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Fallen logs as sources of patchiness in chenopod shrublands of South Australia

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ABSTRACT

While numerous studies focus on heterogeneity created by living plants and animal diggings in arid lands, little information exists on the pattern and role of heterogeneity created by large woody debris. We studied soil nutrient content, volumetric water content, and vegetation associated with the presence of logs in sites subject to different grazing intensity in a chenopod shrubland of South Australia. Soil volumetric water content was lower close to logs, and the soil there dried faster after rains. Organic carbon was higher, but available phosphorus was lower in soil associated with logs. We documented greater seedling emergence, species richness and diversity, and greater annual plant biomass next to logs. Our results were similar in the sites with high and low grazing pressure, the latter having higher numbers of seeds and species in the germinable soil seed bank. Logs in this system create patches that differ in properties from other patches in the system (i.e. those created by perennial plants, depressions, or diggings). Logs constitute a unique microenvironment which affects the plant community structure and may enhance the diversity of the system, and should be considered in management schemes.

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1. Introduction

The distribution of water, nutrients and seeds in arid land ecosystems is highly heterogeneous and this is reflected in small scale heterogeneity in the plant community structure and function (Tongway and Ludwig, 2005). These systems typically contain patches with high resource availability within a matrix of very low resource availability overall (Noy-Meir, 1973; 1981). Studies of the arid lands around the world have found fertile patches associated with animal diggings (James et al. 2009), succulent plants (Stock et al. 1999), shrubs (Facelli and Temby, 2002), long lived trees (Facelli and Brock, 2000) and fallen logs (Pettit and Naiman, 2005). The variety of systems included in these studies and the diversity of patchiness found indicate that resource heterogeneity is a universal characteristic of arid lands when they are highly functional. In addition, they are critical determinants of ecosystem functions, such as resource dynamics, productivity and diversity maintenance (Aguiar and Sala, 1999). However, specific details of the arrangement, distribution, size and longevity of patches depends on the

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intensity and rate of accretion processes occurring around different plant species and other patch-forming entities. The properties of patches may vary widely from system to system, and even within a system, and these changes should have functional importance. While in some patches accumulation of water, nutrients and seeds may be enhanced, in some arid systems the extent and intensity of these effects may vary for the different variables. This difference in patch composition may be a key determinant of the structure of arid land plant communities.

The presence of patchiness is central to plant community dynamics in arid lands. Seedling establishment and survival is usually poor in open spaces, while fertile areas associated with larger plants or micro depressions provide safe sites for seedling establishment (Maestre et al. 2003). The higher emergence rate in enriched patches is most likely due to a combination of the more favorable microclimate and soil conditions (Hastwell and Facelli, 2003), and to the higher resource and seed availability in these patches than in open areas (Facelli and Brock, 2000; Osem et al. 2007). However, just as resources accrete differently around different patches, the properties of patches also vary the size and composition of the seed bank. Specific characters of the various structures that create patches, such as mound heights and differences in branching structure, can affect the ability to trap both resources and seeds (De Soyza et al. 1997). Importantly, this patchiness is a dynamic property of the system.







Abbreviations: VWC, volumetric water content.

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Presently most arid lands are heavily degraded by high densities of introduced grazers (Dregne, 2002), and a prominent feature of this degradation is the destruction of spatial heterogeneity (Lin et al. 2010) through the disruption of transport and accumulation processes (Tongway and Ludwig, 2005). Grazing eliminates features of the landscape that retain water, nutrients and seeds (Emmerson et al. 2012; Landsberg et al. 2003), while erosion dissipates the resources accumulated in patches and lowers the number of fertile patches (Sparrow et al. 2003). In the absence of accumulation patches, or of features able to build them up, vegetation may not recover as soil seed reserves are severely compromised and safe sites scarce (Kinloch and Friedel, 2005b). Degradation by introduced grazers is a result of cumulative impacts of grazing on ecological processes and management by landowners can vary such impacts (Andrew, 1988). The reintroduction of structures such as logs or branches on the surface may mitigate these negative effects or even help the recovery of the system.

