community might provide a greater range of niches and habitats for animals, a homogeneous shrubland or the presence of large areas of shrub-free interspaces could reduce the value of shrublands as potential hot-spots for biological diversity and animal activities.

The tendency of shrubs to accumulate soil nutrients increased with shrub age and size, with more mature shrubs acting as stronger nutrient pumps because of their well-developed canopy cover and branching system. Mature shrubs also generate more positive feedbacks from biological activities of higher trophic levels due to their diverse resources (e.g., perch effect; Pausas et al., 2006). Since most of the accumulated nutrients are found in the surface soil layers (e.g., Wang et al., 2007; Daryanto et al., 2012), maintaining shrubs and to a lesser extent, log or debris mounds, is necessary to prevent erosion-induced soil loss by increasing sink:source ratio (Chapter 4).

While build-up of soil nutrients occurs with shrub development, removal of plant biomass through ploughing and grazing also affect the spatial patterning of soil resources. The presence of grazing reduced the autocorrelation range of shrubs, and with the addition of ploughing, they created a total destruction of biological crust cover. Consequently, changes in the spatial patterns of soil N under grazing were more likely caused by inputs of animal dung rather than biological soil crusts. Similarly, the effects of shrub–litter–nutrient spatial relationships were weaker with disturbance. When there was a well-defined pattern in soil labile C that was related to the distribution of both shrubs and litter cover in the undisturbed (i.e., unploughed–ungrazed) site, the autocorrelation range of soil labile C was less related to litter cover under grazing due to scattering effect by herbivores (Chapter 5).

In addition, ploughing and grazing changed in the spatial patterns of soil infiltrability, bulk density and bare soil cover. The autocorrelation range for semivariograms of soil infiltrability at the undisturbed site was larger than the average diameter of shrubs, indicating that infiltration could occur beyond the shrub canopy. In contrast, areas with high soil infiltrability were localised around the shrubs in the disturbed (i.e., unploughed–grazed and ploughed–grazed) sites. This trend indicated that resource-rich

shrub patches are likely to become more developed with increasing disturbance, further reinforcing the growth and persistence of shrubs at the expense of the bare interspaces (Chapter 6).

Finally, shrub-encroached lands provided other ecological, and to a lesser extent, economic values in relation to C cycling and sequestration. My study showed that a 20-year rest from grazing significantly increased the amount of soil organic carbon (SOC), mostly due to accumulation under mature shrubs. Ploughing, however, resulted in a substantial decline in SOC, but shrub regeneration partly compensated for this loss with increases in aboveground C. In the absence of grazing and ploughing, shrublands accumulated up to $\sim 6.5 \text{ t C ha}^{-1}$, suggesting that the value of shrublands for sequestering C was equivalent to that under grazing, given the current price of C (Chapter 7). With projected changes in climate and continuous positive feedbacks (e.g., vegetation–erosion feedback; D’Odorico et al., 2012), this alternative strategy to manage shrublands is worth considering, although some uncertainties (e.g., C policy) which influence profitability may hinder the implementation of C farming in shrub-encroached lands.

Shrubs maintain ecosystem productivity

In contrast to the commonly held view, we found that shrubs maintained ecosystem productivity by acting as focal points for water infiltration. Water is a key determinant of productivity in semi-arid systems (Le Houérou et al., 1988; Wang et al., 2012), and many studies (e.g., Bhark and Small, 2003; Stavi et al., 2008; Muñoz-Robles et al., 2011) have shown that infiltration is generally greater under the canopies of perennial plants than in their interspaces. The importance of shrubs as foci of infiltration increases with disturbance, where the vegetation–erosion feedback prevents grass regeneration in the interspaces (D’Odorico et al., 2012). Due to grazing-induced soil compaction, infiltration occurs in limited areas with low bulk density around the shrubs.

The same feedback that has been commonly observed in continuously grazed landscapes leads to soil nutrient and soil seed bank depletion (Kinloch and Friedel, 2005; Tessema et al., 2012), and thus reduces the likelihood the reestablishment of grasses after shrub encroachment. Shrubs are able to tolerate low levels of nutrients and

therefore have an advantage where competition from grasses is reduced. The proliferation of shrubs is strengthened by climate (e.g., fluctuating rainfall and increasing CO₂ level; Polley et al., 1997; Dai, 2011), reduction in fire frequency (D’Odorico et al., 2012). Thus shrubs behave as pioneering plants in environments that are already degraded rather than being the cause of such degradation. This is because they have the ability to withstand drought, fire, salinity, and other extreme environmental conditions (Booth et al., 1996).

Shrubs also act as nurse plants, facilitating the growth and survival of understorey protégé species (Howard et al., 2012). They therefore have an important role in the restoration of ecosystem functioning. Many studies (e.g., Padilla and Pugnaire, 2006; Maestre et al., 2009; Howard et al., 2012) have shown that shrubs ameliorate harsh arid conditions by improving soil moisture level and thus support the growth of understorey species. Fertile patches developed by shrubs also provide a range of ecosystem functions such as nutrient and water cycling, C production and the provision of habitat for animals. Maintaining large areas of the world’s shrublands could also become the ‘green solution’ for large-scale removal of greenhouse gasses and the added benefit of restoring degraded landscapes (Lal, 2009).

