



Fallen logs: creating patchiness in chenopod shrublands of South Australia

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A Log Limerick

In arid lands my work does begin,
Rainfall so low it's a sin,
Soil nutrients are poor,
Plants wish there were more!
Survival each day is a win.

So what task do I have in my charge?
After all, arid lands really are large
Not beast- hoof or wing,
No, logs they're my thing,
and the plants that grow on their verge.

But before I go into detail,
Some background I must entail,
For lands that are arid,
Aren't nearly so horrid,
As a Saharan death-defying tale.

Soil nutrients and water are low,
But accumulation occurs, this we know.
In areas all bare,
It's hard to grow there,
But in patches these plants can now grow!

These patches, so varied they be,
Accumulations 'round shrub, grass and
tree,
In holes and in pits,
And animal digs,
Resource islands within a bare sea.

These patches they have what plants need,
Lots of water, nutrients and even seed.
But ecosystem function,
Came to a junction,
For these patches have suffered from our
greed.

We introduced grazing to the land,
Hard hooves this system must withstand,
And where grazers toil,
They churn up the soil!
And those patches they now barely stand.

Now this is where logs play their part,
I've made studying them into an art,
Soil samples and seeds,
Annual plants, even weeds,
Their effects I have teased them apart.

Logs are unique in this system,
Higher nutrients in soils around them,
Many seeds are there,
Much more than the bare,
And plant growth follows this pattern.

Soil temperature is favourable for seed,
Making establishment more likely to
succeed.
Most important of all,
These affects are not small,
And occur at a very great speed.

For time is an important factor,
As restoration really does matter,
Plants grow so slow,
Restoration is low,
Thus fallen logs may just be the answer.

I introduced logs to the ground,
In degraded areas that I found,
Plant response so fast,
Only months had passed,
These logs did truly astound.

So my message to take home today,
If I only had one thing to say,
Is in lands that are arid,
And heavily degraded,
Logs may just save the day.

Abstract

Patchiness of resources strongly affects productivity and diversity of arid systems. Patchiness associated with trees, shrubs, grasses, and animal diggings are well documented but there is very little information on the effect of fallen logs. Fallen logs are one of few documented non-living structures in arid lands that contribute to resource heterogeneity. They can be particularly important in grazed systems, where most resource patches associated with living plants are reduced or destroyed. Further, logs provide a unique opportunity to study aspects of resource patchiness without them having biotic effects on annual plants. My Ph.D. thesis consists of four chapters:

Long term influence of fallen logs on patch formation and their effects under contrasting grazing regimes

Here I studied the long term dynamics of patch formation and the effect of fallen logs in heavily grazed areas. I studied soil nutrient content and soil seed banks associated with the presence of logs in the long ungrazed Koonamore Vegetation Reserve and in adjacent heavily grazed paddock in chenopod shrublands of South Australia. I studied patches associated with fallen logs of unknown age, and others known to have persisted for up to 78 years. Logs acted as traps for soil nutrients and seeds. Organic carbon and total nitrogen were higher in soils next to logs, and also higher inside the reserve than in the grazed paddock. Propagule number and species richness were higher next to logs than in open spaces and viable seeds were in much higher abundance next to logs in the grazed paddock than any other site. Increased time *in situ* of a log had some effect on soil organic carbon, total nitrogen and available potassium. Logs act as resource traps which may enhance the diversity of the system, and may be particularly important for maintaining patches of resources in areas of severe grazing damage.

Microclimate or accumulation of resources: which is the main driver of annual plant communities in a patchy system?

Here I decoupled microclimate and accumulation components of a patch to determine their relative importance for plant communities. I measured soil temperature and soil volumetric water content next to logs and in adjacent open spaces. I then conducted a soil core swapping experiment to separate these soil microclimate conditions from seed and resource accumulation to assess their importance in determining annual plant communities. Soils next

to logs had lower maximum and higher minimum temperatures than open space soils. Also, patches next to logs had lower soil volumetric water content and dried faster after a rainfall event than open spaces. The soil core swapping experiment showed complex interactions on the annual plant community suggesting that each factor has its own impact on annual plant communities.

Spatial and temporal heterogeneity of resources drive changes in community structure of arid annuals

Here I studied the effects of spatial and temporal heterogeneity on density dependence and community structure of annual plant communities. To achieve this I used fallen logs and open spaces coupled with high and low watering regimes in both the field and the glasshouse conducted over two consecutive years, encompassing two growing seasons. I found some evidence of competition among annual plant communities, but community structure of annual plants were strongly influenced by spatial heterogeneity of resources as well as watering regime. My results varied greatly across the two growing seasons, suggesting that both temporal and spatial heterogeneity of resources in arid lands are important determinants of annual plant communities.

Patch formation and patch dissipation associated with fallen logs

To study patch formation I introduced logs and fake logs (large PVC pipes) to open spaces at multiple orientations at two levels of grazing degradation. I assessed soil properties and any changes to annual plant communities over the three following years. I found that three years was not sufficient for creating changes to soil nutrients or annual plant communities when introducing logs, but the destocking which occurred during my experiment had a strong effect on soil nutrient contents. To look at patch dissipation I selected logs in pairs and one of each fallen log was removed. At each of log, open space and removed log I deployed soil temperature and moisture probes. I also collected soil samples to determine soil nutrient contents and soil seed bank across a one year period I found the removal of the log had immediate changes to the microclimate associated with the log, but that one year was not long enough to remove accumulated nutrients or seeds in the seed bank.

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Introduction

1.1 Arid lands

Productivity in arid lands of the world is limited by the very low availability of resources. Precipitation in arid lands is characteristically low and therefore water is the main controlling factor for biological processes. In addition, precipitation is highly variable both within a year, and between years, and this variation in precipitation is largely unpredictable (Noy-Meir 1973). In turn, during the periods when water availability enables biological processes, productivity also limited by low soil nutrient availability. Consequently, one of the most characteristic patterns of arid lands, the highly heterogeneous distribution of these resources, becomes functionally very important.

1.2 Heterogeneity, Jensen's Inequality, and productivity in arid lands

The spatial distribution of resources in arid lands is heterogeneous, consisting of patches of high resource availability within a matrix of very low resource availability. This resource patchiness includes mainly concentrations of water and nutrients (Facelli & Brock 2000) while seeds are also found to accumulate in such patches (Osem *et al.* 2007). If resources were distributed homogeneously throughout arid systems, little or no productivity would occur, however, the presence of patches increases the productivity of the whole system (Noy-Meir 1985). This theory is supported by Jensen's Inequality (fig 1.1), a mathematical principle regarding general properties of non-linear functions. Jensen's Inequality states that the average of the functions of two independent values is different from the function of the average of the said independent values. Thus, in a heterogeneous system the average productivity of open spaces with low resource availability and patches with high resource availability yields a higher productivity than a system with the same level of resources distributed homogeneously.

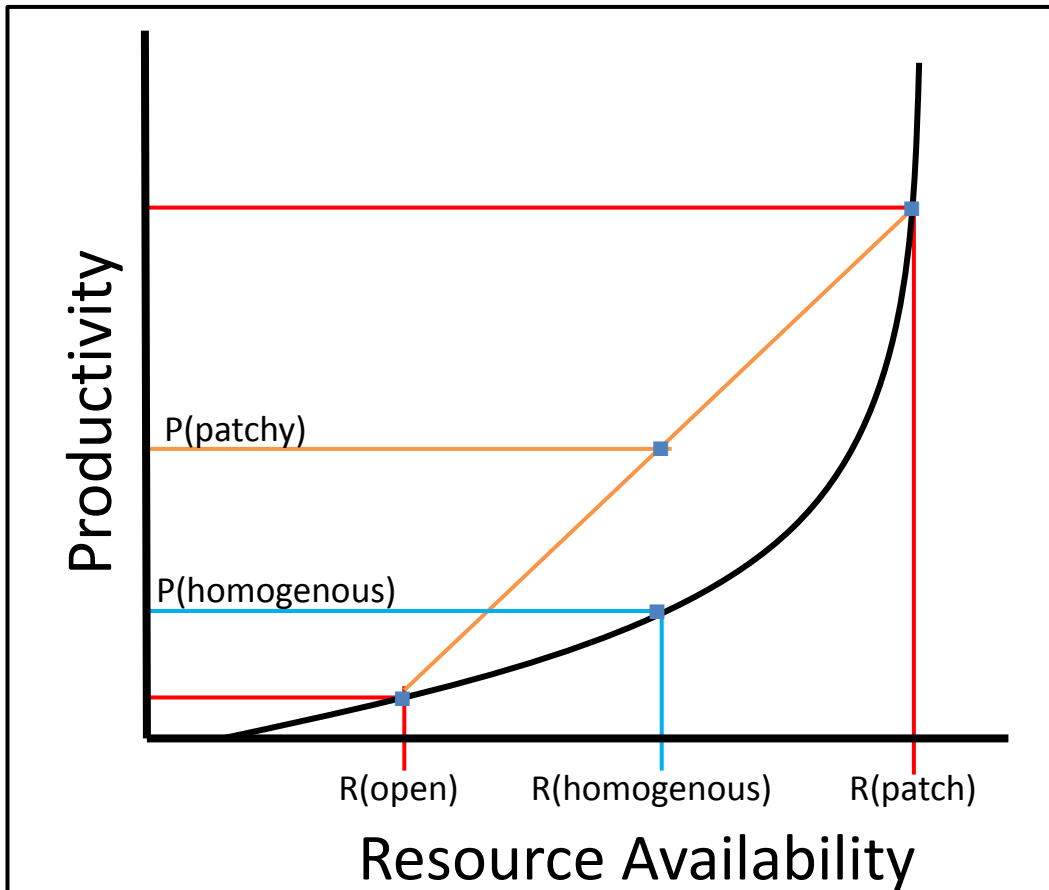


Figure 1.1: Jensen's Inequality. Productivity is a non-linear function of resource availability (black line). The orange line shows geometrically the average productivity of open areas, $R(\text{open})$, and resource patches, $R(\text{patch})$. $R(\text{homogenous})$ is the level of resources in a homogeneous system. The average of $R(\text{open})$ and $R(\text{patch})$ has the same level of resource availability as $R(\text{homogenous})$, yet has higher productivity.

1.3 Resource patches

Patchiness of resources has been extensively studied in arid lands because its presence strongly affects productivity and diversity of arid systems (Noy-Meir 1985). Arid lands generally consist of a two-phase mosaic, with vegetation interspersed in areas of open space (Sala & Aguiar 1996). Studies investigating resource patches include patches associated with trees (Facelli & Brock 2000), shrubs (Schlesinger *et al.* 1996; Facelli & Temby 2002), succulents (Stock *et al.* 1999), grasses (Tongway & Ludwig 1994), animal diggings (Shachak *et al.* 1991; James *et al.* 2009) and fallen branches and logs (Tongway *et al.* 1989; Bowman & Facelli 2013).

Many patch types have been associated with living patch forming entities. Resource patchiness has been associated with trees and shrubs in arid lands on every continent except Antarctica. For example, the tree genus *Prosopis* spp. creates an area of higher nutrient contents and facilitates establishment of other plants beneath its canopy in United States of

America (Barnes & Archer 1996), in India (Singh & Shukla 2012), and in Saudi Arabia (El-Keblawy & Abdelfatah 2014). The long lived tree, *Acacia papyrocarpa*, creates an area of high organic matter and increased water availability under its canopy in chenopod shrublands of South Australia (Facelli & Brock 2000). The area underneath the canopy is occupied by several species of chenopod shrub not present in open areas. Chenopod shrubs in open spaces can also act as resource traps, enhancing soil nutrients, water infiltration rates and microbial activity (Tongway & Ludwig 1994). Two chenopod shrubs *Atriplex vesicaria* and *Maireana sedifolia* are known to act as resource accumulators, but there are differences in the soils under each species (Facelli & Temby 2002). While grass clumps such as *Eragrostis eriopoda* can also act as resource traps, this is at a smaller scale than chenopod shrubs, due to their smaller size, differing shape, and shorter life-span (Tongway & Ludwig 1994).

Living plants are not the only resource accumulators; animal diggings and fallen logs can also create patches. Diggings by *Macrotis lagotis*, *Veranus gouldii*, *Oryctolagus cuniculus* and *Bettongia lesueur* create resource patches in Australian arid lands (James *et al.* 2009). Piles of branches can increase nutrient and water content in surrounding soils (Tongway & Ludwig 1996), as can fallen logs, which increase soil nutrient contents, change soil water content and increase annual plant numbers compared with open spaces (Tongway *et al.* 1989; Bowman & Facelli 2013).

1.4 Properties of a patch

Substantial variation in a wide variety of factors has been found associated with patches. Studies have found patches affect soil nutrient contents (Tongway *et al.* 1989), soil seed bank (Facelli & Temby 2002), soil water availability (Rango *et al.* 2006), and soil temperature (Segoli *et al.* 2012). However, not all studies agree on the directions of these changes: while patches generally increase soil nutrient availability, the type of patch, the species of shrub (Facelli & Temby 2002), or even the shape of a shrub within a species (De Soyza *et al.* 1997) can alter the properties of a patch.

Nutrient contents of patches can be quite varied. In studies on patchiness under *Larrea tridentata*, Schlesinger *et al.* (1996) found higher concentrations of nitrogen in soils under the canopy, however, in a separate study of *L. tridentata*, De Soyza *et al.* (1997) found while soil nutrient contents were higher under hemispherical shaped shrubs, this was not the case for conical shaped shrubs. Analysis of patches under *Sarcopoterium spinosum* found higher soil

nutrients than in open spaces, but that the nutrients were concentrated at the core of the shrub, not the periphery (Segoli *et al.* 2012). Within the same paddock, different shrub species have different effects on soil nutrients; Facelli and Temby (2002) found higher soil nitrogen contents under *A. vesicaria* than in open spaces, and lower soil phosphorous contents under *M. sedifolia*. Similarly, foraging pits made by different animal species also have varied nutrient contents, with diggings by Australian native fossorial mammals having higher soil carbon contents than diggings made by lizard and introduced mammals (James & Eldridge 2007).

Canopies of patch forming plants can also alter the microclimate within a patch. Shading by plants can lower maximum soil temperatures compared with open spaces (Segoli *et al.* 2012). It has also been found that shading can have a moderating effect on both maximum and minimum temperatures: Breshears *et al.* (1998) found soil temperatures were reduced in summer months, but increased in winter months under the canopy of two tree species. Shade is important in arid lands as it can decrease water stress, which may enhance mineral nutrition of plants and reduce water loss (Weedon & Facelli 2008). Even smaller sized patches can have impacts on microclimate with animal foraging pits decreasing maximum daytime temperatures by 17-31% and retaining water longer than open spaces (James *et al.* 2010).

In addition to modifying chemical and physical properties, patch-creating structures can also modify the biotic environment. Many patch types have positive impacts on seed banks and annual plant communities, but this can change to neutral or negative effects depending on the patch type. Seed accumulation and associated seedling emergence have been associated with the presence of chenopod shrubs (Facelli & Temby 2002), in fact, seed density can increase ten-fold under shrubs and seedling emergence three-fold, compared with open spaces (Osem *et al.* 2007). However, just as resources accrete differently around different structures in landscapes, the type of structure affects the size and composition of the seed bank. Specific characters of structures, such as height and differences in branching structure, can affect the ability to trap both resources and seeds (De Soyza *et al.* 1997; Facelli & Temby 2002). For example, Facelli and Temby (2002) found annual plant abundance increased under *A. vesicaria* shrubs and were generally unchanged under *M. sedifolia* shrubs. In a separate study Giladi *et al.* (2013) found *S. spinosum* had negative effects on annual plant communities. Seedling establishment and survival is poor in open spaces in arid lands, but patches with higher resource availability or less physical stress provide safe sites for seedling establishment (Maestre *et al.* 2003). This higher emergence of plants in patches is due to the

combination of accumulation of seed, more favourable microclimate and soil conditions, and also to the higher resource availability in patches (Osem *et al.* 2007).

1.5 Formation and dissipation of patches

The formation of patches has been suggested to be driven both by abiotic and biotic processes. While patches across arid ecosystems can vary in size and shape, the mechanisms behind the formation of patches are thought to be similar, even though some are formed by wind and others by water movement (Aguiar & Sala 1999). A model of resource distribution was developed in mulga dominated arid lands by Tongway and Ludwig (1990), who suggest that it applies broadly to arid lands. They suggest that erosion occurs, mostly in open spaces, and trees, branches, shrubs and grasses slow water movement, allowing greater water infiltration and deposition of soil, litter and other plant matter. Ludwig and Tongway (1995) suggest that this run-on, run-off processes occurs through both water and wind erosion of soils. A subsequent study by Tongway and Ludwig (1996) highlights how structures can act as resource sinks, and showed that branches they placed on the ground accumulated soil and increased soil nutrient contents over a three year period. Studies by Emmerson *et al.* (2010; 2012) show this movement and subsequent deposition in a landscape also occurs with seeds. It is important to note that both of these studies found that grazing regime changes the amount of material transported, as well as the distance. Thompson *et al.* (2014) also demonstrated that a large increase in friction factor associated with the presence of vegetation leads to final seed resting positions being largely tied to vegetation distribution. Yet this model derived by Tongway and Ludwig is based on physical properties and processes, whereas other studies demonstrate the importance of living plants and animals to resource heterogeneity.

The formation of patches by living plants can be much more complex than those formed by inert structures, as plants can directly modify their environments. Plant root systems can modify soil nutrients and moisture through resource acquisition (Sala *et al.* 1989) and hydraulic lift (Horton & Hart 1998). Plant canopies can also change light availability and temperature: several studies have found shrubs create a moderating effect on soil temperatures underneath their canopy (Facelli & Brock 2000; Segoli *et al.* 2012). Additionally, plant litter can alter the physical and chemical environment, both directly and indirectly beneath the canopy (Facelli & Pickett 1991). Shrubs can increase establishment and growth of annual plants beneath their canopy (Pugnaire *et al.* 1996; Osem *et al.* 2007). However, resource patches created by living plants may also have negative effects on plants

through competition when resources are scarce. For example, Facelli and Temby (2002) found shrubs to inhibit growth of annual plants beneath their canopy. Hence facilitation by living plants may be highly dependent on temporal variability as well as the species in question, and it cannot be assumed that the effect of the resource patch created by living plants on other species will always be positive.