Dead plant material has indeed been used in arid landscapes as a tool for rehabilitation in both grazed and ungrazed areas. For example, piles of Mulga branches placed on bare slopes of New South Wales arid lands dramatically increased soil nutrients, and increased water infiltration ten-fold (Tongway and Ludwig, 1996). Plant number and biomass are also enhanced by the presence of logs and branches (Ludwig and Tongway, 1996; Tongway et al. 1989). However, the study of the ecological effects of fallen logs in Australian arid lands has thus far been limited to a few combinations of vegetation types and landscapes (Ludwig and Tongway, 1996; Tongway and Ludwig, 1996; Tongway et al. 1989). Different combinations of land features, vegetation structure and the size and shape of logs may result in very different outcomes. The mulga branches used by Tongway and Ludwig (1996) may have effects that depend on their typical size and branching patterns. Extending the study to other systems is then necessary to further develop this conceptual framework.

The objectives of this study were to establish how logs create spatial heterogeneity in grazed chenopod shrublands of South Australia. We concentrated on the differences in soil nutrients, soil water content, soil seed bank, and plant growth between microsites next to logs and nearby open spaces. We conducted the research in two sections of a single paddock subject to different grazing intensities. The specific questions we addressed were: a) are there any changes in the soil characters associated with the presence of logs?, b) are there any changes in soil seed bank, establishment and plant growth associated with the presence of logs?, c) are there any changes in seedling establishment and growth associated with the presence of logs introduced to open spaces over a short time period?, and d) if there are differences in those variables, are they affected by grazing intensity?

2. Materials and methods

2.1. Study site

Our study was conducted at Middleback Field Research Centre, 16 km North West from Whyalla, South Australia (32°57′S, 137°24′E). The climate of the area is arid, with average yearly rainfall around 250 mm. Interannual variability of rainfall is characteristic of our site, with records varying from 146.8 mm to 510.3 mm over the years. Total rainfall for 2010 was 345.8 mm, which is above average, but not atypical for this area. Rainfall is concentrated in the winter months (June–August) which drives the growth of a diverse annual plant community. The soils are predominantly brown calcareous earths with clay-loam texture, and calcium carbonate accumulated at variable depths. The pH is slightly alkaline, and nutrient availability is generally low (Crocker, 1946). The vegetation at the study site is open woodland dominated by *Acacia papyrocarpa* Benth. with chenopod understorey; *Atriplex vesicaria* Heward ex Benth., *Maireana pyramidata* (Benth.) Paul G. Wilson and *Maireana sedifolia* (F. Muell.) Paul G. Wilson dominate the understorey (Facelli and Brock, 2000). A large number of annual plant species, both native and introduced can be found, and the guild is presently dominated by *Carrichtera annua* (L. Aschers.), an introduced plant from the Mediterranean (Facelli et al. 2005). Fallen logs are abundantly scattered throughout the landscape.

2.2. Site selection

The Purpunda Paddock is extensively affected by sheep and feral rabbit grazing, with a strong grazing gradient radiating from a single watering point. The paddock is 1440 ha and has been continually stocked with approximately 250 sheep since 1966 (Heshmatti et al. 2002). The greatest degradation occurs within 300 m of the watering point, while less degradation is found 1000 m from the watering point, as sheep infrequently travel beyond this distance, and when they do, they are present at low densities. We selected this paddock due to the strong grazing gradient but otherwise homogeneous environment, as well as the abundance of fallen logs. Our study was conducted between 10 May 2010 and 3 Sep 2010, encompassing most of the growing season.

Existing fallen logs (pieces of wood, 3–5 m long and at least 20 cm diameter, henceforth referred to simply as "logs") were located in the paddock to assess their patch forming properties. Five logs were located in the field at 300 m and five at 1000 m from the watering point. We selected logs to be comparable: they had very simple structure, few or no branches and were intact or presented little or no sign of decay. As logs in a similar system are known to persist for at least 75 years (Sinclair, 2004), it is difficult to know their age, but as there presented little decay, it can be presumed that they are relatively young. The open space sites we chose were as close to each log as possible, but leaving a minimum 3 m distance from logs and away from any other living or dead plants.

2.3. Soil properties

To assess if the presence of logs modify soil properties we collected two soil samples (5 cm deep and 9 cm diameter) from the immediate vicinity of three of the logs and from their corresponding open space sites, at both distances from the watering point. As slope was negligible, the side of the log used was chosen at random. The two soil samples from each individual site were combined as a composite sample (1272 cm³ soil for each site) and sent to CSBP soil and plant laboratory (Western Australia) for analyses of soil organic carbon, total nitrogen, available phosphorus and available potassium.