Land management in semi–arid grazed landscapes

While the build-up of fertile patches around shrub hummocks could take a relatively long–time to develop, they can easily be lost by wind or water erosion once the shrubs have been removed (Okin et al. 2006). Such loss occurs because there are no barriers to reduce wind velocity and consequently erosivity, in addition to the lack of sediment deposition around the shrubs (Wolfe and Nickling, 1993). As shrubs occupy a significant proportion of the landscape and contribute greatly to resource capture and retention, removal of shrubs, and to a lesser extent, biological soil crusts during mechanical shrub removal is likely to result in substantial effects on surface stability (Aronson et al., 1993; Shachak et al., 1998; Merino-Martín et al., 2012). This breakdown in surface stability, particularly due to mechanical disturbance, has been shown to occur relatively rapidly after removal (Eldridge and Robson, 1997) and its extent will influence water infiltration, structural, and nutrient loss in the soil, and eventually subsequent plant establishment.

In dense shrublands, the aim of ploughing is to remove shrubs and to allow the recruitment of grasses. The extent to which the desired plant community establishes will depend on post-ploughing levels of grazing and environmental conditions (Sheley et al., 1996). Managing rangelands following shrub removal requires a thorough understanding of the factors likely to influence the ensuing vegetation community. These factors include: (i) management objectives, (ii) characteristics of target species (e.g., density, height, and sprouting ability), (iii) characteristics of secondary species (i.e., the species which will re-grow after disturbance), (iv) topography and terrain, (v) soil characteristics, (vi) site potential and (vii) follow-up treatments (Valentine, 1989). Land managers, however, often fail to sustain long-term management of desired plant communities by failing to control stocking rates; mainly because they need to recoup the cost of shrub removal by continuing to graze (Cox et al., 1984). At the same time, environmental factors such as post-treatment rainfall and temperature often limit the success of many land management programs (Herrick et al., 2006).

Lessons learned from this research

This study showed that a one-off mechanical shrub removal was an inappropriate land management practice to be applied in the studied ecosystem as recovery was generally protracted and there were substantial negative effects on the soil and vegetation. Mechanical removal is also not a practical management strategy to return shrubland to its original grassland condition, particularly in the presence of continuous grazing. Prior to European settlement, sufficient grass cover provided fuel for natural fires. As the connectivity between grasses is reduced by grazing, the bare areas coalesce and result in a discontinuity of fuel loads. At the same time, bare ground results in wind and water erosion and negatively feeds back upon grass establishment (D'Odorico et al., 2012). In contrast, fertile patches and facilitation by shrubs provide sites for improved plant germination, allowing recovery of the degraded landscape (Padilla and Pugnaire, 2006; Howard et al., 2012).

A radical change in perspective is therefore needed in order to manage shrub-encroached land. Alternative enterprises could include, but are not limited to, ecotourism, nature conservation, recreation, goat harvesting and C farming. Climate-friendly approaches such as rotational, rather than continuous grazing and using the land

for C farming during the resting period could offset any financial losses from grazing (White, 2011). Rotational grazing for example, is a climate-friendly approach because land managers can adjust the number or types of stock according to the seasons (e.g., higher number of stock during La Niña seasons and lower number during El Niño), or allow some areas of the property to be released from grazing pressure when there is adequate rainfall to promote recovery. These strategies that involve conservation measures, however, require full support and subsidy from the government since the price of commodity and C tends to fluctuate, thus changing the profitability of C farming accordingly. Moreover, the challenging regulation (i.e., 100 years of continuous C pool increase; Parliament of the Commonwealth of Australia, 2011) may hinder the likelihood of landholders to maintain shrublands as a C farms since variation in climate (e.g., droughts) could generate a slow or even negative accrual of below- and aboveground C.

Future research directions: understanding the dynamics of shrublands

Shrub proliferation has affected the livelihood of millions of people due to its effects on the profitability of grazing enterprises. Since shrublands are likely to maintain their domination at least in the near future, it is necessary to understand their dynamics (e.g., growth, C, and N fluxes) particularly under a scenario of a hotter and drier climate. This study was undertaken at only one point in time, 20 years after removal of shrubs, so it is necessarily limited in its findings. Longer-term studies that integrate shrubs response to La Niña and El Niño cycles with changes in ecosystem structure and functioning would be a high priority. This study was also limited to one ecosystem and soil type and therefore there would be major differences in response across different shrub biomes, likely affecting the response of shrub and their removal on soils and vegetation, and particularly the amount of C sequestered and thus the viability of C farming as an alternative land use. Different ecological response may occur under less conservative management practices that involve herbicides and prescribed fire following disturbance (e.g., Tongway and Hodgkinson, 1992; Vitelli and Madigan, 2004; Noble et al., 2005), particularly if C farming is a management goal.

While the causes of shrub encroachment have been well-documented in many studies, less is known about the consequences of shrub encroachment and the interactions

between shrubs and other organisms. Understanding the complex interactions among different shrubland- and grassland-obligate vertebrates and invertebrates, soil biota, such as biological soil crusts, and plants should be a priority before governments promote shrub removal as a method for enhancing ecosystem structure and function.

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