The effect of resource dynamics on invasive annual and native perennial grasses in grasslands of the mid-north of South Australia

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Abstract

The abundances of invasive annual grasses and native perennial grasses in the mid-north of South Australia are highly patchy. This study aimed to investigate the effects of soil moisture dynamics on the growth and interactions between these grass types. I proposed that different moisture dynamics favour different grass types and aimed to investigate the factors involved.

I measured grass abundances, environmental variables and soil-moisture regimes in several grasslands. At most sites annual grass abundance was positively correlated with rainfall, soil moisture after rainfall and higher soil productivity. Perennial grass abundance was negatively correlated with annual grass abundance and soil moisture after rainfall, and was weakly positively correlated with percentage summer rainfall, elevation, radiation, gravel, and slope.

In a field experiment seed addition or watering, but not removing perennial grasses increased the recruitment of annual exotics in perennial-grass dominated areas. No perennial grasses recruited successfully into areas dominated by annual grasses. In the glasshouse, seedlings of the common native perennial grass *Austrodanthonia caespitosa* (Gaud.) H.P.Linder required high soil moisture to establish. When in competition with a common annual exotic grass, *Avena barbata* (Pott ex Link), *Austrodanthonia* had significantly lower chances of surviving a drought than seedlings without competition.

At low soil moisture *Avena* had similar growth rates to common native perennial grasses but at high soil moisture its growth rates were significantly higher. It performed best in soil moisture regimes that included periods of extreme soil moisture as opposed to constant intermediate moisture. Throughout the soil moisture gradient *Avena* maintained a low root/shoot ratio. The perennial grasses increased growth rates less with increasing soil moisture and increased root/shoot ratios with decreasing soil moisture. In the field, regardless of soil moisture, annual grasses had a strong competitive effect on *Austrodanthonia*, while *Austrodanthonia* had no competitive effect on annual grasses.

Overall, perennial grasses responded little to the environmental variables investigated, but strongly to annual grass abundance, while for annual grasses soil moisture was the driving variable. Except for lower mortality at low soil moisture, there is no evidence that perennial grasses have any competitive advantage at any soil moisture availability during the growing-season shared with annual grasses. Increased perennial grass abundance thus requires decreasing annual grasses or encouraging perennial grasses outside the shared grass growing-season.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give my consent to the copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Tanja Lenz   Date: 15/9/04

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1. Environmental factors and the invasions of temperate grasslands by annual grasses

Plants species that are accidentally or deliberately introduced to new areas are often capable of spreading into agricultural or natural ecosystems. Some plants spread and persist without any apparent negative effects on the composition or structure of local plant communities, whereas others cause significant changes. Such changes include reductions in species diversity and fundamental changes in ecosystem process such as nutrient cycles and fire regime (D'Antonio & Vitousek 1992; Maron & Connors 1996; Crooks 2002; Heidinga & Wilson 2002). Introduced plants that have significant impacts on natural ecosystems are generally referred to as invasive plants or plant invaders (Bazzaz 1986; Cronk & Fuller 1995).

Systems that have been extensively altered by the introduction of new plant species include the temperate grasslands of the Americas and southern Australia. Temperate grasslands are defined here as natural or semi-natural temperate systems, consisting dominantly of a perennial graminoid understorey, with or without scattered woody overstorey. In the Americas and in southern Australia, European settlement resulted in the extensive replacement of perennial graminoids and other understorey species with a relatively small suite of Mediterranean annual grasses and annual dicots (Harris 1967; Mack 1981; Morrow & Stahlman 1984; Dickson *et al.* 1987; Huenneke 1989; Mack 1989; Heady *et al.* 1992; Morgan 1998b).

Changes in grazing regimes, possibly influenced by unusual climatic episodes, are usually correlated with these changes in species composition (Mack 1989; Heady *et al.* 1992; Stromberg & Griffin 1996). The details of the mechanisms driving these changes, however, are not always clear. Conceptual frameworks predict that invasions are more likely to occur in disturbed or productive systems or systems of low diversity and that systems are more likely to be invaded by species that are already invasive elsewhere, are related to other invaders or are clonal (Baker 1965; Fox & Fox 1986; Orians 1986; Kolar & Lodge 2001). Newer frameworks stress the importance of changes in resource dynamics, competitive interactions and stochastic events that favour different species at different times (Johnstone 1986; Davis *et al.* 2000).