We assessed soil water dynamics by measuring volumetric water content (VWC). We deployed Em5b^(R) data loggers with ECH2O EC-10 sensors (Decagon Devices, Washington USA) inserted into the ground to a depth of 10 cm (where most roots of annual plants grow (Harris and Facelli, 2003) in the immediate vicinity of both logs and at adjacent open space sites. Four log replicates and their adjacent open spaces were measured at both 300 m and 1000 m from the watering point. The data loggers measured VWC hourly over a period of 84 days, from 10 Jun until 31 Aug 2010. To compare microsites next to logs and open spaces we analyzed soil water content and the rate of water loss after two typical rainfall events; the first event occurred on 25 Jun 2010 with 7.8 mm of rain and drying for 14 days, the second event occurred on 19 Jul 2010 with 6.7 mm of rain and drying for 9 days. Data were analyzed using log transformed values to linearize the trend.

2.4. Soil seed bank

To determine if there was any difference between the soil seed bank close to the logs and in nearby open spaces, on 12 May 2010 we collected soil samples in the immediate vicinity of all five replicate logs and their adjacent open space sites, at both distances from the watering point. To cover some of the spatial variability in soil seed bank we collected three soil samples in the same way described above at each log and open space site. The three samples from each site were combined and thoroughly mixed. We assessed the germinable seed bank because the approach has the advantage of documenting the actual potential annual plant community, but not all seeds in the soil are quantified. We transported the soil samples to a glasshouse in Adelaide and filled three pots with the soil composites for each site. We repeated this for all five replicates of logs and adjacent open space sites, at both distances from the watering point, giving a total of 60 pots. We watered the pots regularly to maintain suitable germination conditions. Seedling emergence was counted every other day. Seedlings representing the various distinct species were removed, replanted individually and grown for identification. The experiment was concluded after 44 days, since by then little or no new seedling emergence occurred.

2.5. Seedling establishment and growth

To determine if any difference in soil properties associated with the presence of logs was biologically important, we assessed the growth of *C. annua* in soil collected close to logs and adjacent open space sites. After the completion of the soil seed bank study, we planted pre-germinated seeds of *C. annua* in the 60 pots of soil used for assessing soil seed bank. Survival of seedlings was recorded after a five week period, and the above ground biomass of the remaining seedlings was harvested, dried, and weighed.

To assess the effects of logs on seedling establishment and growth in the field, we established plots next to all ten logs and in adjacent open spaces. Each plot was 20×80 cm, with the longest side along the log, or randomly placed in adjacent open spaces. All plots were protected from sheep, kangaroo and rabbit grazing using chicken wire. After a period of four months we counted, harvested, and identified all seedlings. The above ground biomass was then dried and weighed.

We wanted to assess whether some of the effects of logs on plant emergence and growth resulted directly from their presence rather than from the long term changes they may produce in the soil conditions and the soil seed bank. To test this we introduced logs into open space sites on 12 May 2010. Three logs were introduced at 300 m and three at 1000 m from the watering point. All introduced logs were selected to have the same characteristics as pre-existing logs. On 1 Sep 2010 all seedlings within a 20 cm by 80 cm plot at the log were counted, harvested, and identified, and the same was done in a similar plot randomly placed 1 m away from the introduced log. We then dried and weighed the seedlings for above ground biomass.

2.6. Statistical analyses

We analyzed the data using JMP IN 4.0.3 and Graph Pad Prism 5.0.

3. Results

3.1. Soil properties

Organic carbon was higher in soil collected next to logs than from open space sites (Fig. 1a). Unexpectedly, available phosphorus was higher in soil collected from open spaces than from log sites (Fig. 1b). No differences were detected for total nitrogen or available potassium.

The soil water content over an 84 day period showed typical high peaks immediately after rainfall events followed by a drying of soil. Overall, and contrary to our expectation, the soil next to logs had consistently lower soil water content than soil from open spaces. After a rainfall event the soil at log sites dried faster than open space sites as indicated by the difference in the slopes of the log transformed data (Fig. 2). Interestingly, the variance around the mean VWC in soil next to logs was always larger than those from open spaces.