The formation of patches over short time periods has been studied (such as in work by Tongway and Ludwig (1996)), yet very little is known about patch formation in the long term. Using space-for-time substitution, Facelli and Brock (2000) assessed the resource patchiness created by the *A. papyrocarpa* tree and how this patchiness changes with the age of a tree, varying from juvenile to death (at an estimated 400 years). They found the development of the patch is slow (up to 100 years), which suggests that this process of patch development is very different from that caused by non-living features, as reported by Tongway and Ludwig (1996). Similarly, very little information is available on the dissipation of patches. It has been suggested that soil nutrient patches can remain after the patch forming entity is removed (Callaway *et al.* 1991; Barnes & Archer 1996). A few studies have quantified this: Facelli and Brock (2000) found that in patches dominated around *A. papyrocarpa* trees, the soil phosphorus content remained higher than in open spaces for at least fifty years after the death of the long lived tree, while soil nitrogen dissipated sooner; Tiedemann and Klemmedson (1986) found nutrients to remain higher at least thirteen years after shrub canopy removal; and Bechtold and Inouye (2007) found soil nutrients decreased six years after they removed the canopy of a shrub. Studies on dissipation of patches have thus far been limited to living patch forming entities, and given that patch properties can change qualitatively as well as quantitatively, it is important to explore patch dissipation further.

1.6 Effects of introduced grazing on resource patches

Grazing has often detrimental effects on patchiness of resources and hence productivity in arid lands (Bastin *et al.* 1993). Landscape degradation can be natural, such as wind or water erosion, but currently is often human induced or exacerbated, particularly by agricultural practices such as grazing (Dregne 2002). Grazing degradation is multifaceted, with plant defoliation and hoof action each causing negative changes, but together having synergistic negative effect on productivity in arid systems. In degraded arid lands, low densities of plants can cause increased water run-off leading to erosion, decreasing infiltration rates and

lowering the number of resource patches (Tongway & Ludwig 1994; Sparrow *et al.* 2003). Increased grazing degradation changes soil nutrients of patches, dramatically reducing carbon, nitrogen and phosphorus (Li *et al.* 2009). Hoof action by grazers causes soil crust destruction, altering the hydrological functioning of arid land systems, and disrupting or even eliminating the function of patches (Tongway & Ludwig 1990; Eldridge *et al.* 2000; Heshmatti *et al.* 2002). Key nutrients are likely to be lost from a landscape subject to grazing, rather than redistributed in other patches (Sparrow *et al.* 2003). This loss of patches removes an important pattern from arid land systems (Tongway & Ludwig 1994), since resource patches favour landscape stability, maintain nutrient levels, enhance soil stability and maintain favourable soil physical properties (Tongway & Ludwig 1990). Hence, activities by grazing animals may have serious consequences for the system.

Overgrazing can change the distribution and abundance of plants and seeds in arid systems. Patterns produced as a result of grazing can manifest within three months of introducing stock (Andrew & Lange 1986a). Grazing in arid lands can lead to a decline in the distribution and abundance of some plant species, as well as dominance by others, due to direct grazing of plants and trampling of soil (James *et al.* 1999; Facelli & Springbett 2009). Palatable chenopod shrubs, browsed by stock, decrease close to watering points, whilst unpalatable shrubs dominate in close proximity to watering points (Heshmatti *et al.* 2002; Friedel *et al.* 2003). In general, species richness decreases and weed species increase with increased grazing degradation (Landsberg *et al.* 2003). In addition, some plant species are only present at less degraded sites (Landsberg *et al.* 2003). Since resource patches provide favourable sites for seedling establishment, the loss of patches due to grazing affects recovery of vegetation (Kinloch & Friedel 2005b).

Changes in plant distribution due to grazing can also affect the size and composition of soil seed banks. As a result of grazing degradation, both the size and composition of soil seed banks change (Osem *et al.* 2007) and this same pattern can be observed in annual plant communities (Kinloch & Friedel 2005a). Changes in resource patchiness under heavy grazing degradation cause reduction in seed species and density in arid ecosystems (Kinloch & Friedel 2005a; Solomon *et al.* 2006; Kassahun *et al.* 2009). Grazing has a negative impact on the number of seed sinks which lowers the soil seed bank (Kinloch & Friedel 2005b). In addition, reduction in seed abundance can be caused by diminished seed output by adult plants due to grazing (Hunt 2001; Riginos & Hoffman 2003; Tiver & Kiermeier 2006), as

seed banks of palatable shrubs reduce in size from the effects of grazing, as seed production is reduced via the depression of flowering (Andrew & Lange 1986b).

There is ample evidence that the loss of fertile patches due to grazing degradation in arid lands changes important processes in the system (Tongway & Ludwig 1994). Changes in soil and vegetation, as a consequence of grazing, lead to a lack or very slow recovery of vegetation after resting periods of several years (Friedel *et al.* 2003; Sinclair 2005; Lesschen *et al.* 2008). It is quite likely that restoration of degraded arid lands requires the reconstruction of, resource patchiness (Sparrow *et al.* 2003).

1.7 Importance of logs as patch forming entities

It has been established that fallen logs are important in many systems around the world: in South Africa logs in riparian systems increase nutrient contents in soils (Pettit & Naiman 2005); in Japan decaying fallen logs are vital sites for seedling establishment in boreal and subalpine old-growth forests (Narukawa *et al.* 2003); and in Norway it was found that fallen logs are important for fungi diversity in old-growth forests (Lindblad 1998). Throughout Australia fallen logs also play a key role: in a grassy woodland of south-eastern Australia, fallen logs have positive effects on beetle abundance and diversity (Barton *et al.* 2011); in Western Australian jarrah forests fallen logs are important as nesting hollows for ground dwelling mammals (Williams & Faunt 1997); and in Victoria submerged logs are an important habitat for macroinvertebrates in the Pranjip-Creightons Creek system (O'Connor 1992). Yet while the importance of logs has been established in many systems, their contribution to resource heterogeneity in arid lands is poorly established.

While little is known about fallen logs as resource patches, a few studies have established that they do create patches in arid systems. Tongway *et al.* (1989) assessed log mounds in eastern Australia, and established that these mounds increase water infiltration, soil carbon and nitrogen contents as well as favouring annual plant growth. Branch piles placed in eastern Australian arid lands act as resource accumulators too, increasing soil nutrient contents and water infiltration, particularly in grazed areas (Ludwig & Tongway 1996). Previous work in South Australian arid lands also found that logs increase soil nutrient contents and increase seedling emergence and biomass (Bowman & Facelli 2013).

Fallen logs can persist for a very long time in arid lands. The longest recorded time for a fallen log *in situ* is 69 years (Sinclair 2004), although the author commented that this is an underestimate of their persistence, as none of the 46 logs in the study disappeared over this time frame. Fallen logs are one of few documented non-living structures in arid lands which contribute to resource heterogeneity, making them unique in their role as patch-creating structures. We would suggest that this effect is mostly physical, as per the model by Tongway and Ludwig, given that the decomposition of logs in arid lands is so slow, the direct contribution via decay and release of nutrients would be minimal. While plants which create resource patches can have negative, neutral or positive effects on annual plant communities (Weedon & Facelli 2008; Giladi *et al.* 2013), unlike living plants, logs cannot directly compete with annual plants. Most documented resource patches are associated with living plants but the abundance of these is reduced under heavy grazing (Heshmatti *et al.* 2002). As fallen logs are one of few sources of patchiness which withstand grazing impacts they are important in preventing soil nutrients and seeds from leaking from the system.

While the presence of patchiness associated with fallen logs has been studied, the relative contribution of patch characters to productivity remains largely unknown. It is important to further study the mechanisms behind the creation of patchiness associated with fallen logs, as well as the dissipation of resources once a log had been removed. Such studies will not only increase understanding of the ecological function of patches in arid lands, but fallen logs may also be an effective restoration tool. It has been suggested that removal of logs for firewood could alter hydrological properties in arid lands (Berg & Dunkerley 2004), but despite this, fallen logs continue to be treated as a major resource which are removed from natural ecosystems for use as firewood (Vázquez *et al.* 2011). Recovery in arid lands may depend on reconstructing the landscape's natural heterogeneity (Sparrow *et al.* 2003) and as log patches appear to form quickly, the introduction of logs to grazed areas may be an important solution for overcoming the loss of patches.

1.8 References

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Research aims

The overarching aim of my research was to assess resource heterogeneity associated with fallen logs in chenopod shrublands of South Australia. This investigation was conducted at two field sites: Middleback Field Research Centre and Koonamore Vegetation Reserve, both in South Australia. Specific aims for this research are:

- i) Assess long term dynamics of patch formation associated with fallen logs (chapter 2)
- ii) Determine any impacts of grazing on resource heterogeneity associated with fallen logs (chapter 2)
- iii) Quantify soil microclimate effects created by fallen logs (chapter 3)
- iv) Investigate relative contributions of microclimate and accumulated soil conditions on annual plant communities associated with fallen logs (chapter 3)
- v) Determine any impacts of biophysical crust on annual plant communities associated with fallen logs (chapter 3)
- vi) Determine any competitive effects of annual plant communities associated with spatial and temporal heterogeneity (chapter 4)
- vii) Assess changes in community structure of annual plants associated with fallen logs (chapter 4)
- viii) Assess dissipation of accumulated soil properties after removal of fallen logs (chapter 5)
- ix) Examine changes in microclimate post log removal (chapter 5)
- x) Quantify formation of patches associated with logs and fake logs (chapter 5)

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Microclimate or accumulation of resources: which is the main driver for annual plant communities in a patchy system?

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3.1 Abstract

The importance of patchiness in arid ecosystems has been well established, but while many studies have established the different components which constitute a patch, few studies have decoupled these components to determine their relative importance for plant communities. We measured soil temperature and soil volumetric water content associated with patches created by logs and in adjacent open spaces. We then conducted a soil core swapping experiment to separate these soil microclimate conditions from any resource accumulation and increased seed abundance in a patch to assess which is more important in determining annual plant communities. A biological soil crust destruction experiment to eliminate crust properties as a confounding factor was also conducted. We found that logs created an insulation effect on soil temperature, with cooler maximum temperatures and warmer minimum temperatures than open space soils. We also found that patches next to logs had lower soil volumetric water content and dried faster after a rainfall event than open spaces. Disturbance of the biological soil crust did not produce any difference in plant number, biomass, species richness or species diversity. Our soil core swapping experiment showed that complex interactions between microclimate conditions and soil characters on affected the annual plant community. Annual plant numbers were lower when open space soils were transplanted next to logs than controls grown next to logs. However, biomass was highest when soil from next to logs was grown in open spaces. We found species richness to be higher in soils from next to logs (regardless of where they were grown) than open space controls. Additionally, diversity was lowest in open control plots. We found that annual plant communities respond in a complex way to the complex array of resource availability and microclimate conditions modified by the presence of logs.

Key Words: arid lands; fallen logs; resource heterogeneity; soil properties

3.2 Introduction

The importance of patchiness in arid ecosystems has been well established. Resource patches are important for productivity and diversity in arid lands; it has been proposed that if resources were distributed homogeneously throughout arid systems, little or no productivity would occur, but the presence of patches increases the productivity of the whole system (Noy-Meir 1985). These patches come in different sizes and are associated with a variety of features, including trees (Facelli & Brock 2000), shrubs (Facelli & Temby 2002), animal diggings (James *et al.* 2009) and fallen logs (Bowman & Facelli 2013). However, while many studies have determined the presence of different patch types and their composition, little is known about how patches function: a general model for dynamics and mechanisms of patches is yet to be determined.

Substantial variation in a wide variety of factors has been found associated with patches. Studies have found that patches affect soil nutrient content (Tongway *et al.* 1989), soil seed bank (Facelli & Temby 2002), soil water availability (Rango *et al.* 2006), and soil temperature (Segoli *et al.* 2012). But not all studies agree on the directions of these changes: while patches generally increase soil nutrients, the type of patch, the species of plant (Facelli & Temby 2002), or even the shape of a shrub within a species (De Soyza *et al.* 1997) can affect the nutrient contents of a patch.

Many patch types have positive impacts on annual plants: plants which create patches in arid lands are thought to act as ‘nurse plants’, facilitating annual plant growth. This facilitation may have positive impacts on diversity and productivity of plants, as well as determining community structure and permit coexistence of some species (Callaway 1995). Nurse plants can increase establishment and survival of neighbouring plants (Lortie & Turkington 2008), however, temporal dynamics can switch the balance from positive to negative interactions among plants in arid lands (Tielborger & Kadmon 2000). Additionally, different patches can change between being more or less favourable for various species depending on the patch characteristics. Superficially similar patches can have importantly different properties. For example, Facelli and Temby (2002) found that annual plants increased under *Atriplex vesicaria* shrubs and were generally unchanged under *Maireana sedifolia* shrubs (see also Weedon and Facelli). In a different system Giladi *et al.* (2013) found *Sarcopoterium spinosum* had negative effects on annual plant communities. In a previous study (Bowman & Facelli 2013) we documented that the presence of logs on the ground had positive effects on

soil nutrient contents and annual plant communities compared with open spaces. However, it was noted that biological soil crusts next to logs may play a role in the dynamics of this patch.

Biological soil crusts are important for stabilising soil against water and wind erosion in arid lands (Eldridge & Greene 1994), however, they can also impact patch dynamics (Eldridge *et al.* 2000). There is much conflicting evidence regarding the role of biological crusts regarding water infiltration in arid lands: some studies report increased infiltration when crusts are present, while others report a decrease (Belnap 2006). Additionally, the type of crust present can change seed incorporation into soils; smooth crusts increase movement of seeds and organic matter to the next obstacle, while pinnacled and rolling crusts can increase seed retention (Belnap 2003). It is generally regarded that the presence of biological soil crusts change seedling emergence in patches (Prasse & Bornkamm 2000). Soil crusts can influence species composition, plant density and size, as well as community structure of vascular plants (Belnap 2006). Hence it is important to consider soil biological crusts when assessing the effects of different aspects of a patch on annual plants.

Different aspects of patchiness have been measured, as have the effect of patches on annual plant communities, yet we do not know the relative importance of different biotic and abiotic features of patches (e.g. water, nutrients, soil temperature, and seeds) and how these change annual plant communities. Osem *et al.* (2007) implied that it is the increase in seeds in the seed bank which changes annual plant communities in patches, whereas others have suggested changes in resource contents are the main factor affecting annual plants (Bruno *et al.* 2003; Segoli *et al.* 2012). However, Bowman and Facelli (2013) found changes to annual plant communities within four months of introducing logs to the ground, and suggest that these changes could only be produced by microclimate conditions, as it is almost impossible that much nutrient, organic carbon or seeds could accumulate in this time frame. Hence we think it is important to decouple the features of a patch to determine which factors are most important for annual plant communities.

We wanted to determine to what extent annual plant communities are affected by accumulation effects (i.e. soil nutrients and soil seed bank), by microclimate effects (i.e. soil moisture and soil temperature), or if combinations of the two modify plant communities. We chose to use logs for our study, as they are important patch forming entities in chenopod

shrublands. Also, given that shrubs can simultaneously affect annual plants both positively and negatively, and that shrubs can have negative, neutral or positive effects on annual plant communities (Weedon & Facelli 2008; Giladi *et al.* 2013), logs are a patch forming entity that cannot directly compete with annual plants. We asked i) are there any changes in soil temperature and soil volumetric water content associated with patches? ii) is the effect of the patch on annual plant communities a product of microclimate conditions, accumulation properties, or a combination of the two? iii) does the destruction of surface crust associated with patches have an effect on annual plant communities?

3.3 Methods

3.3.1 Site selection

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 230 mm. 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 & 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).

We selected a single paddock (Two Mile Paddock) for this study as while there is some grazing gradient the environment is otherwise homogenous, has low slope and there is an abundance of fallen logs. All fallen logs we selected for this study were comparable: they were 2-3 m in length, 10-30 cm in diameter, had very simple structure, few or no branches and presented little or no sign of decay. Logs were present at a variety of orientations. For each log an adjacent open space area was selected a minimum 3 m from the log and away from any other living or dead plants.

3.3.2 Soil microclimate

To assess soil microclimate conditions associated with fallen logs we randomly selected six logs along a transect on 17 Apr 2012. At each log and its corresponding open space we deployed 5TM© soil moisture and temperature probes attached to EM50© data loggers (Decagon Devices, Western Australia). Soil probes were buried to 2 cm depth; those next to logs were immediately adjacent and the side of the log used was randomly selected. Data for soil volumetric water content and temperature were logged every hour. The experiment was concluded on 29 Sep 2012. The maximum and minimum soil temperatures in each 24 hour period were selected and used to calculate a monthly minimum and maximum temperature.

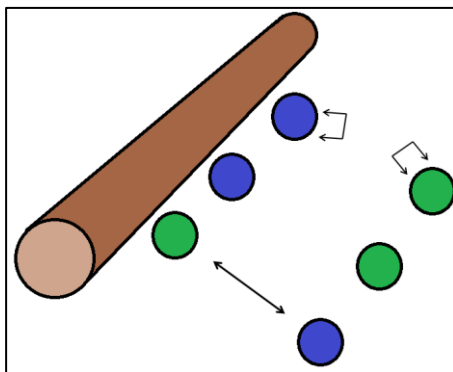


Figure 3.1: diagram of soil core swap experiment. Blue circles indicate soil originating next to the log and green circles are soil originating in the open. Arrows indicate where cores were moved: procedural control was removed and replaced in the same hole, soil was not manipulated for controls, and swap treatments the cores were swapped between the log and open space (each treatment was applied three times at each log).