For most frameworks, however, changes in resource dynamics and effects of resources on resident species are paramount. Variability in resources (whether due to disturbance, productivity effects, species identity or stochastic events) affects recruitment, growth and competitive interactions and in turn is affected by these factors. The differential uptake and accumulation of resources between species can change resource availabilities after invasion (Vitousek *et al.* 1987; Vinton & Burke 1995; Reynolds *et al.* 1997), growth or competitive responses of other plants and community succession (Vitousek *et al.* 1987; Reynolds *et al.* 1997). Independently of the

theoretical framework applied, knowledge of the regulation of recruitment, growth and competitive interactions under different resource availabilities are required to predict the outcome of invasion. The purpose of this research is to examine the effect of resource dynamics on invasive annual and native perennial grasses in grasslands of the mid-north of South Australia. As elsewhere, annual grasses have heavily invaded these systems. This project aims to review the patterns and processes of this trend in other systems, to determine the abiotic factors that correlate with the invasion in the mid-north of South Australia and to determine how fluctuations in the main abiotic factor affect the key plant species involved.

Invasions of temperate grasslands by annual grasses

Few systems would have experienced a similar degree of change since the start of intensive pastoral and agricultural practices about 10 000 years ago than temperate low-lying grasslands. Once major ecosystems in the Americas, Asia, South Africa and parts of Southern Australia, lowland temperate grasslands are now listed as among the most endangered ecosystems in the world (Kirkpatrick *et al.* 1995). Due to their suitability for agriculture and grazing, large areas of natural grassland have been completely cleared and re-seeded with agricultural crops or pasture species (Table 1.1).

The remaining temperate grasslands are classified as semi-natural, i.e. unploughed and with native species present, but generally modified by fertiliser addition, deliberate and accidental species introduction and stock grazing. The invasion of weeds is the largest threat to the remaining temperate grasslands in Australia (Kirkpatrick *et al.* 1995) and recognised as a large problem worldwide (Mack 1989).

Once annual grasses have invaded a perennial grassland, they can cause a variety of changes to the plant species composition and ecosystem processes, such as resource dynamics and fire regimes (D'Antonio & Vitousek 1992). Thus, invasive annual grasses do not simply add a few more species to the species list and compete with resident plants for resources. Rather, they are able to change the entire species composition and dynamics from a diverse perennial system to an annual system of lower diversity. Firstly, annual grasses compete successfully with perennial grasses for soil moisture in most systems, reducing perennial grass growth, reproductive output as well as root formation in deep soil layers (Harris 1967; Romo & Eddleman 1987; Dyer & Rice 1999; Hamilton *et al.* 1999; Ogle *et al.* 2003). Consecutive years of such competition from annual grasses could reduce the populations of perennial grasses and possibly lead to their extinction (Foster 2000). The dense litter layer produced by the annual grasses further affects plant communities. Its physical presence and its potential effects on soil moisture and temperate dynamics and competitive interactions (Grime 1979; Carson & Peterson 1990; Facelli & Pickett 1991; Facelli 1994; Facelli *et al.* 1999) have been shown to decrease plant species richness in

grasslands and other herbaceous communities (Grime 1979; Facelli *et al.* 1988; Carson & Peterson 1990; Foster & Gross 1998; Lenz *et al.* 2003) as well as assist the further establishment of annual grasses themselves or other weeds, creating a potential for positive feed-back cycles. (Whisenant 1990; Lenz *et al.* 2003). The effects of litter on productivity can vary with species and site (Heady 1956; Fowler 1986; Facelli & Facelli 1993).

Region	Original area (km²)	Estimates and descriptions of current status
South Australia	10,000 [1]	0.5% extant [1]
Volcanic Plain, VIC	15,000 [1]	0.3% extant [1]
Wimmera, VIC	1,000 [1]	0.1% extant [1]
Riverina, VIC	10,000 [1]	1% extant [1]
Riverina, NSW	25,000 [1]	1% extant [1]
Monaro, NSW, ACT	2,700 [1]	1.3% extant [1]
Gippsland Plains, VIC	600 [1]	0% extant [1]
Midlands, TAS	125 [1]	6% extant [1]
Total for Australia	**64,004 [1]**	**0.77% extant [1]**
Californian prairie, USA	100,000 [2]	> 10 000 km² cultivated, perennial grasses rare away from coast [2]; 70,000 km² dominated by annuals [3]
Mixed prairie, USA	475,000 [5] - 628,000 [4]	Average of 31% extant [4], but highly variable in space [5]
Mixed prairie, Canada	240,000 [6]	24% extant, half of which is grazed [6]
Short-grass steppe, USA	181,790 [4] - 280,000 [7]	45 [4]-60 [7] % extant
Tall-grass prairie, USA	677,300 [4]	2.8% [4]
Tall-grass prairie, Canada	7,200 [6]	< 1% [6]
Coastal prairie, USA	38,000 [8]	< 1% in pristine condition [8]
Fescue prairie, Alberta	-	< 5% [9]
Fescue prairie, Canada	255,000 [10]	< 5% [10]
Palouse prairie, USA	100,000 [11]	94% cleared[12]; remainder largely dominated by Eurasian annuals[11]
South America	700,000 [13] - > 1,000,000 [14]	1% pristine, condition of remainder generally unknown [13]; grazed Argentinean grasslands often dominated by annual grasses [15]
Northern Asia	2,860,000 [16]	1/3 severely degraded [16]