3.2. Soil seed bank

The number of seedlings emerged from the soil seed bank was determined by the combined effects of proximity to a log and the distance to the watering point. More seedlings emerged from the soil seed bank collected next to logs at 300 m than in the open (Fig. 3a). Soil from next to logs at 1000 m had greater emergence of seedlings than open spaces (Fig. 3b). Species richness was significantly greater from soil next to logs than from soil collected at adjacent open spaces at the 300 m distance (Fig. 3c). Species richness was also greater next to logs at the less degraded 1000 m site than the open spaces (Fig. 3d).

3.3. Seedling establishment and growth

In the glasshouse, seedlings of *C. annua* had much higher survival in soil from next to logs than from open spaces (Fig. 4a). Survival was also higher in soil collected 1000 m from the watering



Fig. 1. Soil properties of samples collected next to logs () and in nearby open spaces () for (a) organic carbon (p = 0.026), and (b) available phosphorus (p = 0.034) (bars indicate SD, nested ANOVA).



Fig. 2. Drying of soil after two major rainfall events (a) and (b) at log sites (\blacksquare) and open space sites (\bigcirc) (bars indicate SE, data transformed using \log_{10}). The slopes for both events are significantly different (ANCOVA and Johnson–Neyman procedure, p < 0.001).

point than from 300 m, from both logs and open space soil. For the surviving seedlings, biomass was greater for those growing in soil collected next to logs than from open spaces at 300 m (Fig. 4b), and greater next to logs at 1000 m (Fig. 4c).

3.4. Annual plant community next to logs in the field

The biomass of plants that established next to logs was significantly greater than from open space sites (Fig. 5a). No difference was detected for seedling emergence, however, when data was reanalyzed excluding *Crassula colorata* (which due to the sheer number of small individuals it was deemed to overwhelm the outcome), the number of emerged seedlings was significantly greater at logs sites than open space sites (Fig. 5b). Species richness was significantly greater next to logs than in open space sites (Fig. 5c), and species diversity, using Shannon's diversity index, had the same pattern, with significantly more diversity next to logs than in the open (Fig. 5d).

3.5. Annual plant community next to introduced logs

There was no difference detected for biomass, species richness or emergence of seedlings in plots next to introduced logs. However, Shannon-Weiner species diversity was significantly higher next to introduced logs than adjacent open space sites (Fig. 6). Given the very low replication, and the consequent low power of this part of the study, this issue deserves further attention.

4. Discussion

Our data indicates that logs create unique sites for seedling establishment and growth in the chenopod shrublands of South



Fig. 3. Emerged seedlings from soil samples collected next to logs (\square) and from nearby open space sites (\square) at 44 days from initial watering of soil for (a) emergence number at 300 m (b) emergence number at 1000 m (nested ANOVA, site p < 0.001, distance (site) p = 0.043) (c) species richness at 300 m and (d) species richness at 1000 m (nested ANOVA, site p < 0.001, distance (site) p = 0.043) (c) species richness at 300 m and (d) species richness at 1000 m (nested ANOVA, site p < 0.001, distance (site) p = 0.043) (c) species richness at 300 m and (d) species richness at 1000 m (nested ANOVA, site p < 0.001, distance (site) p = 0.043) (c) species richness at 300 m and (d) species richness at 1000 m (nested ANOVA, site p < 0.001, distance (site) p = 0.045) (bars indicate SD).



Fig. 4. Seedlings of *C. annua* in soil collected close to logs (\blacksquare) and from open spaces (\blacksquare) after 5 weeks in the glasshouse (a) percentage survival of seedlings (b) biomass at 300 m and (c) biomass at 1000 m (nested ANOVA, site *p* < 0.001, distance (site) *p* = 0.007) (bars indicate SD).



Fig. 5. Seedlings in the field growing next to logs (\blacksquare) and in open spaces (\blacksquare) for (a) biomass (p = 0.026) (b) seedling number excluding *Crassula colorata* (p < 0.001) (c) species richness (p = 0.003) and (d) species diversity (p = 0.017) (bars indicated SD, nested ANOVA).



Fig. 6. Species diversity for introduced logs and open space sites (p = 0.006 nested ANOVA, bars indicate SD).

Australia. These patches are different from those created by shrubs (Facelli and Temby, 2002) and trees (Facelli and Brock, 2000) in this system, and thus important in their own right for increasing qualitative spatial heterogeneity. Logs affect soil conditions, soil water content, the germinable seed bank, and the growing annual plant community. Importantly, the patterns of these changes are substantially different to those recorded in other systems (Pettit and Naiman, 2005; Tongway et al. 1989).