3.3.3 Effects of microclimate and accumulated materials on annual plant communities

To assess the importance of microclimate and accumulation conditions on annual plant communities associated with fallen logs, a soil core swapping experiment was conducted (see fig 3.1). On 25 Mar 2013 ten logs were randomly selected along with adjacent open spaces. At each log three sets of three treatments were conducted, at positions randomly allocated along each log. Treatments consisted of a soil core swap, a procedural control and a control. PVC pipes of 10 cm diameter and 10 cm depth were used to isolate soil cores. The pipes were driven into the ground and the isolated cores were carefully removed. Soil cores from immediately adjacent to fallen logs were then swapped with cores from the open spaces. A set of procedural controls was also conducted where cores were removed and then replaced in the same hole. Controls were undisturbed soil circles of the same size as the swapped cores. While some cores were able to be removed intact directly from the hole, many cores required to be dug out. Where cores needed to be dug out from next to logs, the digging was conducted at the side of the core furthest from the log. Any dug areas were filled in with spoil as cores were replaced. All treatments were marked out so each plot could later be identified. At each log and open space site the treatments were protected from grazing and trampling

using chicken wire fences. This experiment was concluded on 1 Sep 2013 when all annual plants which had grown in the plots were harvested. Annual plants for each treatment were pooled together and each species was identified, plants were counted and then dried and weighed for above ground biomass.

3.3.4 Biological soil crust

A further ten logs were selected on 8 May 2013 in Two Mile Paddock to assess the effect of disturbance of biological soil crust on annual plant communities associated with fallen logs. At each log and corresponding open space, two plots of 30 cm x 20 cm were marked out. One of each pair of plots was randomly allocated to have the surface crust broken while the other plot remained intact. To disturb the crust a piece of wood with 20 nails (3 cm long and spaced 3 cm apart in a 4 x 5 arrangement) was lightly pressed into the surface and wiggled to gently break the crust without creating excess damage to the soil. Plots next to logs and in the open were then protected against grazing and trampling using chicken wire fences. The experiment was completed on 2 Sep 2013 when all plants were counted, identified, then dried and weighed for above ground biomass.

3.3.5 Statistical analyses

Data were analysed using Graph Pad Prism 6 and PCord 5. Soil temperature data were analysed using split plot two-way ANOVA for each month followed by Tukey's multiple comparison tests (data from August required square root transformation to equalise variances, all other months used raw data). The selected rainfall event had a best fit of an exponential one phase decay, but was Ln transformed for linear regression analysis. Soil core swap data were analysed using nonparametric MANOVA. The crust destruction data were analysed using split plot two-way ANOVA.

3.4 Results

3.4.1 Soil microclimate

Fallen logs affected soil temperature in all months, with the daily maximum being higher in open soils than next to logs and the daily minimum being lower in open soils than next to logs (fig 3.2a, $p < 0.0001$). Soil volumetric water content was generally higher in soils in open spaces than soils next to logs (fig 3.2b). When we analysed a single rainfall event (fig 3.3a, Jul 10 2012, 44.8 mm, indicated by bracket) and subsequent drying of the soils over 33

days (one small event of 1.4 mm occurred during the period) we found that soil next to logs dried faster than soils in open spaces (fig 3.3b, $p < 0.001$).

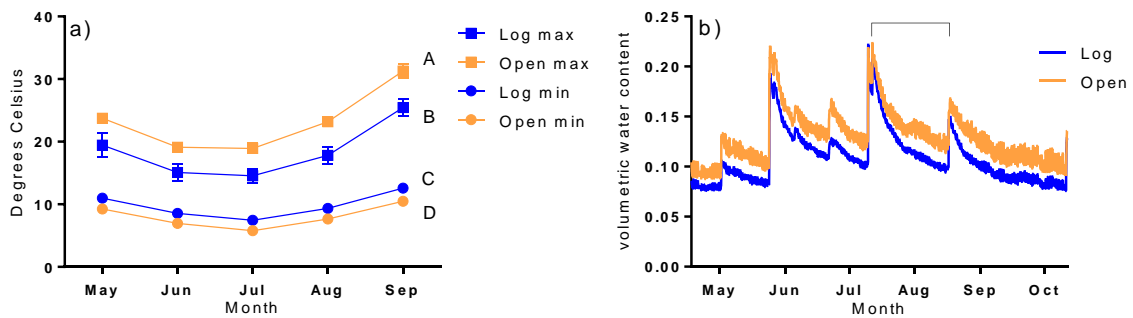


Figure 3.2: a) average daily maximum and minimum soil temperature next to logs and in the open (each month analysed separately, split plot ANOVA and Tukey's multiple comparisons test, $p < 0.0001$) and b) volumetric water content of soils next to logs and in the open from 17 Apr- 29 Sep 2012 (bracket indicates rainfall event used in figure 3.2).

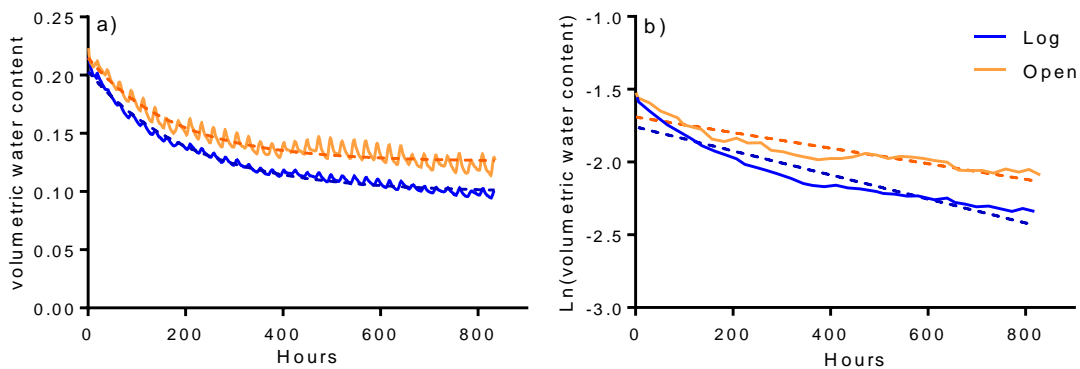


Figure 3.3: volumetric water content of soils next to logs and in the open for an isolated rainfall event of 44.8 mm on Jul 10 2012 followed by 33 days drying (with one small 1.4 mm event at approximately 500 hours) a) with exponential fit (for log $r^2 = 0.89$ for open $r^2 = 0.80$) and b) Ln transformed using only peaks of the curve (for log $r^2 = 0.78$ for open $r^2 = 0.66$, slopes are significantly different $p < 0.0001$).

3.4.2 Effects of microclimate and accumulated materials on annual plant communities

The number of plants emerged from soil was significantly lower in open space soil transplanted next to logs than either control or procedural control plots next to logs, as well as soil from next to logs transplanted into open spaces (fig 3.4a, $p = 0.0044$, $p = 0.006$ and $p = 0.0226$ respectively). There was no difference in emergence from all treatments with soils originating in open spaces, nor was there any difference detected for plant emergence from soils grown in open spaces ($p > 0.05$). The biomass for emerged plants was significantly higher when soil next to logs was transplanted into open spaces than all other treatments except the procedural control next to logs (fig 3.4b). No difference was detected for all other

treatments (fig 3.4b, $p > 0.05$). The species richness of annual plants was higher in all soils originating next to logs, than the control treatment in the open (fig 3.4c, $p = 0.0146$, $p = 0.0062$, and $p = 0.0368$ respectively). All treatments which originated from open soil were statistically similar (fig 3.4c, $p > 0.05$). Species diversity of annual plants was higher when originating or growing in soil next to logs than the control treatment in the open (fig 3.4d, $p < 0.05$). The dominant species by number and biomass (fig 3.5) shows little change in species performance between each treatment.

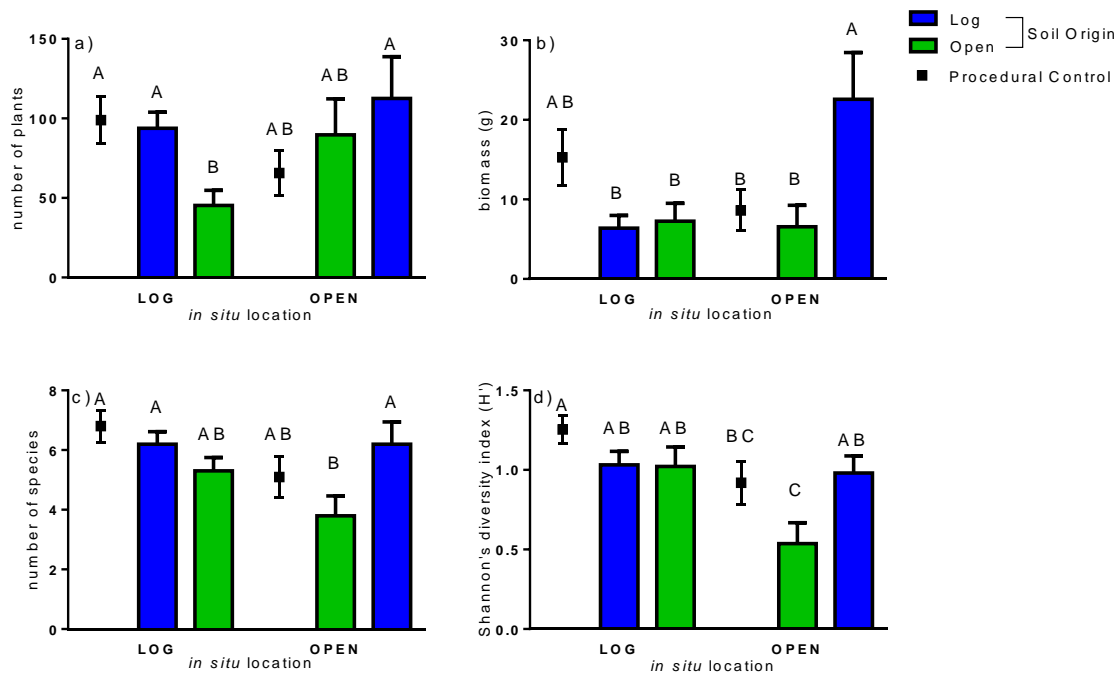


Figure 3.4: a) number of emerged seedlings, b) seedling biomass, c) species richness of emerged seedlings, and d) Shannon's Diversity Index for treatments grown next to logs and in open spaces, with soils originating next to logs and in open spaces (and with a procedural control) (perMANOVA).

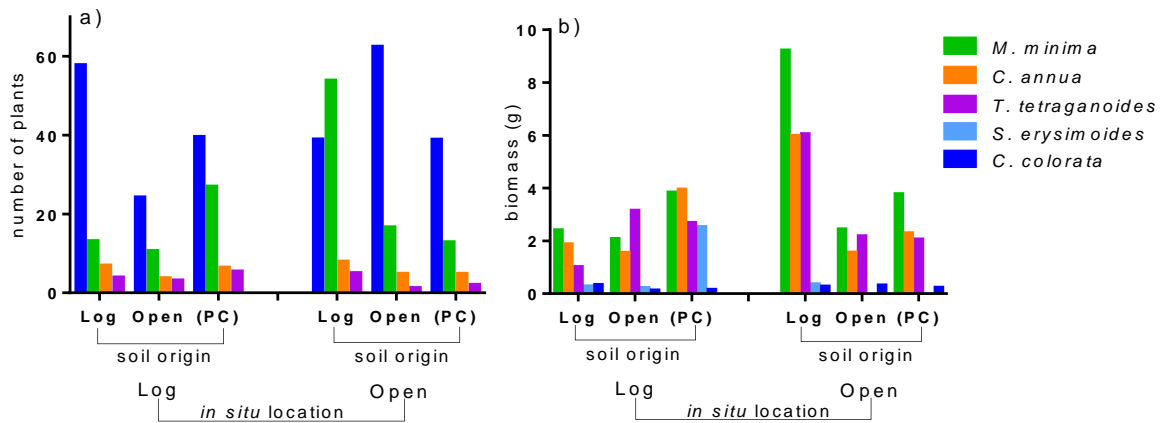


Figure: 3.5: a) number of individual plants for the four dominant species and b) biomass for the five dominant species for each treatment.

3.4.3 Biological soil crust

As we expected, more plants emerged next to logs than in the open (fig 3.6a, $p = 0.0012$), as well as having higher biomass (fig 3.6b, $p = 0.0053$) and a higher species richness (fig 3.6c, $p = 0.0009$). Shannon's diversity was also higher next to logs than in open spaces (fig 3.6d, $p = 0.0006$). Yet, no effect of breaking the crust was detected for emergence, biomass, species richness or diversity ($p > 0.05$).

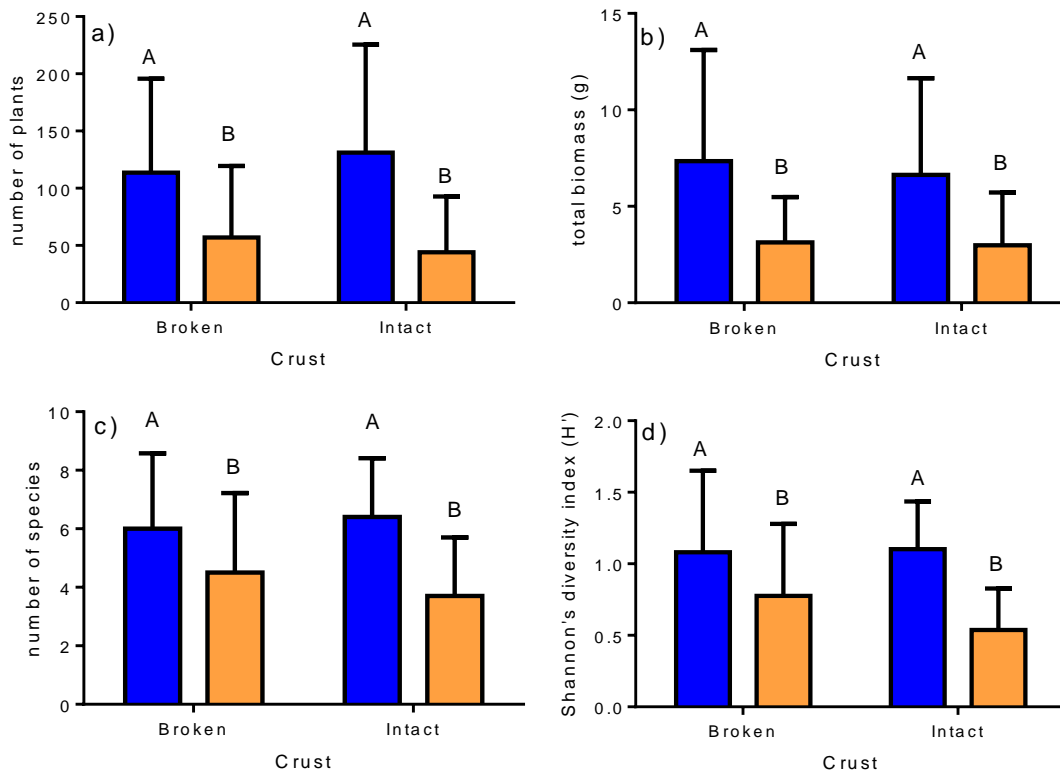


Figure 3.6: a) number of emerged seedlings, b) seedling biomass, c) species richness, and d) Shannon's diversity index for emerged seedlings next to logs (■) and in the open (■) with broken or intact crust (bars indicate SD, split plot two-way ANOVA).

3.5 Discussion

Our data gave us interesting (and to some extent unexpected) information on patches, but the attempt at separating the effects of soil and seed bank accumulation from the microenvironmental effects on annual plant communities did not provide an unequivocal result. The moderated effect on soil temperature created by logs is similar to that found in patches created by shrubs (Breshears *et al.* 1998; Segoli *et al.* 2012), where plant litter is present (Facelli & Pickett 1991) and also in animal diggings (James *et al.* 2010). This microclimate effect of the log patch is important for plant communities, as lower maximum temperatures can promote seed longevity in the seed bank (Baskin & Baskin 2014) and can reduce water stress, which may enhance mineral nutrition of plants and reduce water loss (Weedon & Facelli 2008). We expected that soil water content would also follow the trend shown in other patch types, with more soil water present in patches than in open spaces (Ludwig *et al.* 2005; Rango *et al.* 2006), yet this was not the case. Our soil volumetric water content was not only generally lower next to logs, but decreased faster after a rainfall event. Since higher volumes of water increase annual plant biomass, number and species richness

(Lundholm & Larson 2004), our volumetric water content data would suggest that open spaces are favourable for annual plant growth, but the combinations of the other log patch properties (soil temperature, nutrients and accumulated seeds) creates higher plant emergence next to logs.

We have suggested in a previous study (Bowman & Facelli 2013) that a reduction in water content next to fallen logs may result from the presence of intact biological soil crust, as they can reduce water infiltration (Eldridge & Greene 1994; Maestre *et al.* 2002). However, intact biological soil crusts are also known to decrease seedling emergence of some species (Prasse & Bornkamm 2000). The experiment where we destroyed crust showed no effect on annual plant communities, which may suggest that in this case the effect of the log is greater than that of the crust in this system, or simply that species which thrive next to logs also establish well in crusted soils.

This study shows that there are differences in microclimate between soils next to logs and open spaces. We also know from previous studies that logs accumulate soil nutrients and seeds (Bowman *et al.* in press), however, when we attempted to isolate the accumulative effects of fallen logs from the microclimate effects the outcomes were not clear cut. There was a large amount of variation within treatments which made it difficult to tease apart the effects. Additionally there also appears to be some effect of disturbance when swapping the cores (fig 3.4, note the procedural controls) which further complicates interpretation of the results. We suspect that the soil was sufficiently aerated when cores were moved to accelerate organic matter oxidation (Rasmussen & Collins 1991). This may account for some of the positive effect on plant biomass when cores were relocated from log to open sites, as oxidation of organic matter can produce a release of nutrients, particularly nitrogen (Schnitzer & Khan 1975). Disturbance aside, we did find some changes to annual plant communities when decoupling patch effects.