Table 1.1: Available estimates and descriptions of temperate grassland cover adapted from various sources. Website estimates (March 2003) based on government data or diverse publications, some not referenced. 1) Barlow (1999, in Ross 1999); 2) Heady (1992); 3) Huenneke (1989); 4) http://www.npwrc.usgs.gov/resource/2000/grlands/pastpres.htm; 5) Reed & Peterson (1961, in Coupland 1992); 6) http://www.mb.ec.gc.ca/nature/whp/prgrass/df03s33.en.html; 7) Lauenroth & Milchunas (1992); 8) Smeins *et al.* (1992); 9) http://www.albertapcf.ab.ca/changing_prairies.htm#4; 10) http://www.mb.ec.gc.ca/nature/whp/prgrass/df03s34.en.html; 11) Daubenmire (1992); 12) http://biology.usgs.gov/luhna/chap10.html; 13) Fundación Vida Silvestre Argentina (2003). Identification of the last wild grasslands of the South American Southern Cone. http://www.vidasilvestre.org.ar/pastizales/index_eng.asp; 14) Zhou (2002); 15) D'Antonio (1992); 16) Soriano (1979, in Mack 1989).

Beyond changes in species composition, some invasive annual grasses (as well as invasive perennial grasses) can change the fire regime of a grassland. The invasive annual cheatgrass (*Bromus tectorum*), for example, increases both the size and the frequency of fires in Idaho and it is estimated that the frequency increased from one fire per 60-110 years to one fire per 3-5 years

(Whisenant 1990, in D'Antonio & Vitousek 1992). Consequent changes included increased likelihood of flooding, soil erosion and the destruction of otherwise intact systems (D'Antonio & Vitousek 1992).

Models of invasion

A variety of ecological models have been used to explain or predict the occurrence of plant invasions, such as this large-scale invasion of temperate grasslands. These models can be separated into two categories: models based on systems being in equilibrium, *i.e.* with stable attributes, and models based on systems with stochastic or non-equilibrium attributes.

Equilibrium models of invasion

Traditionally, plant invasions have been viewed either from the perspective of the invader or the perspective of the invaded systems almost exclusively. Baker (1965) published a set of characteristics that invasive plants seem to share, such as high growth rates and high reproductive output. Although these characteristics proved useful in detecting potential invaders (Newsome & Noble 1986), not all invasive species show these characteristics nor do all species that show these characteristics become invasive (Baker 1965). More recent research confirmed that there are few general characteristic traits of invaders. The only general characteristics common to plant invaders are: having a history of invasion elsewhere; having other invasive members in the family or genus; and vegetative reproduction (Kolar & Lodge 2001). Specific predictions, however, are difficult. For example, related pairs of exotic invasive, exotic non-invasive and native tall grassland plants in the United States show few physiological and morphological differences (Smith & Knapp 2001).

Whether ecosystems that are susceptible to invasion share similar characteristics is also unclear. Attributes that have been found to correlate to invasibility are disturbances, diversity, and productivity (which are in turn autocorrelated). Disturbances, especially, have often been viewed as an important or essential precursor for plant invasion (Fox & Fox 1986; Orians 1986). Although plants are more likely to invade disturbed communities (Hobbs 1989), disturbances are not essential for invasion to occur (Huenneke *et al.* 1990; Cronk & Fuller 1995). Indeed, disturbances will only promote invasion if they increase the availability of a limiting resource for the invader (Hobbs 1989).