Nitrogen and phosphorus are particularly limiting in Australian arid land soils, and therefore accretion of these nutrients in fertile patches is particularly important. It was expected that there would be an increase in these nutrients next to logs, as has been recorded in other studies (Pettit and Naiman, 2005). However, whilst we did find an increase in organic carbon, total nitrogen was not different for sites next to logs and open spaces, and available phosphorous was significantly lower in soil from next to logs. Our soil available phosphorus results are very different to those found by Tongway et al. (1989), who found higher phosphorus in soils from log mounds compared with open spaces. The lower availability of phosphorus in our study is perhaps an effect of termite activity, as termite activity has been reported to increase phosphorus leaching from soils (Okwakol, 1987), but the invertebrate community is yet to be documented at this site. Alternatively, the reduction in soil phosphorus may be a result of visible lichen crust remaining intact next to logs (A. Bowman, personal obs.), as lichen-moss crusts have been negatively correlated with phosphorus in soils due to uptake of phosphorus and conversion to unavailable organic forms (Bowker et al. 2006).

In spite of these unexpected results, both field and glasshouse studies showed increased seedling establishment and growth at log sites, where organic carbon is higher. Soil organic matter maintains soil stability and porosity, allowing better root movement through soil, thus giving roots better access to soil nutrients (Brady and Weil, 2008). Yet soil nutrients are not the only determinant for plant growth. There may be different soil microbial composition and activity next to logs that may promote plant growth (Bever et al. 2010). However, as the differences occurred in both field and glasshouse experiments, microenvironment and water alone cannot explain these differences, further enforcing that soil chemistry or microbial activity could be important. The soil nutrient results are very intriguing, suggesting that there are other factors at play in the patchiness created by logs, and warrant further research.

As water is considered to be one of the most limiting factors for plant growth in arid lands, it was assumed that increased plant establishment would be a response to higher water content of soils. Yet, volumetric water content was consistently lower next to logs, where the greater plant establishment occurred. It seems that sheep avoid logs as they move to and from the watering point, as sheep tracks are perturbed by the presence of obstacles (Lange, 1969), and as suggested by the visible lichen crust remaining intact next to logs (A. Bowman personal obs.). Since lichen crusts can reduce local water infiltration (Eldridge and Greene, 1994), this may cause the reduction in VWC we documented. However, we also know that macropores created by plants and invertebrates can significantly increase infiltration into soils (Colloff et al. 2010), thus further investigations are required to determine the cause of our unexpected VWC results. The lower VWC documented in the field suggests that for these species, conditions other than water are enhancing seedling establishment and growth next to logs.

We expected increased seedling establishment and growth at logs, although it was originally thought that increased water and nutrient availability would be the key factor, as was found in New South Wales and South African arid lands (Ludwig and Tongway, 1996; Pettit and Naiman, 2005). Not only was species diversity greater at logs, but also seven species were only documented at log sites. This suggests that these species may not have been in open spaces, either because they are not retained and incorporated in the soil, or because under open soil conditions they die faster. Alternatively these species may rely on microclimate conditions created by logs, such as soil temperature or protection from wind, to establish and may not be able to persist in the system in the absence of this source of patchiness.

Interestingly, logs placed experimentally in open spaces produced significantly greater species diversity after only four months, suggesting that some of the effects of logs may occur over a very short time scale. The study was conducted during a particularly wet winter, which may have sped up some of the effect caused by the logs on seedling establishment and growth. Yet it is almost impossible that there was a substantial increase in the level of organic carbon in the soil, or an accumulation of seeds in the soil seed bank, similar to what happens next to logs present for many years. Indeed no species set and released seeds during the period of the study. The most likely explanation is that the presence of the log produces changes to some microclimate conditions. Many seeds in this system have dormancy controlled by fine-tuned responses to soil temperature (Facelli et al. 2005). Modification of soil temperature regime can be a factor in this heterogeneity. This effect of logs has not been studied before and deserves attention.