Our data indicate that different aspects of annual plant communities were affected by different properties of the log patch. Plant number was higher if soil originated next to logs than open space soil grown next to logs. Species richness was similar, with more species in plots originating next to logs than open space controls. As soil origin had a greater effect on emergence than *in situ* location, this would suggest that an accumulation property of the log patch caused this increase; in this case we presume the accumulation of seeds would play a

stronger role in emergence than soil nutrients. This is consistent with previous findings, as we (Bowman *et al.* in press) found much higher numbers of seeds in the soil seed bank next to logs than in open spaces.

Biomass of annual plants was higher in plots when soil from logs was moved to open spaces than in the control plot. This indicates that high biomass has resulted from accumulated seeds and nutrients in the soil, and higher water content and temperatures, all combined with movement of the soil core potentially aerating the soil, as mentioned previously. When soil from next to logs was transplanted to open spaces, the plants which grew would consequently have had access to the higher soil nutrients in the soil core, coupled with higher sunlight, and even potentially higher volumetric water content, which are known to produce higher biomass of annual plants (Goldberg & Miller 1990; Lundholm & Larson 2004). Given that the biomass of species had little effect on the dominance species rank, we could argue that small changes in patch characters will not immediately change community structure of patches. However, perhaps over time small changes in patch characteristics could alter positive feedback by plants in log patches, and hence the patch effects would slowly change.

Species diversity was lowest in open control plots, indicating that accumulation of nutrients and seeds, and microclimate conditions both have some positive effect on species diversity. However, the dominant species responded similarly to the changes produced by logs, suggesting that log patches are important at the ecosystem level function rather than just community structure level. While resources can affect species diversity, we should note that we did not measure any effects of density dependence in this study, which can have strong impacts on species diversity and community composition (Rajaniemi *et al.* 2009). However, our results suggest that density is not high enough to affect biomass or diversity, as we would expect these to be lower in plots with higher plant numbers. This was not the case, yet the effects of resource patches on density dependence and community structure needs to be explored further.

The effect resource patches play on plant productivity is arguably the most important role for these patches, given that the presence of patchiness increases the productivity of arid systems (Noy-Meir 1985). The relative contributions of patch characteristics created by logs, while not conclusive, does indicate that plant establishment will occur provided there are some favourable patch characters present. The changed microclimate conditions next to fallen logs

may indicate that even small structures in arid systems may give a higher chance for plants to establish and grow. Knowing that logs create this moderating effect, they may be useful in degraded areas with low patch numbers at facilitating plant establishment. It would be highly beneficial to determine if these microclimate characters develop in a short time frame, and if these microclimate effects develop next to other introduced structures, as they may be a useful tool for rehabilitation.

Fallen logs create a unique patch in arid lands by inducing changes in both microclimate and accumulation of materials- namely nutrients and seeds. While we have documented important information regarding soil temperature and volumetric water content associated with logs, our results regarding the relative contribution of accumulation and microclimate effects on annual plant communities are somewhat inconclusive. It is evident from our results that the changes to the patch properties produced by a fallen log are more complex than originally anticipated. Isolating the effects of different patch properties may give us a better understanding of limiting factors for main species in arid systems. It is important to further this work, as the relative contributions of patch factors on annual plant communities is key to better understanding diversity maintenance in patchy systems.

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Density dependence and community structure of annual plants associated with spatial heterogeneity in a chenopod shrubland of southern Australia

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4.1 Abstract

Resource heterogeneity is a well-established pattern in arid lands, creating patches of favourable conditions for annual plant growth. While conditions may favour individual plants (i.e. nutrient accumulation and moderated soil temperatures), resource patches also favour higher densities of annual plants (i.e. through accumulated seeds and higher emergence). We query how these two affect balance: is there an overall increase in fitness for the individual plant? Several studies have recently focused on the effects of temporal pulses of resources on plants, yet studies looking into the spatial availability of resources on competition and community structure of annual plants are noticeably absent. In this study we used spatial heterogeneity associated with fallen logs, coupled with high and low watering regimes, to look into the effects of spatial variation of resources on annual plant communities. Our studies were conducted over two consecutive years, encompassing two growing seasons. In the field we found strong evidence that community structure of annual plants changes with spatial heterogeneity and water availability. There was some evidence of competition among annual plant communities in the glasshouse, but not in the field. We found quite varied results across the two growing seasons, suggesting that both temporal and spatial heterogeneity of resources in arid lands are important determinants of annual plant communities. Overall we found that resource patchiness does indeed put the balance in favour of the individual plant.

Keywords: arid lands; competition; fallen logs; microenvironment; nutrient accumulation; rainfall pulses; soil patchiness

4.2 Introduction

The existence and importance of competition among plants in arid lands has long been debated (Grime 1973; Tilman 1982). While there is some evidence that competition does occur in arid lands (Maestre & Cortina 2004), it is generally accepted that under severe environmental stress competition will not occur, as plants are adapted to be highly stress tolerant, rather than highly competitive (Thompson & Grime 1988; Goldberg & Novoplansky 1997). The stress-gradient hypothesis predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients, with facilitation being more common when stress is high (Maestre *et al.* 2009). Research on plant facilitation in arid systems has been quite extensive: in South Australian chenopod shrublands the long-lived *Acacia papyrocarpa* and the chenopod shrubs *Atriplex vesicaria* and *Maeriana sedifolia* have facilitative effects on surrounding plants, and not only are the effects different from species to species, but so are the mechanisms (Facelli and Brock 2000; Facelli and Temby 2002). However, there is evidence that negative species interactions are prevalent in arid systems much more than expected by chance (Bowker *et al.* 2010).

The possibility of competition is restricted by absence or little overlap in plant resource acquisition zones, and given open spaces are prevalent in arid zones competition may be less prevalent. Although competition may be less frequent in arid lands, Fowler (1986) suggests that it is no less important. As competitive abilities of plant species vary according to the conditions in which they grow (Grime 1977), it is important to consider that resources in arid lands vary both spatially and temporally. Competition should be stronger for species that complete their cycle during periods of high resource availability, such as annual plants that germinate and establish after rainfall events, or those in patches of high resource availability.

Arid lands are characteristically low in rainfall, and this rainfall is often quite variable. Temporally varied pulses of rainfall can change plant number, biomass, species richness (Lundholm & Larson 2004), and survival of annual plants (Sher *et al.* 2004), as well as competitive hierarchies (Novoplansky & Goldberg 2001). Temporal availability of resources for annual plants in arid lands occurs with rainfall, making both water and soil nutrients readily available through increased root uptake (Hodge 2004). Despite numerous studies assessing effects of temporal heterogeneity of resources on annual plant communities, the effect of spatial heterogeneity on density dependence of annuals has been largely overlooked (but see Cahill & Casper 1999).

Arid lands are characterised by their low rainfall and poor soil nutrient contents. It is suggested that if resources in arid lands were distributed homogeneously they would be below the threshold for plant growth, however, the typical heterogeneous pattern of the distribution of resources makes productivity possible (Noy-Meir 1973). Spatial heterogeneity is a well-established pattern of arid lands. Studies of spatial heterogeneity have been quite intensive and include patches of resources associated with long trees (Facelli & Brock 2000), shrubs (Facelli & Temby 2002), animal diggings (James *et al.* 2009) and fallen logs (Bowman & Facelli 2013). Resource patches have accumulations of soil nutrients (Tongway & Ludwig 1990; Facelli & Brock 2000) and increased water infiltration (Tongway *et al.* 1989; Tongway & Ludwig 1994), as well as an accumulation of seeds in the soil seed bank (Bowman *et al. in press*). There is also some evidence suggesting that resource heterogeneity can change the structure of annual plant communities: Facelli and Temby (2002) found abundances of annual plants were higher in resource patches under chenopod shrubs, and found that different annual plant species were in higher abundances depending which shrub they were growing under. Additionally, Bowman and Facelli (2013) found annual plant biomass, number, richness and diversity were all higher in resource patches next to logs than in open spaces.

Fallen logs are one of few documented non-living structures in arid lands which contribute to resource heterogeneity, making them unique in their role as patch-creating structures. Fallen logs can persist for a very long time in arid lands; the longest recorded time for a fallen log *in situ* is 69 years, however, Sinclair (2004) commented that this is an underestimate of their persistence. Soils next to logs have increased water infiltration, soil carbon and nitrogen contents as well as favouring annual plant growth compared to open spaces (Tongway *et al.* 1989) and these effects are more pronounced in grazed areas (Ludwig & Tongway 1996). In our previous work in South Australian arid lands, in addition to increased soil nutrient contents, we also found that logs increase numbers and species richness of seeds in the soil seed bank (Bowman *et al.* 2014). Despite patches creating an increase in herbaceous plants, resource patches alone may not be the main determinant for changes in community structure; density dependence may affect annual plant communities in arid lands too.

Resource patches may favour individual plants (i.e. nutrient accumulation and moderated soil temperatures), and patch conditions also favour higher densities of annual plants (i.e. through accumulated seeds and higher emergence). Therefore we ask here how these affect balance for the individual plant in the environmental created by fallen logs: is there an overall

increase in fitness? This is an important question since the Storage Effect Model (Chesson 2000b) predicts that under some combinations of density dependent effect and environment favourability variability can favour coexistence of species. The model requires that the favourable conditions that increase density have a non-linear combinatory effect with the favourable effect on the individual fitness. Over or under-additive effects of density and environmental favourability lead to species coexistence (Chesson 2000a). Importantly the model works for temporal heterogeneity as well as for spatial heterogeneity. To answer our question we looked into the effects of spatial heterogeneity on density dependence of annual plant communities in a chenopod shrubland under high and low water regimes. We also assessed changes in the community structure of annual plants in resource patches. The aims of this study were to determine if there are any changes in annual plant communities associated with spatial resource heterogeneity under high and low watering regime, including: a) density dependent effects and b) changes in community structure.

4.3 Methods

4.3.1 Site Selection

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 230 mm. 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 of scattered *Acacia papyrocarpa* trees with chenopod understorey dominated by *Atriplex vesicaria*, *Maireana pyramidata* (Benth.) (Paul G. Wilson) and *Maireana sedifolia* (Facelli & 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.) DC., an introduced plant from the Middle-East (Facelli *et al.* 2005). Fallen logs, abundantly scattered throughout the landscape, are known to increase soil nutrient availability and plant emergence (Bowman & Facelli 2013). Thus, when water is availability is ample there could be more density dependent negative effects.

4.3.2 Field experimental design

To assess any impacts of spatial heterogeneity on density dependence or community structure of annual plants, field studies were conducted over the winter growing season in 2012. On 16 Apr 2012, before rains triggered any substantial emergence of annual plants, twenty logs were selected in the field (all of similar size: 10-30 cm diameter and 2-3 m long with no branches). At each fallen log, three plots (30 cm by 20 cm) were pegged out immediately adjacent to the log with a 10 cm buffer between them. The same methods were conducted in adjacent open space sites, away from any other living or dead trees or shrubs. For each of the three plots at log and open space sites, one of three treatments was randomly allocated to annual plant growth: every third plant removed, two of every three plants removed, and a control where no plants were removed. This procedure effectively reduces density without substantially modifying the proportion of the different species in the community. Removal of annual plants in the treatments was conducted once a fortnight. The experiment was concluded on 12 Oct 2012.

Further assessment of impacts of spatial heterogeneity on density was assessed over the winter growing season in 2013 due to the very low rainfall and subsequent low plant numbers and biomass. On 6 May 2013 twenty fallen logs and matching open spaces nearby were located in the field. At each log and open space four 30 cm by 20 cm plots were marked out. One of four treatments was randomly allocated to each plot: increased density of the dominant species, natural density, reduced density and control. To increase density, a block of wood with 20 nails set 3 cm apart (in a five by four configuration) was pressed into the plot and one *C. annua* seed was planted in each of the holes left by the nails. We chose to augment the density by increasing *C. annua* as it is the dominant annual species in the area (Harris & Facelli 2003). Natural density plots did not have density of plants altered. Reduced density plots were mapped as seedlings emerged and every second plant was removed. To ensure there was no effect of procedure the block with 20 nails was also pressed into the natural and reduced density plots but no seeds were added. The control plot had no treatment applied. The experiment was concluded on 1 Sep 2013.

For both experiments all plots were fenced with chicken wire to protect them from grazing by sheep, kangaroos and rabbits. Additionally, ten of the log and open space plots for each experiment were watered regularly (fortnightly 2012, monthly 2013) with the same amount of rain as had fallen in the area for that month, thus doubling the water to these plots. The

experiments were completed when the majority of plants were flowering. For each plot all plants were harvested, counted, identified and dried for three days in an oven at 70° C. Above ground biomass of seedlings was then weighed.

4.3.3 Glasshouse experimental design

To assess the impact of soil from sites at logs and in open spaces on density dependence of annual plants glasshouse studies were also conducted over the two growing seasons of 2012 and again in 2013 due to the very low rainfall and subsequent low plant numbers and biomass. On 16 Apr 2012 36 additional fallen logs were located in the field. At each log and adjacent open space two soil samples (measuring 5 cm deep and 9 cm diameter) were collected and mixed as a composite sample for an interspecific competition glasshouse experiment, while two other samples were collected and mixed for an intraspecific competition glasshouse experiment, totalling 72 composite samples per experiment. The experiments were set up in glasshouses back at the University of Adelaide (South Australia). For information on soil properties for sites next to logs and in open spaces see Chapter 2 (Bowman *et al.* in press).

The set up for both experiments was the same: for each sample a plastic container (17 x 17 cm and 9.5 cm depth) with drainage holes drilled in the base was used. A weed mat sheet and 250 cm³ of washed sand were added and then the composite soil sample was placed on the top and watered. For the interspecific experiment each log and open soil sample was allocated a treatment of high or low water and of every third plant removed, two of every three plants removed, or control, where no plants are removed. The experiment was concluded on 27 Jul 2012. For the intraspecific experiment *C. annua* seeds were germinated in a separate container and were then sown in pots in a high or low water treatment, and with one, five or ten seedlings per pot. The experiment was concluded on 21 Jul 2012. For both experiments all pots were watered regularly and monitored for the first week to ensure all seedlings took to their new substrate. After the first week, high water treatments were watered twice a week and low water treatments once a week until saturated. After three weeks, when seedlings were well established, the watering treatments were reduced to once a week and once a fortnight respectively. The experiments were concluded when the majority of plants had flowered, all plants were removed from the pots, identified, dried for three days at 70° C and then total biomass was weighed.

To assess if density dependent effects were different for plants growing in soil from sites next to logs and open spaces with minimal disturbance to the soil profile, further glasshouse experiments were conducted. On May 8 2013 soil cores were collected immediately adjacent to 35 fallen logs and their corresponding open spaces. At each log and open space a PVC pipe of 10 cm diameter and 10 cm depth was hammered until the lip was level with the ground. Cores were then dug out by hand and a cap was carefully placed on the bottom of the core without losing any soil from the core. The cores were transported back to the University of Adelaide's glasshouse and watered to saturation. Log and Open soil cores were then randomly allocated a high or low water treatment, and increased or natural density. High water treatments were watered twice as often as low water treatments. Increased density treatments had six *C. annua* seeds planted in the pots. On 26 July all plants were harvested when the majority of plants were flowering and dried at 70° C for three days, then weighed for biomass.

4.3.4 Statistical analyses

For all primary plant data (plant number, biomass, species richness and species diversity), density treatments were combined (except procedural control in 2013 field experiments) prior to analyses to assess any differences in log and open soils, and high and low watering regimes. Primary plant data were analysed using split-plot two way ANOVA (2013 plant number and biomass were log transformed to equalise variances for analysis) in Graph Pad Prism 6.0. Where required, a post hoc Newman-Kuels multiple comparisons test was conducted. Biomass per capita data for all years was analysed in Graph Pad Prism 6.0 with linear regressions, except in 2013 when the open space, high water data was more suited to an exponential fit. Intraspecific competition of *C. annua* in the glasshouse was analysed in JMP IN 4 using a three-way ANOVA and post hoc Newman-Kuels multiple comparison test. Indicator species analyses, determining whether species were associated with specific site and/or water regime more than expected by chance, were run in PCORD to determine community structure of annual plants, using pooled treatments as per alpha data.

4.4 Results

4.4.1 Rainfall

The season's rainfall was higher in 2012 than in 2013 (261.8 mm and 226.8 mm respectively). However, during the actual period of the experiments rainfall was 139.8 mm (for 180 days) and 162.7 (for 119 days) for the growing seasons in 2012 and 2013 (fig 4.1).

Further, much of the rainfall in the 2012 season concentrated in a large event, possibly leading to high run-off and less infiltration.

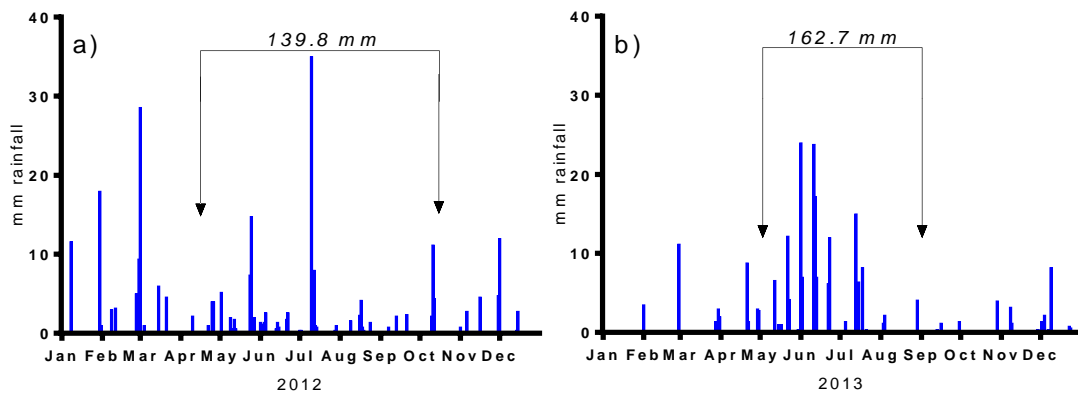


Figure 4.1: Daily rainfall at Whyalla Aero station (located 6 km from experimental set up) during a) 2012 and b) 2013. Arrows indicate beginning and end of each field experiment (Apr 16- Oct 12 2012 and May 6- Sep 1 2013 respectively). Rainfall data sourced from the Australian Bureau of Meteorology.