Productivity may also be positively correlated with invasibility. Invasions of less productive systems such as arid systems are less frequent than of other systems (Fox & Fox 1986; Rejmánek 1989; Cronk & Fuller 1995). On a large spatial scale, it is not clear whether this is due to fewer species introductions or a lower likelihood that invasions occur in these systems. However, on a smaller spatial scale, the addition of resources often promotes invasion (Huenneke *et al.* 1990;

Harrington 1991; Hobbs & Mooney 1991; Burke & Grime 1996; Davis *et al.* 1999; Thompson *et al.* 2001; Brooks 2003), although, like disturbance, resource addition is not necessary for invasions to occur.

The correlation between diversity and invasibility is hotly debated. Some researchers argue that low diversity communities have more spare resources. This, combined with a decrease in resource use for any invaders due to lack of enemies, should lead to more invasions than in diverse communities (Shea & Chesson 2002). Positive correlations seen in larger scale studies may be due to other indirect effects. The results of various small-scale experiments support the hypothesis that increasing diversity correlates with decreasing invasibility (Tilman 1997; Naeem *et al.* 2000; Diemer & Schmid 2001; Hector *et al.* 2001; Kennedy *et al.* 2002; Stachowicz *et al.* 2002). Other researchers insist that these correlations do not prove direct cause-effect relationships and do not apply to large scales (Johnstone 1986; Rejmánek 1989; Cronk & Fuller 1995; Levine & D'Antonio 1999; Lonsdale 1999; Levine 2000; Moore *et al.* 2001). Troumbis *et al.* (2002), for example, used several measurements of invasibility for a system and concluded that correlations between diversity and invasibility depended on the response variable used. Other studies concluded that species identities were more important to invasion success than overall diversity (Van der Putten *et al.* 2000; Dukes 2001). Foster *et al.* (2002) found that, although invasion was greatest in high diversity microsites, further analysis suggested that this correlation was due to extrinsic abiotic factors such as the light environment and soil disturbances and not diversity *per se.*

The only traditional framework that takes interactions between the invader and the invaded system into account is the Enemy Release Hypothesis, which states that new arrivals can become invaders due to the lack of predators or herbivores. There is little direct experimental evidence for this (Keane & Crawley 2002). However, the success of many biological control programs (McFayden, 2000 in Myers & Bazely 2003) suggests that this mechanism can contribute to some invasions.

Non-equilibrium models of invasion

More recently, the theoretical frameworks that deal with plant invasions have changed from these broad-scale equilibrium models to non-equilibrium models that explicitly take species interactions and stochastic events into account, regardless of climate, productivity, diversity or disturbance regimes. These frameworks rely less on the general assumption of the existence of equilibrium in a system, and the necessity of disturbance by an external factor to promote invasion (Hengeveld 1988). Rather, invasion is seen as a stochastic event that relies on a 'window of opportunity' to open after any barriers to invasion have been removed (Johnstone 1986). Such occurrences are system- and species-specific. These models do not predict system- or species-

specific characters that promote invasion, but rather characters that influence the likelihood of 'windows of opportunity' to open. The 'fluctuating resource availability theory', in particular, states that '*a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources*', propagules are present and the characteristics of the species are suitable for this particular habitat (Davis *et al.* 2000). The model predicts that (1) systems that experience resource fluctuations are more likely to be invaded than systems with stable resource levels; (2) systems are more likely to be invaded after an abrupt change (disturbance, disease or pest outbreak) in the rate of supply of a limiting resource due to increased influx or decreased uptake by present vegetation; (3) invasibility increases with the interval between an increase in resource supply and capture of resources by present vegetation.

Few studies pursue detailed changes in recruitment of new arrivals and resource dynamics over time, thus direct experimental evidence for this particular model is still uncommon. Davies *et al.* (2001) found that different changes in resource availability over relatively short periods resulted in different invasion levels of native plant species in a weedy North American grassland. Pérez-Fernández (2000), while not directly testing the theory, concluded that the recruitment success of native and introduced plants in a Western Australian woodland depended not only on soil moisture levels, but also on variation in soil moisture levels. The theory also ties in well with all other models (Davis *et al.* 2000) and several other studies have stressed the importance of combinations of resource fluctuations, propagule availability and competitive interactions due to indirect evidence or the lack of other explaining factors (Buckland *et al.* 2001; Thompson *et al.* 2001; Troumbis *et al.* 2002).