Some evidence for the effect of distance from watering point, a proxy for degradation (Heshmatti et al. 2002), was detected in this study. This was mostly evidenced in the differences in germinable seed bank, where seedling number and richness were higher at 1000 m sites than in the more degraded 300 m sites. It is likely that there is less seed accumulation in the soil due to overgrazing at 300 m sites, as the seed banks are likely to have been depleted by reduced seed output (Kinloch and Friedel, 2005a), or because there are fewer obstacles to retain them (Emmerson et al. 2012). Thus, even though germinable soil seed bank was studied, the extractable soil seed bank could provide more information, particularly across the grazing gradient around the watering point (see, however Meissner and Facelli (1999)).

Our results have multiple implications for studies of resource heterogeneity and plant community structure in arid lands, as well as for rehabilitation of degraded sites. The results make it evident that further research is required to understand better the effects of logs in arid landscapes. For this system in particular, a better understanding of soil properties and processes next to logs is necessary. Soil compaction as well as lichen cover and properties of the lichens may further clarify the results, probably explaining the differences in volumetric water content of soil between logs and open spaces. Further studies on the invertebrate activity at logs could also explain some variation in the soils at logs. In this study we could not determine the age of the logs, but they are known to persist for many decades (in some species > 75 years) (Sinclair, 2004). Studies on the age of logs and the rate of decomposition may provide important information on the dynamics of the formation of patches and their eventual dissipation. Such studies are currently very scarce (see Sinclair, 2004). Also, since there is higher seedling emergence at log microsites, it is possible that competition may be stronger in these sites and that increases in density and intensity of competition could vary with seasonal condition. In general the relative balances between high site quality and density dependent negative effects are not well understood in arid lands.

Logs create unique sites for establishment and growth of seedlings in the chenopod shrublands of South Australia. There are, however, still several critical questions about the biotic and abiotic factors influencing this establishment and growth. Several further studies are required to better assess the effect of logs on patchiness in the chenopod shrublands of South Australia. Such studies may lead to logs being used as a tool to revert degradation in arid lands around the world and provide incentives for managers to curtail dead wood collection from sensitive sites.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http:// dx.doi.org/10.1016/j.jaridenv.2013.05.014.

References

- Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology & Evolution 14, 273–277.
- Andrew, M.H., 1988. Grazing impact in relation to livestock watering points. Trends in Ecology & Evolution 3, 336–339.
- Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C., Stock, W.D., Tibbett, M., Zobel, M., 2010. Rooting theories of plant community ecology in microbial interactions. Trends in Ecology & Evolution 25, 468–478.
- Bowker, M.A., Belnap, J., Davidson, D.W., Goldstein, H., 2006. Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model. Journal of Applied Ecology 43, 152–163.
- Brady, N.C., Weil, R.R., 2008. The Nature and Properties of Soils, fourteenth ed. Pearson Prentice Hall, New Jersey).
- Colloff, M.J., Pullen, K.R., Cunningham, S.A., 2010. Restoration of an ecosystem function to revegetation communities: the role of invertebrate macropores in enhancing soil water infiltration. Restoration Ecology 18, 65–72.
- Crocker, R.L., 1946. An introduction to the soils and vegetation of Eyre Peninsula, South Australia. Transactions of the Royal Society of South Australia 70, 83–105.
- De Soyza, A.G., Whitford, W.G., Martinez-Meza, E., Van Zee, J.W., 1997. Variation in creosotebush (*Larrea tridentata*) canopy morphology in relation to habitat, soil fertility and associated annual plant communities. American Midland Naturalist 137, 13.
- Dregne, H.E., 2002. Land degradation in the drylands. Arid Land Research & Management 16, 99–132.
- Eldridge, D., Greene, R., 1994. Microbiotic soil crusts a review of their roles in soil and ecological processes in the rangelands of Australia. Soil Research 32, 389– 415.
- Emmerson, L.M., Facelli, J.M., Chesson, P., Possingham, H., Day, J.R., 2012. Changes in seed dispersal processes and the potential for between-patch connectivity for an arid land daisy. Ecology 93, 544–553.
- Facelli, J.M., Brock, D.J., 2000. Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of South Australia. Ecography 23, 479–491.
- Facelli, J.M., Chesson, P., Barnes, N., 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology 86, 2998– 3006.
- Facelli, J.M., Temby, A.M., 2002. Multiple effects of shrubs on annual plant communities in arid lands of South Australia. Austral Ecology 27, 422–432.
- Harris, M.R., Facelli, J.M., 2003. Competition and resource availability in an annual plant community dominated by an invasive species, *Carrichtera annua* (L. Aschers.), in South Australia. Plant Ecology 167, 19–29.