4.4.2 Primary plant data

No significant difference was detected between logs and open spaces, watering regime or any interaction for plant number or biomass in the 2012 growing season (fig 4.2a and 4.2c, $p > 0.05$). In the 2013 growing season plant number and biomass were significantly higher next to logs than in open spaces (fig 4.2b, $p = 0.0019$ and fig 4.2d, $p = 0.0104$ respectively). Species richness was higher next to logs than in open spaces for both growing seasons (fig 4.2e and f, $p = 0.0006$ and $p < 0.0001$ respectively). Shannon's diversity index was higher next to logs than in open spaces for both growing seasons (fig 4.2g and h, $p < 0.0001$ and $p = 0.0005$ respectively). No significant difference was detected for watering regime nor was there any interaction for any of these parameters in both growing seasons ($p > 0.05$).

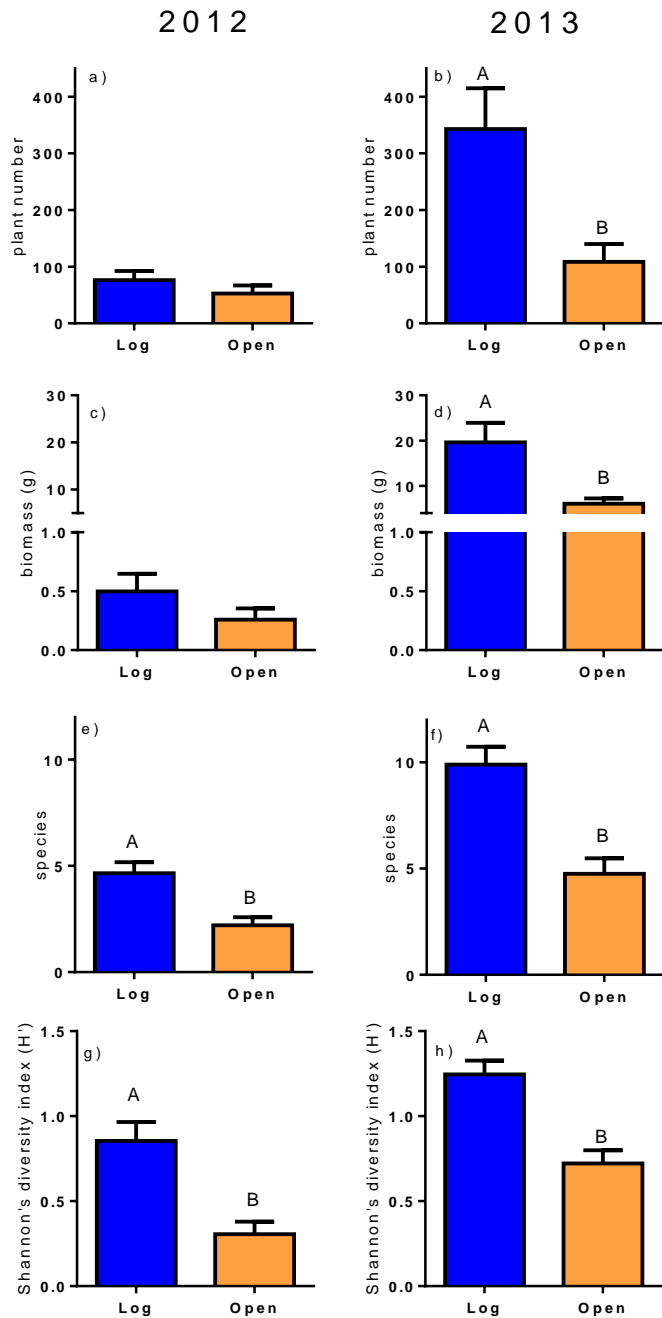


Figure 4.2: annual plants in the field for the growing season in 2012: a) plant number, c) biomass, e) richness, and g) Shannon's diversity index, and in the 2013 growing season: b) plant number, d) biomass, f) richness and h) Shannon's diversity index for all annual plants in plots grown next to logs and in open spaces (bars indicate SE, letters denote significant difference). Because of the lack of any effect, the watering regimes are pooled into the sites.

In pots in the glasshouse during the 2012 growing season an interaction was detected for number of plants emerged in soil next to logs and in the open and under high and low water regimes (fig 4.3a, $p = 0.22$). Species richness was higher in soils next to logs than soil from open spaces, and there was no effect of watering regime (fig 4.3b, $p = 0.004$). Biomass was

higher in soils from next to logs (fig 4.3c, $p < 0.0001$) and biomass was higher under high water regime (fig 4.3d, $p = 0.44$). Diversity was also higher in soils from next to logs (fig 4.3e, $p = 0.0002$), and diversity was higher under high water regime than low water regime (fig 4.3f, $p = 0.02$).

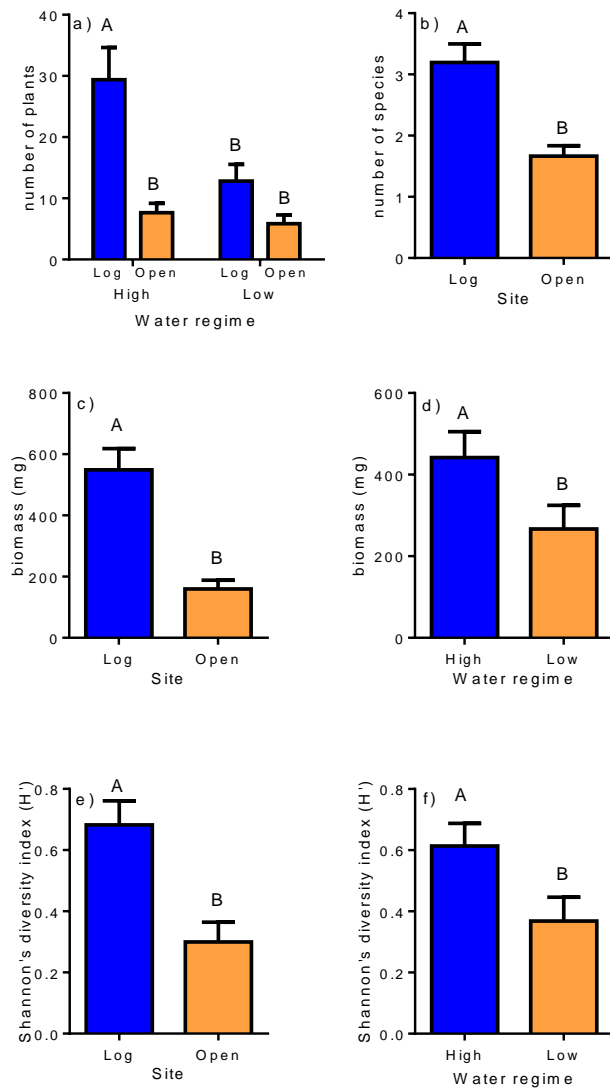


Figure 4.3: annual plants in the glasshouse for the growing season in 2012: a) plant number, b) species richness, c) biomass pooled for site d) biomass pooled for water regime, e) Shannon's diversity index pooled for site and f) Shannon's diversity index pooled for water regime (bars indicate SE, letters denote significant difference).

In pots in the glasshouse during the 2013 growing season the number of plants emerged, biomass, species richness and diversity were all higher in soils next to logs than soils in the open with no effect of watering regime (figs 4.4a-d, $p = 0.006$, $p = 0.003$, $p < 0.0001$, and $p = 0.0005$ respectively).

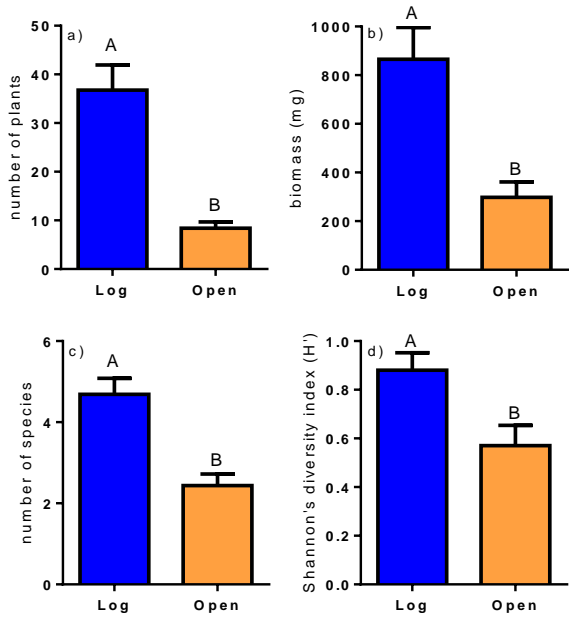


Figure 4.4: annual plants in the glasshouse for the growing season in 2013: a) plant number, b) biomass, c) species richness, and d) Shannon's diversity index (bars indicate SE, letters denote significant difference).

4.4.3 Density dependence of annual plants in the field

Even with large differences in biomass and number of plants across the two growing seasons, there was no significant effect of resources on per capita biomass in either year of field studies next to logs or in open spaces, under high or low water conditions (fig 4.5, $p > 0.05$).

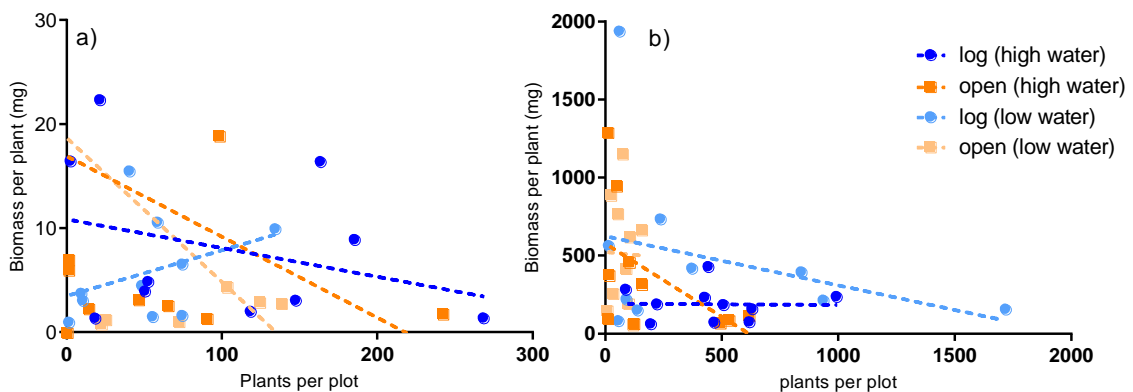


Figure 4.5: Biomass per capita (mg) for annual plants in the field next to logs and in the open, under high and low water regimes, for: a) the 2012 growing season (log, high water ($r^2 = 0.10$, slope = -0.03 , $p = 0.37$), log, low water ($r^2 = 0.13$, slope = 0.04 , $p = 0.30$), open, high water ($r^2 = 0.05$, slope = -0.08 , $p = 0.52$), open, low water ($r^2 = 0.05$, slope = -0.14 , $p = 0.52$)) and b) the 2013 growing season (log, high water ($r^2 = 0.01$, slope = -0.01 , $p = 0.95$), log, low water ($r^2 = 0.10$, slope = -0.31 , $p = 0.37$), open, high water ($r^2 = 0.28$, slope = -0.16 , $p = 0.11$), open, low water ($r^2 = 0.01$, slope = -0.94 , $p = 0.96$)).

4.4.4 Density dependence of annual plants in the glasshouse

Some evidence of density dependence was detected for per capita biomass in 2012 next to logs under the high watering treatment (fig 4.6a, $p = 0.0047$). No density dependence was detected for any other treatments ($p > 0.05$). *C. annua* plants had varied responses to density, site and water regime, with interactive effects between the three treatments (fig 4.6b).

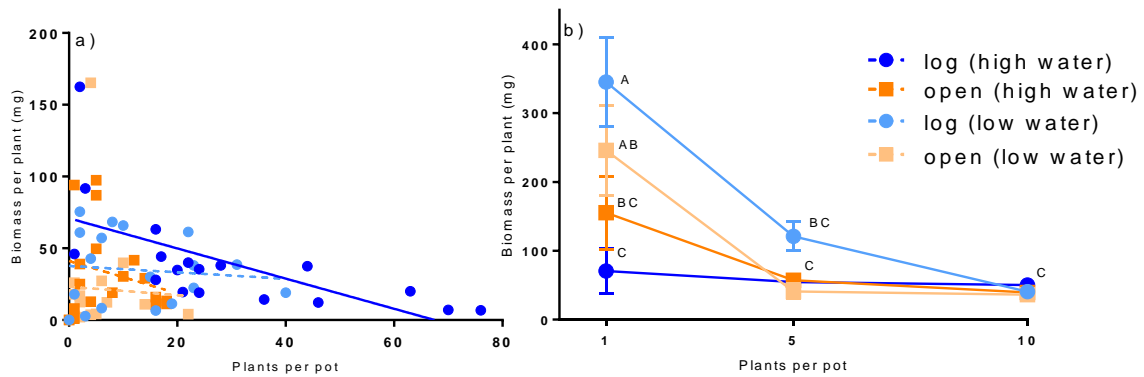


Figure 4.6: Biomass per capita (mg) of plants in the glasshouse in the 2012 growing season, in soil from next to logs (circles) and from the open (squares) under high (filled) and low (open) water regimes: a) for all species (log, high water ($r^2 = 0.40$, slope = -1.05 , $p = 0.0047$), log, low water ($r^2 = 0.01$, slope = -0.23 , $p = 0.68$), open, high water ($r^2 = 0.06$, slope = -1.13 , $p = 0.35$), open, low water ($r^2 = 0.01$, slope = -0.29 , $p = 0.85$)), and b) for *C. annua* plants of varied densities.

In the second growing season (2013) further evidence of density dependence of annual plants was detected in soil from next to logs under both high and low water treatments (fig 4.7a, $p < 0.05$). No evidence of density dependence was detected in soil from open spaces.

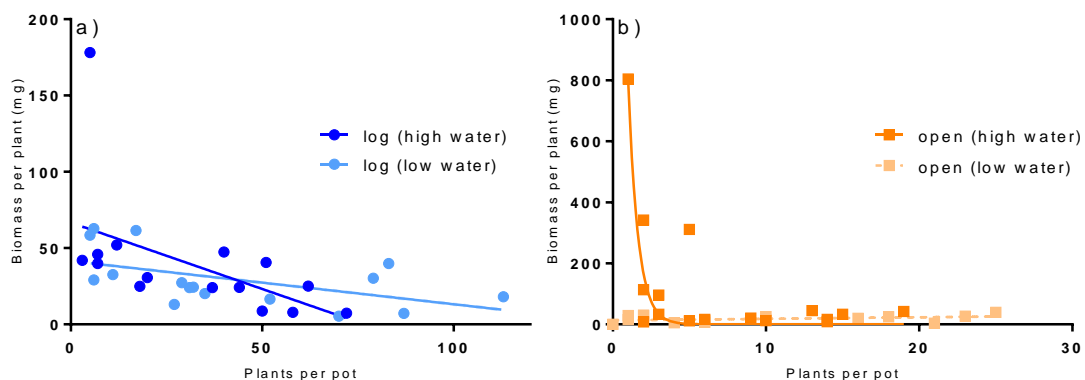


Figure 4.7: biomass per capita of annual plants in the glasshouse in 2013 subject to high and low water treatments: a) in soil cores from next to logs (high water ($r^2 = 0.27$, slope = -0.87 , $p = 0.04$), low water ($r^2 = 0.28$, slope = -0.28 , $p = 0.03$)), and b) in soil cores from open spaces (high water ($r^2 = 0.75$, $p = 0.13$), low water ($r^2 = 0.13$, slope = 0.50 , $p = 0.17$)).

4.4.5 Community structure of annual plants

In each growing season several species were found associated with certain site and water regime combinations more than expected by chance (ISA analysis). In the 2012 growing season, eight of fifteen emerged species were significantly associated with sites next to logs under high or low water regime, or irrespective of water regime (table 4.1, $p < 0.05$). In the 2013 growing season 19 of 35 emerged species were found associated with specific site and water regime combinations more than expected by chance (table 4.1, $p < 0.05$). Interestingly, some species were associated with a different site depending on the growing season.

Table 4.1: p values from an indicator species analysis for species associated with site and watering regime more than expected by chance for both growing seasons.