Controlling processes in temperate grasslands

Non-equilibrium theories do not allow 'quick and easy' predictions about particular species or particular systems, since they rely on the interactions between the two. Thus, they require knowledge of the resource dynamics in a system and the responses of potential invaders and resident species to these resource dynamics. Next to grazing, factors that influence resource dynamics, such as climate, soil factors, topography and fire and their interactions, are the main factors that control species composition and function of grassy ecosystems (Moore 1964; Ripley 1992). The influences of environmental and biotic factors on grasslands are not easily separated, since they both interact. Grazing, for example, not only changes population dynamics of resident species (Facelli *et al.* 1989; Dyer & Rice 1997; Morgan 1998c; Peco *et al.* 1998) but also tends to increase bulk density and decrease soil infiltration rates resulting in lower soil moisture (Willatt & Pullar 1984; Dormaar *et al.* 1989; Naeth *et al.* 1990; Naeth *et al.* 1991; Chanasyk & Naeth 1995; Greenwood *et al.* 1997; Renzhong & Ripley 1997; Lutge *et al.* 1998; Gibson *et al.* 2000). Further, overgrazing can promote erosion (Hewitt 1996; Mwendera *et al.* 1997; Lutge *et al.* 1998; Li Sheng *et al.* 2000), decrease organic carbon levels (Li *et al.* 1997; McIntosh *et al.* 1997; Renzhong &

Ripley 1997; Hiernaux *et al.* 1999) and change nitrogen, phosphorus and potassium dynamics (Lutge *et al.* 1998; Hiernaux *et al.* 1999; Frank *et al.* 2000). Fire, similarly, affects resource availability, often decreasing organic carbon levels (Agrawal & Tiwari 1987; Ross *et al.* 1997; Materechera *et al.* 1998). For the purpose of this section, correlations of grassland species composition with climate, soils and topography will be considered as evidence for the importance of environmental factors, whereas correlations with grazing and fire history will be considered as evidence for the importance of a mixture of environmental and biotic factors.

The importance of environmental factors versus biotic factors in controlling species composition in grasslands can vary along a productivity gradient. In general, studies on bottom-up versus top-down controls *sensu* Fretwell (1977) and Oksanen *et al.* (1981) find that the importance of top-down forces in regulating plant growth increases with increasing primary productivity (Forkner & Hunter 2000) due to changes in predation pressure (Oksanen *et al.* 1981). Whether or not this generalisation is applicable to grasslands is questionable, since in most of these systems external forces regulate grazing regimes and predation is discouraged. However, similar predictions have been made for grasslands in general. Milchunas *et al.* (1988) suggest that the effect of grazing intensity on species composition and diversity depends on both rainfall and the evolutionary length of time the system has been grazed by large herbivores. They suggest that the effect of grazing on plant community structure increases with rainfall from semi-arid to subhumid grasslands. Thus, in some systems grazing can have strong effects on grassland species composition, regardless of current management. However, the longer the systems have been exposed to grazing by large herbivores, the smaller the effect of grazing will be on species composition as well as the invasion by exotics (Milchunas *et al.* 1988; Milchunas *et al.* 1989; Milchunas *et al.* 1992). Furthermore, a significant number of studies of semi-arid or temperate grasslands report environmental factors to be at least equally important (Ayyad & Dix 1964; Kemp & Dowling 1991; McIntyre & Lavorel 1994; O'Connor & Roux 1995; Harrison 1999; Stohlgren *et al.* 1999). In these studies, environmental factors explained most of the variation (> 50%) in species composition, or if grazing was included as an explanatory variable, they explained as much or more variation than grazing. In addition, while the effects of grazing in semi-arid grasslands can control crucial processes such as perennial grass recruitment (Austin *et al.* 1981; Defosse *et al.* 1997) and survival of some perennial grass species (Austin *et al.* 1981). Burke *et al.* (1998) suggest that soil water availability is the dominant factor controlling species composition in grasslands receiving less than 700 mm annual rainfall. With increasing rainfall, this gradually changes to other factors, such as soil nitrogen, grazing, fire and light. In grasslands with rainfall above 1200 mm these factors become the dominant factors in controlling the system.

In grasslands with annual rainfall less than 700 mm, where environmental factors strongly control species composition, they presumably can have a strong influence on the invasion of

perennial grasslands by annual grasses. The following sections will examine environmental factors that control the recruitment and growth of and interactions between annual and perennial grasses in general.

General controlling factors of annual and perennial grass abundance on large scales

<u>Climatic factors:</u> Rainfall, both in its timing and amount, is one of the main factors controlling the number of annual and perennial grass species as well as their abundance in grassy systems. For example, in Californian grasslands the number of perennial species increases and the number of annual species decreases with increasing elevation, which in turn is correlated to increasing rainfall and decreasing temperature (Bartolome 1980, in Heady *et al.* 1992). Similarly, the abundance of perennial grasses increases with increasing rainfall and altitude in "improved pastures" in NSW, and at the same time is negatively correlated to annual grass abundance (Kemp & Dowling 1991).