- Hastwell, G.T., Facelli, J.M., 2003. Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. Journal of Ecology 91, 941–950.
- Heshmatti, G.A., Facelli, J.M., Conran, J.G., 2002. The piosphere revisited: plant species patterns close to waterpoints in small, fenced paddocks in chenopod shrublands of South Australia. Journal of Arid Environments 51, 547–560.
- James, A.I., Eldridge, D.J., Hill, B.M., 2009. Foraging animals create fertile patches in an Australian desert shrubland. Ecography 32, 723–732.
- Kinloch, J.E., Friedel, M.H., 2005a. Soil seed reserves in arid grazing lands of central Australia. Part 1: seed bank and vegetation dynamics. Journal of Arid Environments 60, 133–161.
- Kinloch, J.E., Friedel, M.H., 2005b. Soil seed reserves in arid grazing lands of central Australia. Part 2: availability of 'safe sites'. Journal of Arid Environments 60, 163–185.
- Landsberg, J., James, C.D., Morton, S.R., Muller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. Journal of Applied Ecology 40, 1008–1024.
- Lange, R.T., 1969. The piosphere: sheep track and dung patterns. Journal of Range Management 22, 396–400.
- Lin, Y., Hong, M., Han, G., Zhao, M., Bai, Y., Chang, S.X., 2010. Grazing intensity affected spatial patterns of vegetation and soil fertility in a desert steppe. Agriculture Ecosystems & Environment 138, 282–292.
- Ludwig, J.A., Tongway, D.J., 1996. Rehabilitation of semiarid landscapes in Australia. II. Restoring vegetation patches. Restoration Ecology 4, 398–406.
- Maestre, F.T., Cortina, J., Bautista, S., Bellot, J., Vallejo, R., 2003. Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. Ecosystems 6, 630–643.
- Meissner, R.A., Facelli, J.M., 1999. Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. Journal of Arid Environments 42, 117–128.

- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4, 25–51.
- Noy-Meir, I., 1981. Spatial effects in modelling of arid ecosystems. In: Goodall, D.W., Perry, R.A. (Eds.), 1981. Arid-land Ecosystems: Structure, Functioning and Management, vol. 2. Cambridge Press, Sydney).
- Okwakol, M.J.N., 1987. Effects of *Cubitermes testaceus* (Williams) on some physical and chemical properties of soil in a grassland area of Uganda. African Journal of Ecology 25, 147–153.
- Osem, Y., Konsens, I., Perevolotsky, A., Kigel, J., 2007. Soil seed bank and seedling emergence of *Sarcopoterium spinosum* as affected by grazing in a patchy semiarid shrubland. Israel Journal of Plant Sciences 55, 35–43.
- Pettit, N.E., Naiman, R.J., 2005. Flood-deposited wood debris and its contribution to heterogeneity and regeneration in a semi-arid riparian landscape. Oecologia 145, 434–444.
- Sinclair, R., 2004. Persistence of dead trees and fallen timber in the arid zone: 76 years of data from the T.G.B. Osborn Vegetation Reserve, Koonamore, South Australia. The Rangeland Journal 26, 111–122.
- Sparrow, A.D., Friedel, M.H., Tongway, D.J., 2003. Degradation and recovery processes in arid grazing lands of central Australia Part 3: implications at landscape scale. Journal of Arid Environments 55, 349–360.
- Stock, W.D., Dlamini, T.S., Cowling, R.M., 1999. Plant induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. Plant Ecology 142, 161–167.
- Tongway, D.J., Ludwig, J.A., 1996. Rehabilitation of semiarid landscapes in Australia. I. Restoring productive soil patches. Restoration Ecology 4, 388–397.
- Tongway, D.J., Ludwig, J.A., 2005. Heterogeneity in arid and semiarid lands. In: Lovett, G.M., Turner, M.G., Jones, C.G., Weathers, K.C. (Eds.), Ecosystem Function in Heterogeneous Landscapes. Springer, New York, pp. 189–205.
- Tongway, D.J., Ludwig, J.A., Whitford, W.G., 1989. Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia. Austral Ecology 14, 263–268.