Species	Log * High Water	Log * Low Water	Log (no interaction)	Open * High Water
<u>2012 Experiment (n=15)</u>				
<i>Actinoble uliginosum</i>			0.0044	
<i>Atriplex vesicaria</i>	0.0242			
<i>Austrostipa</i> spp.		0.0102		
<i>Brachycome linearilobia</i>		0.0034		
<i>Calandrinia eremaea</i>		0.008		
<i>Crassula colorata</i>		0.0396		
<i>Medicago minima</i>		0.0208		
<i>Sysimbrium erysimoides</i>	0.007			
<u>2013 Experiment (n=35)</u>				
<i>Austrostipa</i> spp.	0.001			
<i>Brachycome linearilobia</i>			0.0054	
<i>Calandrinia eremaea</i>			0.001	
<i>Calotis hispidula</i>		0.006		
<i>Carrichtera annua</i>	0.0008			
<i>Crassula colorata</i>	0.0018			
<i>Gnephosis burkittii</i>		0.0002		
<i>Herniaria hirsuta</i>			0.0002	
<i>Lepidium</i> spp.	0.0004			
<i>Medicago minima</i>		0.0002		
<i>Mollugo cerviana</i>			0.0276	
<i>Omphalolappula concava</i>	0.001			
<i>Ptilotus</i> spp.		0.0406		
<i>Rytidosperma</i> spp.	0.0082			
<i>Sclerolaena</i> spp.		0.0164		
<i>Sysimbrium erysimoides</i>			0.0002	
<i>Tetragonia tetraganoides</i>		0.0456		
<i>Wahlenbergia</i> spp.				0.0002
Unidentified	0.007			

4.5 Discussion

We found annual plants were strongly influenced by rainfall regime and spatial heterogeneity of resources, however, little evidence of density dependence was found and this was restricted to glasshouse experiments, suggesting that it may only occur under very favourable conditions. Interestingly, even the results in the glasshouse varied across the two growing seasons, which can be related to the strong variation in year-to-year germination of arid land annuals (Pake & Venable 1996); in addition, the samples were treated differently: the 2012 soil was mixed prior to potting, where the 2013 soil was collected as intact cores. In this case we expect the intact cores would give a better approximation of relevant field processes. The first growing season only showed effects of density under high water and nutrient conditions, where the second growing season showed density effects in both high and low water treatments in soil from next to logs. Interestingly, *C. annua* in the intraspecific competition experiment had a mixed interactive effect at varied levels of density to water and nutrient treatments. While per capita biomass was lowest at high densities as expected, biomass was also lowest under high nutrient and high water conditions, which was contrary to our expectations. However, the individual response of *C. annua* cannot be expected to mirror other species' responses, nor even directly affect other species, as *C. annua* has a significantly deeper rooting depth than other annuals at this site (Harris & Facelli 2003). While generally these results may infer that higher water and nutrient treatments can increase density dependent effects, this did not translate into the field, and so it seems that root restriction or some other glasshouse factor may have exacerbated the effect.

While we found no evidence of density dependence differing between log or open space sites in the field, we did find our plant numbers and biomass to reflect those found in previous studies on spatial resource heterogeneity (see Bowman & Facelli 2013). More noticeable was the difference in plant biomass and number between years. Interestingly, while our second year had lower total rainfall than the first, plant biomass and numbers were much higher. However, the period when the experiments were conducted saw more rainfall in a shorter period in 2013 than in 2012. In 2013 rainfall occurred at regular intervals during winter ranging between 10-20 mm along with a few smaller events. In 2012 the rainfall was much more sporadic with multiple small events at irregular intervals and one very large rainfall event of 35 mm in July (see fig 4.4). It is also likely that the majority of the large rainfall event in July would not have infiltrated. Taking the size and frequency of rainfall events into account, our study shows the same trend as found by Lundholm and Larson (2004), where

pulse frequency and size can have large effects on plant number and biomass. They found pulse frequency and the total amount of water added can affect annual plant number, richness and biomass: biomass is highest under high volume of water and high pulse frequency and plant number and species richness are highest under high water volume and low water frequency. Further research to clarify the interactive effects of spatial heterogeneity (such as produced by logs) and specific patterns of water availability are warranted.

Changes in rainfall pulses may have contributed to the differences we found in species richness and biomass of annual plants across the two years, but no density dependent effects were detected with these varied pulses of rainfall. There is much evidence that water pulse frequency and size can shape population dynamics, species interactions, and ecosystem processes in arid ecosystems (Schwinning *et al.* 2004; Sher *et al.* 2004). Others have found specific species become the dominant competitor under varied water pulses (Novoplansky & Goldberg 2001), yet we did not find competition to be such a factor. In fact, Novoplansky and Goldberg (2001) suggested that pulsing regime has strong effects on relative competitive abilities, and that this would be more likely to influence field distribution patterns, but this did not prove to be the case in our study. It is possible that the plants in our study are avoiding resource competition by displaying root system plasticity and using different resources to their neighbours (Hodge 2004). However, we think it is simply a case of stress avoidance, where rather than compete for resources, the annual plants' survival mechanism is to set seed before dying after pulsed resources recede (Chesson *et al.* 2004).

As expected, we found that the community structure of annual plants changed with site and water availability. We expected this as specific germination requirements can provide fine temporal niche partitioning (Bazzaz 1996). Germination responses to temporal variation in resources are species specific (Pake & Venable 1996), and spatial heterogeneity may be particularly important in determining community structure because the strength of different biotic interactions can be modulated by environmental conditions (Reynolds *et al.* 1997). Previous studies have found soil samples incubated under different temperature and watering regimes produced different plant communities (Facelli *et al.* 2005). However, finding certain species associated with site and water regime more than expected by chance may not just be due to fine niche partitioning, but localised dispersal could mean that an individual species would tend to build up in spatial locations that are favourable to it (Facelli *et al.* 2005).

Spatial and temporal heterogeneity of resources both had significant impacts on annual plant community structure. Our study highlights the importance of conducting multi-year studies, particularly in arid systems where conditions can change dramatically between years. Given the difference in our results across the two years it would be beneficial to assess density dependence in subsequent years, particularly given the years we studied did not deviate greatly from the average rainfall for the area. We are not the first to fail to detect competition in arid ecosystems (see Mangla *et al.* 2011). Goldberg and Barton (1992) state that documenting when competition occurs does not necessarily imply that it is ecologically important, yet we would argue that determining under what conditions competition is active is still important. We agree with an old argument by Grime (1973), which suggests that species in arid lands are limited to those which are tolerant to specific conditions limiting their productivity, rather than to competitive effects. It appears that annual plants in this system are growing when conditions are most favourable and setting seed as conditions decline, as per the Storage Effect Model (Chesson *et al.* 2004). However, this is an interactive effect, as not only are these plants growing when temporal conditions are favourable, but also where the spatial conditions are favourable. Fallen logs create better conditions for annual plants in good years, as not only is water availability (which is lower around logs) not as critical, but logs create patches which can alleviate nutrient and temperature stress which may otherwise limit plant growth. This study highlights the importance of fallen logs: they are an excellent example of interactions after death, where the remains of plants can still have an effect on communities. While there may be some evidence for density dependence in annual plant communities next to logs, we found that resource patches and pulses of rainfall are much more important for determining annual plant community structure.

4.6 Acknowledgements

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Contribution to the Paper	Designed experiments, conducted all field work, conducted all statistical analyses and wrote the manuscript.		
Signature		Date	7/12/14

Name of Co-Author	Jose M. Facelli		
Contribution to the Paper	Advice on experimental design, statistical analyses, and help in drafting process.		
Signature		Date	7/12/14

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Contribution to the Paper			
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Contribution to the Paper			
Signature		Date	

The dynamics of formation and dissipation of patches associated with fallen logs in a chenopod shrubland of southern Australia

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5.1 Abstract

Resource heterogeneity is a prominent feature of arid systems, and affects their functional properties. While many studies have documented the presence of this patchiness and described their properties, just a few have looked into the dynamics of their formation or their dissipation. Previously we have characterised the patches of resources, seeds and soil conditions around fallen logs in chenopod shrublands of South Australia. Here we report on patch formation and dissipation associated with introducing and removing fallen logs in the same system. We hypothesised that patches will quickly accumulate seeds and more slowly nutrients, and that they would dissipate fairly rapidly after log removal. This process should be faster in heavily grazed areas because of more intense transport processes. To assess the formation of patches we introduced logs and artificial logs (large PVC pipes, to rule out the contribution of the decaying log) to open spaces at various orientations and at two distances from a watering point. We took soil samples upon initial deployment and three years later. We also assessed any changes to annual plant communities after logs and artificial logs had been deployed for three years. To look at dissipation of a patch, fallen logs in pairs were selected with an adjacent open space area and one of each pair of fallen logs was removed. At sites corresponding to each remaining log, adjacent open space and removed log we deployed soil temperature and moisture probes. We also collected soil samples to determine soil nutrient contents and soil seed bank initially and also one year later. We found three years was not enough to create measurable changes to soil nutrient contents or annual plant communities when introducing logs, but instead found a temporal change in nutrients, potentially due to unplanned destocking which occurred during our experiment. Our patch dissipation results were quite intriguing, as the removal of the log produced immediate changes to the microclimate associated with the log, but we found that one year was not long enough to dissipate accumulated nutrients or seeds from the soil.

Key Words: annual plants; arid lands; resource heterogeneity; seed bank; soil nutrients; soil water content

5.2 Introduction

The presence and functional importance of resource heterogeneity in arid lands is well established. If resources were distributed homogeneously throughout arid systems, little or no productivity would occur, however, the presence of resource patches increases the productivity of the whole system (Noy-Meir 1985). These patches can be associated with trees (Facelli & Brock 2000), shrubs (Facelli & Temby 2002), grasses (Tongway & Ludwig 1994), animal diggings (James *et al.* 2009) and fallen logs (Tongway *et al.* 1989; Bowman & Facelli 2013). Generally these studies of patches have largely focused on documenting the existence and characteristics of patches, but there is relatively little information available on how these patches form or dissipate over time. Patchiness is an important driver of productivity and diversity of arid systems (Noy-Meir 1985), hence information about patch dynamics is critical to enhance our understanding and ability to manage them.

The formation of patches has been suggested to be driven both by biotic and abiotic processes. Ludwig and Tongway (1995) suggest that resource patches are created by both water and wind erosion of soils and subsequent deposition next to features in a landscape, such as shrubs and logs. Studies by Emmerson *et al.* (2010; 2012) showed similar transport and subsequent deposition in the landscape also occurring with seeds. Additionally, while modelling seed dispersal in patchy landscapes, Thompson *et al.* (2014) demonstrated that vegetation traps seeds. This deposition of materials has been demonstrated in studies which have reported a substantial and rapid accumulation of soil within experimental plots with vegetation and branches (Tongway & Ludwig 1996; Reid *et al.* 1999). However, a patch formed by living plants can be much more complex than one formed by inert structures, as plants can directly modify their environments. Plant root systems can modify soil nutrient and moisture contents through resource acquisition (Sala *et al.* 1989) and hydraulic lift (Horton & Hart 1998). Plant canopies can change light availability and temperature (Facelli & Brock 2000), and dead plant material can change many soil properties (Facelli & Pickett 1991). While some studies have considered how patches may form, information about the timing of patch formation is largely absent from the literature.

Very few studies have looked into dynamics of patch formation. Facelli and Brock (2000) used space-for-time substitution to assess the resource patchiness created by the *Acacia papyrocarpa* tree and how this patchiness changed with the age of a tree. They found the development of the patch is slow (up to 100 years) around this long lived tree (maximum age estimated conservatively at 400 years). In contrast, Tongway and Ludwig (1996) found changes in soil nutrient contents after introducing branch piles for just three years, and Bowman and Facelli (2013) found increased annual plant species diversity on introducing logs to open spaces after just four months.

Similarly, very little information is available on the dissipation of patches. It has been suggested that soil nutrient patches can remain after a patch forming entity is removed (Callaway *et al.* 1991; Barnes & Archer 1996). A few studies have quantified this: Facelli and Brock (2000) found that patch soil nutrient contents remain higher than in adjacent open spaces for at least fifty years after the death of a long lived tree; Tiedemann and Klemmedson (1986) found nutrients to remain at least thirteen years after canopy removal; and Bechtold and Inouye (2007) found soil nutrient contents decreased six years after they removed the canopy of a shrub. Again, all of these studies involved living patch forming entities, and patch dissipation after the removal of a non-living patch forming structure, such as a log, may elicit different results.

Fallen logs are a unique patch forming entity, as they are one of few that are non-living. Fallen logs increase soil nutrient contents, lower volumetric water content and increase annual plant numbers (Bowman & Facelli 2013). Patches formed by logs can be particularly important in grazed areas, as grazing reduces vegetation, thus increasing transport of material, and reduces the number of resource patches, disrupting or even negating the function of resource patches (Heshmatti *et al.* 2002; Sparrow *et al.* 2003; Popp *et al.* 2009). Changes in soil and vegetation as a consequence of grazing can lead to a lack of vegetation recovery even after resting periods of several years (Friedel *et al.* 2003; Sinclair 2005). To restore degraded arid lands resource patches need to be reconstructed (Sparrow *et al.* 2003). Fallen logs are known to create patches (Bowman & Facelli 2013) and their introduction to grazed areas could help to re-establish patches. Additionally, it has been noted that fallen logs are a major resource which are often removed from natural ecosystems for use as firewood (Vázquez *et al.* 2011). Hence we query the effects of both formation and dissipation of a patch associated with fallen logs. Another study using long term information in a similar

system suggested that patches around logs reach a fairly stable condition 12 years after a log falls to the ground (Bowman *et al.* in press). This suggests that there must be some rapid changes and strong accumulation of materials soon after a log is deposited.

The objectives of our study were to assess the dissipation and formation of patches associated with fallen logs. We chose to focus on short term effects on soil properties. We conducted our research at the Middleback Field Research Centre in South Australia. The key questions we chose to ask were: i) are there any changes in soil microclimate, soil nutrients and soil seed bank after removal of a fallen log over a one year period, and ii) are there any changes to soil nutrients and annual plant communities associated with the introduction of fallen logs into open spaces over three years. In addition we introduced artificial logs (PVC pipes) of similar diameter to the natural logs to determine if the decomposition of log material contributed to the formation of patches.

5.3 Methods

Our study was conducted at Middleback Field Research Centre, 16 km North West of Whyalla, South Australia (32°57'S, 137°24'E). The climate of the area is arid, with average yearly rainfall around 230 mm. Rainfall is concentrated in the winter months (June-August), which drives the growth of a diverse annual plant community. The winters are mild (July mean 16.9° C) while the summers are hot (January mean 30.2° C) and usually dry, but can be punctuated by drenching rains during La Niña events. The soils are predominantly brown calcareous earths with clay-loam texture, and have 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 & 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). Throughout the area dead individuals of *A. papyrocarpa* are common and the logs frequently found on the ground most likely belong to this species.

5.3.1 Dissipation of a patch

The Two Mile Paddock was selected for this part of the study, as while there is some grazing degradation the environment is otherwise homogenous and there is an abundance of fallen logs. To determine any changes when removing a log from its environment existing fallen logs (pieces of wood 2.5-4 m long and 10-30 cm diameter, henceforth referred to simply as “logs”) were located in the paddock on 24 Mar 2013. We selected logs to be comparable: they had very simple structure, fairly straight, with few or no branches and had no sign of decay. Logs were present at a variety of orientations. Logs were selected in pairs with an adjacent open space area, leaving a minimum 3 m distance from logs and away from any other living or dead plants. The position on the ground of one of each pair of logs was marked out using roofing nails and then the log was removed (henceforth referred to as “removed log”). For the duration of the experiment the site of the removed log was always treated as if the log was still present. The remaining log was left *in situ*. Ten replicates of log, open space and removed log were used for this part of the study.

To assess any changes in microclimate associated with the removal of fallen logs, 5TM© soil temperature and moisture probes (Decagon Devices) attached to EM50© data loggers (Decagon Devices) were deployed at six sets of log, open space and removed log sites. Soil probes were deployed at 5 cm depth in open spaces, immediately adjacent to logs and next to removed logs. The data loggers were set to measure soil temperature (°C) and soil volumetric water content (%) every hour from 23 March 2013 until 22 May 2014.

To assess any dissipation of accumulated nutrients and seeds from the patches around fallen logs, soil samples were collected for further analysis. Soil collection from removed log sites was treated as if the logs were still present, thus soil was collected immediately adjacent to where logs were originally positioned, not directly underneath the removed log. After collecting a soil sample the hole was filled in with soil from the area to decrease effects of microtopography and a marker was placed in the centre so the same area was not used for subsequent sampling. On 24 March 2013 one soil sample (collected using a cookie cutter 5 cm deep and 9 cm diameter) was collected from the immediate vicinity of the logs, removed logs and from their corresponding open space sites. This sample was sent to CSBP soil and plant laboratory (Western Australia) for determination of soil organic carbon, total nitrogen, nitrate nitrogen, ammonium nitrogen, available phosphorus, available potassium, sulphur, electrical conductivity, and pH. Further soil samples were collected in the same way and sent

for the same analysis as described above, on 6 May 2013, 1 August 2013, 5 November 2013 and 22 May 2014. Soil samples collected as above on 24 March 2013 and on 24 March 2014 were retained for seed extraction. Seed extraction was conducted as per Malone (1967) within the week post collection and a cut test was used to determine viability of seeds.

5.3.2 *Formation of a patch*

The Purpunda Paddock (3 km from the Two Mile paddock) was selected for this part of the study due to the abundance of fallen logs and the presence of a piosphere effect (see Heshmatti *et al.* 2002). The stocking rate in Purpunda Paddock was reduced throughout the experiment until September 2013 when stock was completely removed. We chose two distances from the watering point: 400 m and 2 km, respectively representing a heavily grazed situation and a good rangeland condition. In open spaces at both distances we introduced logs and artificial logs on 22 May 2011. Logs were obtained from standing dead trees; they were 2-3 m in length and 10-30 cm diameter with simple branching structure. We also introduced pieces of PVC pipe of 22.5 cm diameter and 2 m length with caps on the ends as structures physically equivalent to logs, but without producing effects such as nutrient and organic material leaching that could be produced by logs. Henceforth we refer to these PVC pipes as “artificial logs”. At each distance we walked along an arc, maintaining the set distance from the watering point, and at random distances along the curved transect we deployed logs and artificial logs to open spaces. Before placing a log or artificial log we collected two soil samples (using a cookie cutter 5 cm deep and 9 cm diameter) approximately 50 cm apart and combined these for further analysis. The log or artificial log was then placed over where samples had been collected. At each distance from the watering point, six logs and six artificial logs were introduced, half in a north-south orientation, and half in an east-west orientation. Slopes are minimal in the area, and orientation with respect to sunlight was considered more likely to affect patch characteristics

To assess any accumulation of soil nutrients associated with the introduction of logs and artificial logs, we collected a further two soil samples (as above) approximately 1 m apart along a randomly selected side of each log, as well as two samples in open spaces. We collected these samples precisely three years after the initial samples were collected (22 May 2014). All soil samples collected throughout the duration of the experiment were sent to CSBP soil and plant laboratory (Western Australia) for determination of soil organic carbon,

total nitrogen, nitrate nitrogen, ammonium nitrogen, available phosphorus, available potassium, sulphur, electrical conductivity, and pH.