Differences in the timing of rainfall, both from area to area and from season to season, also affect the abundance of annual & perennial grasses. Annuals with their characteristic ruderal life history are favoured by cool season rainfall. The invasive annual cheatgrass (*Bromus tectorum*), for example, is favoured by rainfall during autumn and spring, whereas summer rainfall enhances the growth of *Agropyron spicatum*, a perennial grass that has been replaced by cheatgrass in many grasslands in North America (Harris 1967). In their native Mediterranean habitat, annual grasses also tend to be more abundant in areas where winter rainfall is high and summer rainfall low (Jackson 1985).

These differences are caused by the different life histories of annual and perennial grasses. By definition annuals complete their life cycle in a few months. This life history, coupled with fast initial growth and reproductive output under cool and wet conditions enables annual grasses to grow in climates with long droughts, since they can in general complete their life cycles before the onset of the next drought (Ewing & Menke 1983). In an experiment on Southern African grasses, for example, annual grasses completed their life cycle in a few months (75-125 days), whereas the perennial grasses did not flower within the first growing season (Ernst & Tolsma 1992). Under optimal experimental conditions, the annual grasses investigated in this study had also 3-4 times faster RGR than perennial grasses for the first 50 days after germination. In contrast, the increased abundance of perennial grasses with increasing rainfall or increasing summer rainfall, on the other hand, tends to be attributed to their higher growth rates and better competitive ability (Harris 1967; Hamilton *et al.* 1999). Once perennial grasses are established, annual grasses can have difficulty in colonising areas unless a disturbance such as overgrazing or drought result in patch mortality (Peart 1989).

Temperatures also affect the growth of annual and perennial grasses differently, even when they have the same photosynthetic pathways. In several comparisons between cool-season annual and perennial grasses, low temperatures tend to decrease perennial grass growth more than annual grass growth (Harris 1967; Harris & Wilson 1970; Jackson & Roy 1986).

Nutrient availability: Annual grasses have up to 3-4 times higher growth rates than perennial grasses at high nutrient availability (Muller & Garnier 1990; Ernst & Tolsma 1992; Claassen & Marler 1998). At low nutrient availability, however, this trend is reversed, with annual grass growth rates dropping, while perennial grass growth rates remain steady (Muller & Garnier 1990; Claassen & Marler 1998). Consequently, annual grasses can have a competitive advantage over a perennial grass at high nutrient availability and vice versa (Claassen & Marler 1998). Accordingly, in many instances, annual grass invasion correlates with higher nutrient availability or follows the addition of nutrients (Lauenroth & Dodd 1978; Huenneke *et al.* 1990; Kotanen 1997; Morgan 1998b; Chiarucci *et al.* 1999; Paschke *et al.* 2000). Similarly, management practices that decreased nutrient availability resulted in a decrease in annual grass abundances and an increase in perennial grass abundance in a Colorado oldfield (Paschke *et al.* 2000).

The effect of a pulse of nutrient addition to a grassland can result in a variety of long-term changes in nutrient availability. Annual and perennial grasses affect the nutrient dynamics of a system differently. Levels of nitrogen leaching, for example, are higher under annual grasses in both their native Mediterranean habitat and in other habitats that they have invaded (Joffre 1990; Maron, 2001, c.f. Svejcar & Sheley 2001). Perennial grasses in semi-arid grasslands, on the other hand, are often associated with resource islands of increased soil organic matter and mineralised nutrients (Hook *et al.* 1991; Vinton & Burke 1995; Schlesinger *et al.* 1996). Experimentally induced invasion of annual species can erase these resource islands, resulting in lower nutrient heterogeneity in the system (Vinton & Burke 1995). Since such resource islands can have facilitative effects on other species (Maestre *et al.* 2001), their disappearance or reduction could create further long-term changes in the species composition. However, the long-term effects of both changes in nutrient heterogeneity as well as nutrient dynamics are largely unknown.