To determine if there were any changes to annual plant communities after logs and artificial logs were introduced, we harvested all annual plants next to the logs and in open spaces on 2 Sep 2013. At each log or artificial log we collected annual plants within a plot of 80 x 20 cm on both sides of the log and the same sized plot in an adjacent open space. Plants were counted, identified, oven dried and weighed to determine above-ground biomass.

5.3.3 Statistical analyses

Differences in soil temperature were determined using split plot one-way ANOVA (after log transformation of the data to equalise variances). To determine if soil dried at different rates after a rainfall event, data were log transformed and linear regressions were performed. Soil nutrient analyses were analysed using split plot one-way ANOVA (after data were log transformed to equalise variances). Seed bank differences were determined using split plot one-way ANOVA, total propagules and total viable seeds were log transformed for analysis. We used Jmp In 4 to conduct analyses of variance to assess any differences in annual plant communities three years after introducing logs and artificial logs. To assess any differences in soil nutrient contents three years after introducing logs year we conducted split plot two-way ANOVA in Graph Pad Prism 6.

5.4 Results

5.4.1 Dissipation of a patch

Average maximum daily soil temperature was higher in open space soils than next to logs or, surprisingly, removed logs for June, July, August (winter in the southern hemisphere) and April while all other months showed a similar trend (fig 5.1). Average minimum daily soil temperature was higher next to logs than in the open for May, Jun, Jul, Aug, Dec and Apr. No difference in minimum temperatures was found between soils next to logs and removed logs, nor between open spaces and removed logs. These trends were consistent across all months.

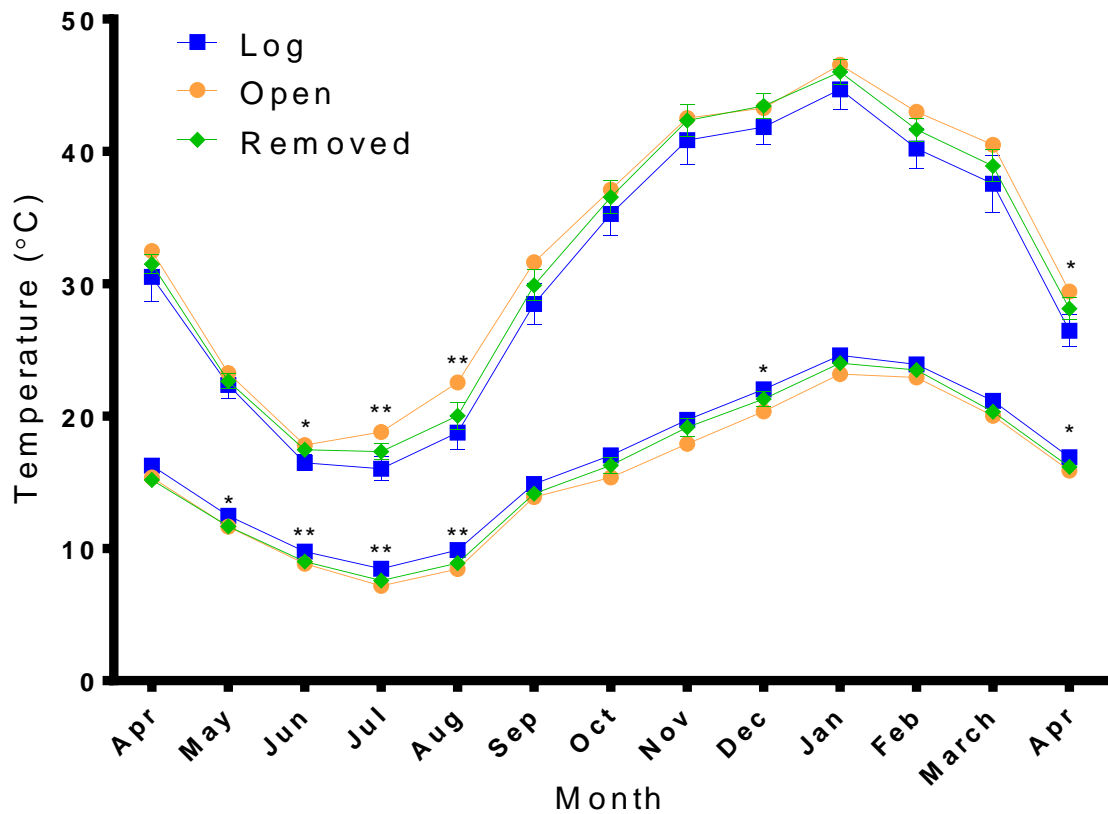


Figure 5.1: Average maximum and minimum daily soil temperature at 5 cm depth for sites next to logs, open spaces and where logs were removed, encompassing April 2013 to April 2014 (* $p < 0.1$, ** $p < 0.05$, data log transformed for analysis, bars indicate SE- note that values are so low the symbols often obscure SE).

Soil volumetric water content was generally higher in soils in open spaces than soils next to logs or removed logs (fig 5.2a). When a single rainfall event (of 23.8 mm) and subsequent drying was analysed, open space soil had a significantly different slope, showing soil dried more slowly than next to log and removed log soils (fig 5.2b, $p < 0.0001$). Soils next to logs and removed logs dried at the same rate, but the water content of soils next to logs was consistently higher than for soils next to removed logs (fig 5.2b, $p < 0.0001$, data log transformed for analysis).

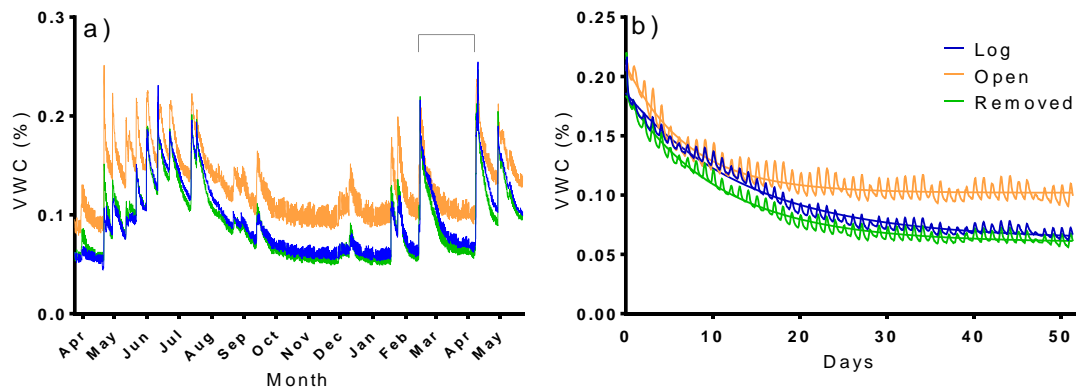


Figure 5.2: Soil volumetric water content at 5 cm depth for log, open and removed log a) hourly between 24 Mar 2013 and 22 May 2014 (bracket indicates rainfall used for b) and b) immediately following a single rainfall event of 23.8 mm on Feb 13 2014 and subsequent drying.

Soil nutrient analyses showed no significant effect of the removal of logs. Organic carbon (fig 5.3a) and total nitrogen (fig 5.3b) contents were consistently lower in open spaces than next to logs or removed logs, but no significant differences were found between logs and removed logs at any time. No significant differences were detected for any other nutrient across the three treatments.

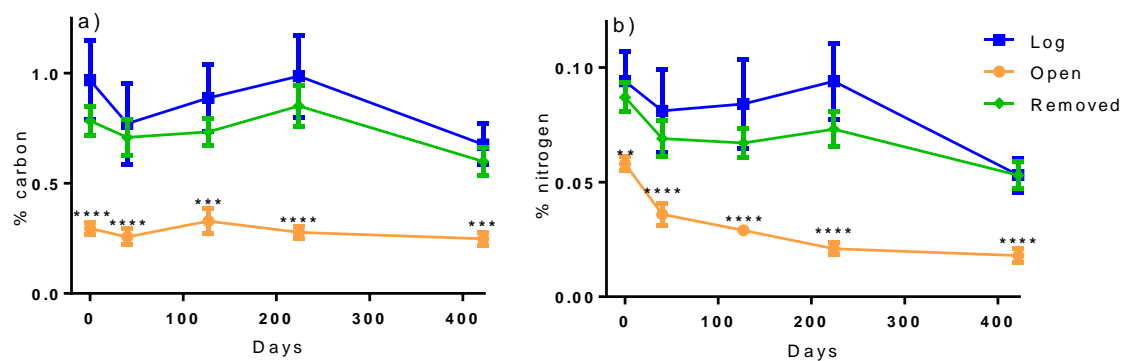


Figure 5.3: a) organic carbon and b) total nitrogen contents in soils collected next to logs, removed logs and in open spaces periodically over 422 days (** $p < 0.05$, *** $p < 0.01$, **** $p < 0.001$, data log transformed for analysis, bars indicate SE).

No difference in the soil seed bank variables was ever detected between logs and removed logs but sites corresponding to these two treatments had consistently higher seed bank parameters than open space sites (fig 5.4). These results were expected in 2013, as logs had not yet been removed, but we did expect some change in 2014. The number of propagules,

propagule species richness, viable seed numbers and viable seed richness were all higher next to logs and removed logs than open spaces in 2013 and 2014 (figs 5.4a-h, $p < 0.01$).

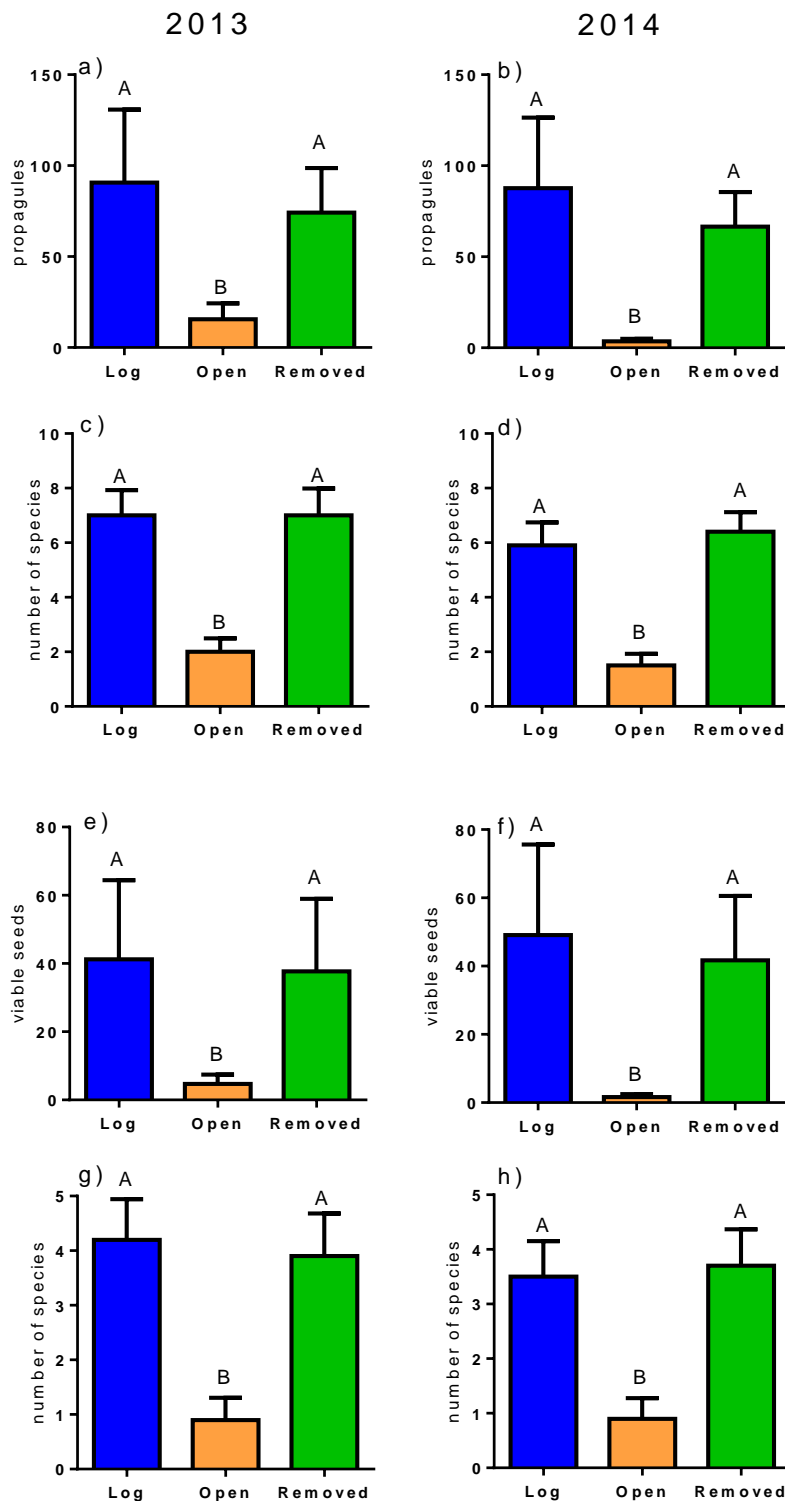


Figure 5.4: a and b) Propagule numbers, c and d) propagule species richness, e and f) viable seed numbers and g and h) viable seed species richness, for 2013 (prior to log removal) and 2014 (one year post log removal) (split plot one-way ANOVA, bars indicate SE).

5.4.2 Formation of a patch

We did find some changes in soil nutrient contents, but not in the direction we expected. No difference was detected between introduced log and open soils for organic carbon in 2014, but soil collected in 2014 had significantly higher organic carbon contents than soil collected in 2011 (fig 5.5a, $p = 0.0001$). We similarly found no difference in log and open space soils in 2014 for all soil nutrient contents. We did find initial soils to have higher total nitrogen, available phosphorus and available potassium than log and open space soils collected in 2014 (figs 5.5b, 5.5c and 5.5d, $p < 0.0001$, $p = 0.0151$ and $p = 0.0143$ respectively). We also found that regardless of log or open site, organic carbon contents of soils were higher in the good condition area than in the degraded area (fig 5.6, $p = 0.0254$). No effect of introducing logs or pipes to the ground was found on annual plants after three years. We detected no effect for analyses using plant number, species richness or biomass when looking at log, artificial log or open, pristine or degraded, and orientation (see appendix for figures comparing artificial logs and natural logs, and log orientations).

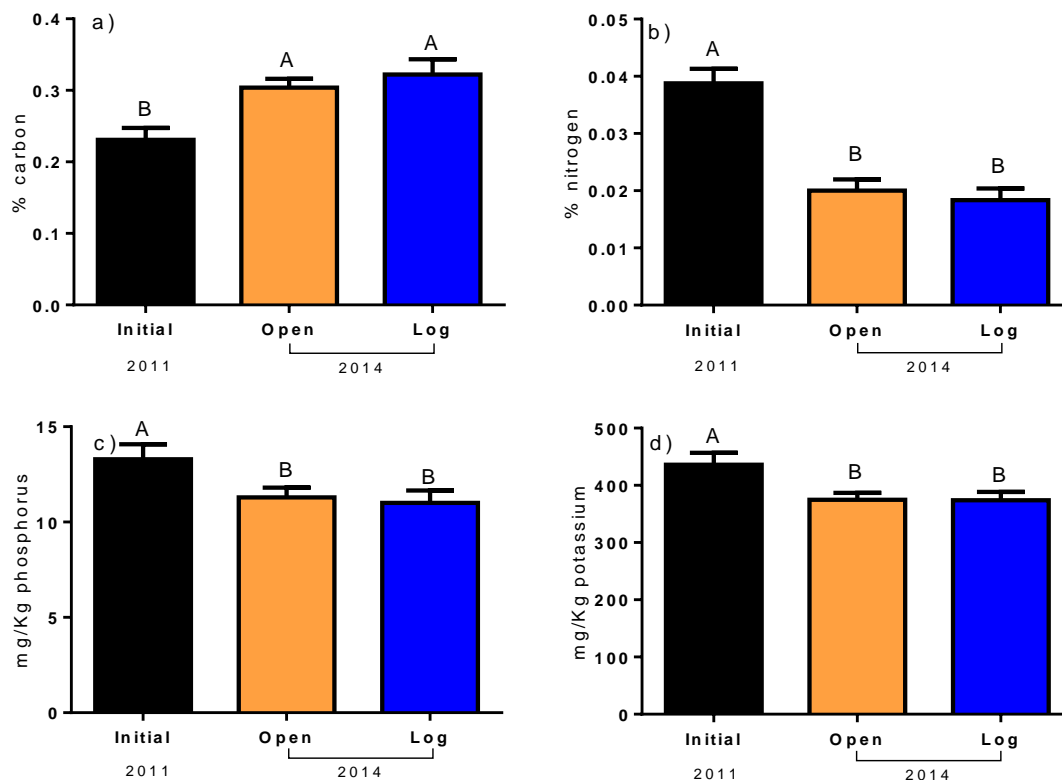


Figure 5.5: a) organic carbon, b) total nitrogen, c) available phosphorus and d) available potassium contents of initial soil samples in open spaces, and for post log deployment at open spaces and next to introduced logs (split plot two-way ANOVA, bars indicate SE).

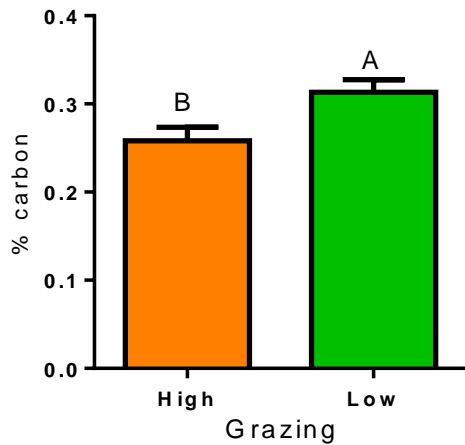


Figure 5.6: organic carbon contents of soils in high and low grazing areas (split plot two-way ANOVA, bars indicate SE).