Controlling factors of annual & perennial grass abundance on neighbourhood scales

Although the differences in life forms and growth rates of annual and perennial grasses result in predictable patterns over large climatic or edaphic scales, the invasion of particular perennial grasslands by annual grasses, and their re-invasion by perennial grasses after the cessation of the disturbance is less predictable (Harris 1967). Firstly, temperate grasslands are characterised by large spatiotemporal heterogeneity in environmental factors such as temperature and rainfall. These environmental and climatic fluctuations are usually responsible for the small-scale year-to-year changes in species composition commonly observed in temperate grasslands with otherwise

stable management regimes (Collins *et al.* 1988; Tilman & El Haddi 1992; Silvertown *et al.* 1994; Morgan 1998c, 2001; Kammer 2002). Thus, in different systems, an increase in rainfall or soil moisture may favour perennial grass growth (McIntosh & Allen 1998; Hamilton *et al.* 1999), the growth of only some, but not all perennial grasses (Ayyad & Dix 1964), or may enhance growth of annual grasses (Hobbs & Mooney 1991; Nicholson & Hui 1993; Hamilton *et al.* 1999). This section will investigate the main causes of environmental heterogeneity in grasslands, their effects on species composition and some of the possible reasons for the complex responses observed.

Large seasonal differences in temperature and rainfall, together with varying soil types, are among the environmental factors that favour the development of grasslands (Moore 1964). In addition, grasslands often exhibit strong spatial heterogeneity in soil moisture, temperature or nutrient availability due to physical factors such as topography (Ayyad & Dix 1964; Defosse *et al.* 1997; Famiglietti *et al.* 1998; Hook & Burke 2000), and biological processes by plants and animals (Gurevitch 1986b; Afzal & Adams 1992; Jaramillo & Detling 1992; Vinton & Burke 1995; Semmartin & Oesterheld 1996; Reynolds *et al.* 1997; Burke *et al.* 1998). Plants can redistribute and accumulate nitrogen and carbon, resulting, for example, in the resource islands under individual perennial grasses (Hook *et al.* 1991; Vinton & Burke 1995; Schlesinger *et al.* 1996) or in larger areas underneath dominant species where nitrate availability is changed (Reynolds *et al.* 1997). In turn, grazing and burrowing animals can redistribute these nutrients (Afzal & Adams 1992; Jaramillo & Detling 1992; Stromberg & Griffin 1996).

Underlying these biological processes are physical factors such as topography and small-scale soil variations. Grasslands in undulating areas, for example, have a range of microclimates, as exposed aspects are generally warmer and drier than sheltered aspects (Ayyad & Dix 1964), windward aspects are drier than sheltered upland sites, and aspects in rain shadows are drier than other aspects (Coronato & Bertiller 1996). Slope positions can differ in soil moisture dynamics due to short-term run-off and the long-term hydrological redistribution of particles, especially finer particles, to lower slope positions. Although there is a tendency for soil moisture to be higher in lower slope positions (Ayyad & Dix 1964; Gurevitch 1986b; Knapp *et al.* 1993), run-off in grasslands in lower rainfall areas may not be sufficient to distribute soil particles and soil moisture availability depends solely on soil texture, independently of slope positions (Singh *et al.* 1998).

The correlations between invasive annual grass abundance with lower rainfall, winter rainfall or high nutrient availability and perennial grass abundance with higher rainfall, summer rainfall and lower nutrient availability on large spatial scales only translate partially to small spatial scales. Studies that have correlated the abundance of annual and perennial grasses with environmental factors on small scales suggest that annual grasses are more abundant on drier microsites such as

exposed aspects and higher slope positions and perennial grasses are more abundant on sheltered aspects and lower slope positions (McIntosh & Allen 1998; Peco *et al.* 1998; Singh *et al.* 1998). Also, increasing soil moisture can improve the competitive ability of the perennial grass *Nassella pulchra* over invading annual grasses (Hamilton *et al.* 1999). Since annual and perennial grasses often compete for soil moisture (Harris 1967; Harris & Wilson 1970; Melgoza *et al.* 1990; Dyer & Rice 1999; Hamilton *et al.* 1999), it is possible that on the small scales, at which plant-plant interactions are most important (Singh *et al.* 1996) perennial grasslands can resist invasion by annual grasses in sites and times of higher soil moisture. However, contrary examples can also be found. For example, in the same system where higher soil moisture improved the competitive ability of a perennial grass, a drought killed a lower proportion of perennial grass seedlings than annual grass seedlings (Hamilton *et al.* 1999). Even at low nutrient availability, annual grasses can grow at least equally well (Muller & Garnier 1990; Claassen & Marler 1998) or even better (Kolb *et al.* 2002) than perennial grasses. Similarly, the abundance of some invasive annual grasses increased significantly during unusually wet years and decreased during a severe drought (Hobbs & Mooney 1991; Nicholson & Hui 1993).