5.5 Discussion

5.5.1 Dissipation

Results from our patch dissipation experiment indicated that removing a fallen log did not immediately change soil properties around logs and, surprisingly, that the temperature microclimate conditions associated with fallen logs were not affected by the removal of the log during the study period. The water dynamics, on the other hand, were changed: patches with logs removed retained less water and lost it faster than patches around logs.

Fallen logs have a moderating effect on soil temperatures with lower maxima and higher temperature minima compared with open spaces. This moderating effect is similar to that found associated with shading created by shrubs in arid systems (Segoli *et al.* 2012). Interestingly, the removal of fallen logs appeared to have only a very small immediate effect on this moderation: while maximum soil temperatures remained lower in removed log patches than in open spaces, no difference was detected for minimum soil temperatures between log and removed log soil or between removed log and open space soils. We did observe that there were abundant annual plants next to logs and removed logs over winter but not in the open, which may explain the reduction in maximum temperature, particularly during winter months, where logs were removed (A. Bowman personal observation).

While removing the logs only had minimal effect on soil temperature, the changes to soil volumetric water content were significant. While log and removed log soil patches were consistently drier than open space soil, we had predicted that removing logs would trigger

changes making the patch more similar to open space soils. This was certainly not the case; instead soil volumetric water content was even lower in removed log patches. We suggest that the presence of logs can have two opposing effects on water infiltration: on the one hand they may change the surface of the soil in ways that reduce infiltration, most likely by creating a hydrophobic surface (e.g. because of organic matter properties or presence of a dense microphytic crust). On the other hand, during a rainfall event that triggers rainfall runoff, the physical presence of the log results in pooled water on the surface which will slowly infiltrate, increasing soil water content. Indeed structures such as logs on the ground obstruct runoff from open spaces and can favour infiltration (Ludwig *et al.* 2005). After removing a fallen log, surface soil properties could still reduce infiltration, but as there is no physical barrier to cause pooling, the microsite of the removed log ends up with even lower water content than the soil in the log patch.

Changes to microclimate conditions when a log is removed may be particularly important for germination and soil seed bank dynamics. There is evidence that higher soil temperatures can decrease seed viability and compromise bet-hedging strategies (Ooi 2012). We would expect that the moderating effect that logs have on soil temperatures create more favourable conditions for soil seed bank persistence than open spaces, and removing fallen logs would also reduce how favourable the environment is for seeds. Additionally, while seed dormancy for most species in this system is controlled by soil temperature (Facelli *et al.* 2005), germination success is generally determined by moisture (Baskin & Baskin 2014) and our findings show that removing a log would seem particularly unfavourable for seedling germination. Yet despite these speculations, we did not find any changes in the soil seed bank one year after removing fallen logs.

As expected we found no difference between log and removed log soil seed banks in 2013, as samples were taken prior to log removal, hence in 2013 removed log treatments were simply log treatments. Similar to Bowman *et al.* (in press) we found stark differences in the number and species richness of seeds between log and open space soils. Kinloch and Friedel (2005) also found lower seed densities associated with bare soil surfaces compared to areas with vegetation or depressions. However, we did expect that there would be some changes to the soil seed bank one year post log removal, as we expected the balance between germination, longevity and accumulation/removal would change, but this was not the case. The lack of change when a log is removed may simply be due to most species forming the soil seed bank

in Australian arid lands having small and variable germination fractions, resulting in little fluctuation in seed bank size (Ellner 1985; Pake & Venable 1996). However, Facelli *et al.* (2005) reported changes in soil seed bank composition over 18 months, but the dynamics was strongly species specific. Several species at our field site are known to have long persistence in the seed bank, with half-life estimated between 5-10 years, which is important during times unfavourable for germination and seed production (Facelli *et al.* 2005; Kinloch & Friedel 2005).

We did not find any changes in soil nutrient contents between log and removed log soils. This is consistent with previous studies that found soil nutrients in patches to take several years to dissipate. Bechtold and Inouye (2007) found the contrast in soil nutrients between shrub and open spaces decreased six years after they removed the canopy of the shrub, and Tiedemann and Klemmedson (1986) found similar changes, but 13 years after canopy removal. Facelli and Brock (2000) looked into the dissipation of soil nutrients after the death of a long lived tree, and they found soil nutrients remained higher than open space soils for at least 50 years. Additionally, we expect if grazing had been present during the study the patch may have dissipated at a faster rate through increased surface erosion where logs had been removed, but not next to logs as sheep avoid obstacles in the landscape (Lange 1969).

5.5.2 Formation of a patch

We were surprised to find that introducing logs to open spaces had no effect on soil nutrient contents or annual plant growth after three years. In our previous work we found changes in annual plant diversity after introducing logs to the same paddock after only four months (Bowman & Facelli 2013). Similarly, Tongway and Ludwig (1996) introduced piles of branches to the ground for three years and they found clear increases in soil carbon and nitrogen contents, as well as improved water infiltration rates and promotion of growth and establishment of perennial grasses (Ludwig & Tongway 1996).

The overall changes in soil nutrients over the three year period of the study were most unexpected. Rather than finding any changes produced by introducing logs, we found that soil contents of carbon, nitrogen, phosphorus and potassium all changed over a relatively short time. While these changes may reflect destocking of the paddock, they may also simply be a product of temporal variability. The stocking rate in Purpunda Paddock was reduced throughout the experiment until September 2013 when stock were completely removed.

However, current literature suggests that changes to soil properties after destocking are quite slow (Lesschen *et al.* 2008), and studies with grazing exclusion found organic carbon, total nitrogen and total phosphorus in soils all increased over time (Rong *et al.* 2014), while in our study only organic carbon increased, while other elements declined.

5.5.3 Conclusions

Our findings show patch formation and dissipation to be more complex than originally anticipated. Patch accumulation did not occur within a three year period, yet logs are known to create patches at twelve years *in situ* (Bowman *et al.* in press), suggesting that a log patch develops roughly between three and twelve years. After removing a log we found immediate changes to soil microclimate, but soil seed bank and soil nutrients continued to persist unchanged for at least one year. Given that our site had little topographic gradient, few large rainfall events (none of them torrential) and low or no grazing present, we are not surprised that soil nutrients and seed bank were unchanged. We predict that faster rates of dissipation will be found from removed patches in areas with greater topographic gradient and higher stocking rates. Our changes in microclimate conditions were highly unexpected, particularly regarding soil volumetric water content. The removal of a fallen log creates a patch that is unique in the environment and very different to any others in the system, as areas of log removal still retain some properties of the patch, but develop some new ones. More information is needed on the role of this patch type and about its length of its persistence. Given other patch types take several years to dissipate it is important to continue to monitor how this patch type changes with time. The dynamics of formation and dissipation of patches depend on the patch forming entity, yet there are still many questions unanswered about the dynamics of patchiness. Given the prevalence of grazing in arid lands this remains an important area for future research and ultimately a general model of patch formation and dissipation in arid lands is required for enhancing our ability to manage and restore these fragile ecosystems.

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Conclusion

The focus of this thesis has been the assessment of the spatial heterogeneity associated with fallen logs in chenopod shrublands of South Australia. While patchiness in arid lands is well documented, most current literature focuses on patches created by living organisms (i.e. by plants or activity of animals) and little is known about other patch types. Some early work by Tongway *et al.* (1989) and work completed in my Honours year (Bowman & Facelli 2013) established that resource heterogeneity is associated with fallen logs, yet these studies only documented differences in nutrient contents and annual plant growth. Until now the mechanisms behind the differences between patches associated with fallen logs and the nearby open spaces have been unknown. The relative contributions of patch factors (i.e. seed bank, soil properties and microenvironment) on plant growth next to logs were also yet to be determined. Additionally, there is very little information available on the formation and dissipation of resource patches across all resource patch types. Hence my work on resource heterogeneity associated with fallen logs has aimed to fill an important knowledge gap in arid land ecology.

6.1 Key findings

Several key findings of this project have important implications for studies on resource heterogeneity. I was able to confirm studies conducted by Tongway *et al.* (1989) and my own previous work by establishing that fallen logs do create resource patches, increasing soil nutrient contents and annual plant growth. Consequently I began to analyse in detail the patch characteristics. I established that fallen logs are important sites for seed accumulation in the soil seed bank, particularly in heavily grazed areas where other patch types have been reduced under grazing pressure. I also looked at microclimate effects which are largely unknown in all patch types; fallen logs create a moderating effect on soil temperatures (making a more favourable site for seed longevity), and interestingly reduce soil volumetric water content, which makes logs a very unique patch type indeed.

Fallen logs are an example of plants continuing to interact with the environment after death, similar to plant litter (Facelli & Pickett 1991). While facilitation of annual plants is arguably one of the most important features associated with resource patches, fallen logs are able to create positive effects on plant establishment and growth despite no longer being alive. Given that the properties of patches are relatively unknown, I delved further into which

characteristics of patches associated with logs are contributing to increased plant establishment and growth. Here I found some particularly interesting results: the presence of lichen crust next to logs does not change the plant growth; the increased plant establishment and growth associated with logs does not create density dependent effects; and fallen logs create changes in the community structure of plants. Interestingly, one experiment where I separated accumulation of nutrients and seeds from microclimate effects showed that plant numbers, species richness and species diversity were relatively similar provided the plants experienced the accumulative patch effects, the microclimate effects, or both. Only biomass of the plant communities next to logs was much higher when accumulation and microclimate effects were combined. This suggests that even the simplest patch types may be able to increase plant establishment, provided there is some effect of microclimate or accumulation of materials.

One of the most unique contributions to our knowledge on patch dynamics is my work on formation and dissipation of the patch. Unfortunately, being a doctoral project, my work was somewhat time restricted. I was fortunate to have use of the long term data set from the Koonamore Vegetation Reserve. From the thesis data I established that fallen logs after 12 years *in situ* already have substantial associated resource and seed accumulation in patches, but there is no detectable change for logs of ages between 12 years and 78 years *in situ*. However, it is important to note that there was substantial natural variability in the logs used for this study (such as size, structure, orientation and slope) which could not be standardised due to the small size of the long-term data set. I also introduced logs and monitored their contribution to soil nutrient contents and changes in plant establishment for three years. No changes were found for these characters in the three year period, and unfortunately no data were available for the time period between three years and twelve years *in situ*. However, this does allow us to speculate that the formation occurs somewhere in this time window. As these logs continue to remain *in situ*, it will be possible to continue to acquire information to clarify this issue. Similarly, my work on patch dissipation proved quite intriguing. Removing a fallen log had some immediate effects on microclimate conditions, but no effect on accumulated resources one year after removal. This study in particular would require from further monitoring to determine at what point the patch dissipates and becomes similar to open spaces.

The characterisation of resource heterogeneity associated with fallen logs has important implications for patchiness throughout this system. Resource patches can be quite dynamic and each patch has different characteristics and can favour different plant assemblages. Patches created by logs are particularly important in grazed areas as they cannot be removed directly by browsing stock, nor do they fail to grow when hooves trample the surrounding soils. However, it is also important to note that logs are regularly collected for firewood in many arid and semi-arid systems, and this removes an important patch type from these systems.

6.2 Conceptual framework

Patchiness created by fallen logs is important for the function of the ecosystem. As suggested by Noy-Meir (1985), if resources were distributed homogeneously throughout arid systems, little or no productivity would occur, however, the presence of patches increases the productivity of the whole system. My work on patchiness created by fallen logs supports the model of resource distribution derived by Tongway and Ludwig (1990); they suggest that erosion occurs, mostly in open spaces, and trees, branches, shrubs and grasses slow water movement, allowing greater water infiltration and deposition of soil, litter and other plant matter. Fallen logs cannot actively acquire resources as living resource patches may, hence patches created next to fallen logs would be formed by abiotic processes. Water and wind move soil particles and seeds which accumulate next to fallen logs, creating a patch of higher nutrient availability and seed densities, and facilitating plant establishment and growth. Once these patches are established it is probable that there is some level of positive feedback, as once logs favour higher densities of plants, the higher density would hence favour more accumulation of materials, particularly the incorporation of seeds into the seed bank.

Fallen logs are one of many patch forming entities in arid lands, but compared with other patch types they have some very unique properties. While other patch types have been documented to contain higher soil nutrient contents and more seeds in the soil seed bank, they also generally have higher soil water content. While fallen logs do have higher soil nutrient contents and more seeds in the soil seed bank, it is the microclimate conditions of this patch that make logs unique. In soils next to logs a moderating effect in temperature is created, similar to that found under shrubs and trees in arid lands. This could create more favourable conditions for seed viability and longevity. Additionally, contrary to the model by Tongway and Ludwig, fallen logs have lower soil water content than surrounding open space soils.

These surprising microclimate properties certainly raise questions about the effect this patch type has on plant communities.

The accumulation of seeds next to logs, probably along with increased seed longevity as a by-product of moderated soil temperatures contributes to increased seedling emergence and diversity maintenance. Not only would seeds which may not survive in the open now reside in a log patch, but the different combination of environmental factors next to logs would give germination cues which may not occur otherwise in the system. Given that the effect of the log is stronger than any effects created by biological soil crusts, and that we did not detect any effect of density dependence in annual plant communities next to logs, the unique combinations of properties next to logs are very important for diversity maintenance. Diversity maintenance is particularly important in areas of grazing degradation.

Introduced grazing has had wide spread impacts in arid systems all over the world. Not only can direct browsing reduce plant biomass, numbers and seed output, but damage to soils by trampling can be quite extensive. These changes to soil surfaces have significant implications for transport and deposition processes in arid systems. While there may be lower soil nutrients, less plants and seeds in an area, there are also less patch-forming entities and greater movement of particles throughout a system. This would make any remaining structures particularly important for diversity maintenance, as there would be fewer resource patches and hence fewer areas for plant establishment. With increased transport and reduced retention areas, resources will be removed from the system or accumulate at levels lower than the saturation point for productivity. Under these conditions logs would be very important, as they cannot be removed through grazing practices and they provide favourable sites for seedling establishment. Unfortunately, fallen logs are often not common in arid systems as logs are removed for human uses, such as building and for firewood.

Future studies should also focus on the practical applications of fallen logs in arid lands. Particularly in areas subject to heavy grazing degradation, the introduction of fallen logs may assist to restore land through creating resource patches in a relatively short timeframe (3-12 years). Further, it is still important to address the timing for dissipation and formation of patches associated with logs. The formation of a patch next to a log would need to be monitored further to determine how long it takes to form. It is important to consider that patches may form faster in areas where material movement is enhanced, either through

grazing, large rainfall events, moderate topographic gradients or a combination of these. Similarly it would be beneficial to monitor the dissipation of a log patch over a longer time frame to determine when the patch becomes the same as open spaces. Given removing a fallen log decreased soil water content even further, it would be beneficial in the future to determine why soil water content is lower in log patches but not in other resource patches.

There is a need for a general framework for patch dynamics: there is very little information available about the formation and dissipation of patches, nor is there any information about the relative importance of different patch types: does size matter, or are other properties more important? The relative contributions of different patch types to a specific system have yet to be determined. Within the chenopod shrublands of South Australia patchiness associated with long-lived trees, shrubs and logs have all now been studied extensively, yet there has been no comparison across these patch types. Is the patch associated with the long-lived *Acacia papyrocarpa* more important because it persists for longer and has higher concentrations of soil nutrients than a patch next to a chenopod shrub? Or is it possible that each patch type with its different properties provide sites of establishment which are specific to certain species? If this is the case certainly the maintenance of multiple types of patch is very important for ecosystem function. While some species may be quite liberal in their germination requirements, if other patches have species associated with them more than expected by chance (as found next to fallen logs) specific patch types may be necessary for the persistence of some species. Certainly it is important to maintain multiple types of patches, increasing the diversity of a system, in times of changing environmental conditions.

Similarly, no comparison has been made across systems where resource patches are a common feature. While a tree may be the dominant driver for species diversity in one system, it may be a different patch type which promotes facilitation in another system. A comparison of the difference between patch and open spaces across systems may show that patches are more important depending on the system: if patches accumulate a higher proportion of resources in one system, they may be more important than a system where the open matrix may have slightly more allocation of resources, and hence more ability to promote seedling establishment. This comparison across systems could be conducted using current literature and a simple equation to compare between patch types and systems: using soil nitrogen contents as an example, $(N_{(\text{patch})} - N_{(\text{open})}) / N_{(\text{open})}$ would give a comparable value. Additionally, some systems may contain many small patches while others have few but larger patches,

hence some proportion of patch to open area comparison may allow across system comparisons.

Further it would be beneficial to investigate the role of fallen logs across environmental gradients. This thesis now firmly places importance on fallen logs in arid systems. Additionally, logs are established as important features in many ecosystem types: they create refugia in river systems for macroinvertebrates and juvenile fish species; they are important in grasslands for invertebrates and vertebrates as shelter, as well as providing protection from grazers to plant species; and in forests they provide important sites for fungi and seedlings to establish. Logs are functionally important in many systems, but they are important for different reasons: a study of logs across environmental gradients may determine in which conditions logs change their role from resource accumulator, to a decaying site for seedling establishment.

6.3 Concluding remarks

My work on fallen logs has made an important contribution to our knowledge on resource heterogeneity, and consequently to the ecology of arid lands in general. Fallen logs are often an overlooked structure in arid lands, as they are non-living and often removed for firewood, yet logs are important creators of resource heterogeneity and hence may have important implications for land management. Fallen log resource patches are particularly unique given the microclimate conditions associated with them. There are still some mechanisms behind formation and dissipation that are unknown, as well as these unique microclimate conditions which require further investigation. Despite this, fallen logs can be firmly placed into existing conceptual framework for resource heterogeneity in arid lands, making an important contribution to productivity of the whole system.

6.4 References

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