The above examples suggest that the effects of environmental factors on annual and perennial grasses can be species-specific and vary with life stage. Not all perennial and annual grass species respond to soil moisture in the same manner. Different species of perennial grasses, for example, can react very differently to soil moisture (Ayyad & Dix 1964; Knapp 1984; Singh *et al.* 1998) and competitive hierarchies can shift between perennial grass species due to changes in soil moisture (Nernberg & Dale 1997). Secondly, the importance of competitive interactions versus other processes such as recruitment may change in time or space. If the effects of soil moisture on recruitment are very different to its effects on competitive interactions the invasion of annual grasses into perennial grasslands will not be controlled by single factors but by a complex mixture of controlling variables changing in space and time.

A theoretical framework for the invasion of temperate grasslands with annual grasses in the mid-north of South Australia

The attributes of temperate grasslands, such as the frequent disturbances, the large environmental fluctuations and the introductions of the same suite of Mediterranean annual grass species suggest that temperate grasslands are highly susceptible to invasion. The strong environmental fluctuations in time and space due to intrinsic factors and due to changes in resource dynamics with the introduction of European grazing systems suggests that equilibrium theories are not generally applicable to invasions of annual grasses, especially on small scales. I thus propose that non-equilibrium theories that include details of resource dynamics are better suited to explain invasions in temperate grasslands with annual rainfall below 700 mm. I predict that the recruitment, growth and survival of native perennial grasses and invasive annual grasses

in this system, as well as their competitive interactions, are closely connected to resource dynamics at a variety of scales. Non-equilibrium theories predict that a combination of resource levels, propagule supply and seasonal timing exists, such that each 'suitable' species can invade an area. A species may be 'suitable' regardless of whether it is native or exotic to an area – opening the possibility of re-invading areas dominated by exotic species with native species (Davis, 2001).

The practical applications of using this theoretical framework in this system are apparent. Equilibrium theories predict either that invasive plant species are superior competitors at all times at all sites or, on the other hand, that the removal of disturbance or the cessation of resource addition will stop further invasion. The first prediction allows only for one post-invasion management option (active species removal), while the second prediction has lead to the management practice of removing all stock from an area to stall further invasion or promote restoration. Destocking temperate grasslands may result in decreases in annual grasses in some cases (Grove *et al.* 2002) or has mixed effects, such as increasing perennial grass abundance, but lower native plant diversity (Grove *et al.* 2002; Osem *et al.* 2002). However, in other cases destocked grasslands continue to be dominated by annuals (Harris 1967; Heady *et al.* 1992, and references therein; Stromberg & Griffin 1996; McIntosh & Allen 1998).

Non-equilibrium theories, on the other hand, predict that fluctuations in resources or conditions can have a range of effects on species composition, favouring either invasive annual grasses or native species at different points in time. In this case, management options are more flexible and can include grazing, slashing, or propagule addition at different times to create conditions that either promote desired native species and/or discourage the further invasion of undesired exotic species. To be successful, however, this requires detailed knowledge of the resource dynamics in the system and how they affect the invasive and the native species at different spatiotemporal scales.

Overview and objectives of research

Like other temperate grasslands, the grasslands of the mid-north of South Australia have been extensively invaded by annual grasses (Chapter 2). There is little knowledge on ecological patterns and processes of the mid-north grasslands in general and to my knowledge no published information on the dynamics of essential resources in this system exist. In this thesis I aim to determine the most appropriate theoretical framework to further investigate the invasion of grasslands by annual grasses in this area. I will use a series of surveys and experiments to establish the resources that drive annual grass invasion, the dynamics of these resources and how they affect annual and perennial grass recruitment, growth and their competitive interactions.

To address these objectives I aim to answer the following questions:

1. Which resources or environmental factors correlate to the recruitment and growth of perennial versus annual grasses, both at large scales (within the lower mid-north region) and small scales (within the same site) (Chapter 3)?

2. How does the availability of a resource that correlates well with grass abundance affect the recruitment of annual and perennial grasses and thus their likelihood of invasion success in 'uninvaded areas' (Chapter 4)?

3. How does the timing and amount of a resource that correlates well with grass abundance affect the growth and competitive abilities of both annual and perennial grasses? How is this resource affected by grass abundance? Are annual grasses superior competitors in most conditions or do the competitive hierarchies between annual grasses and perennial grasses change under certain conditions (Chapter 5 & 6)?

2. Temperate grasslands in the South Australian mid-north

Introduction

Temperate grasslands and grassy woodlands are a major vegetation type of southern Australia (Figure 2.1). In South Australia, the mid-north region in particular was dominated by grassy ecosystems. However, the precise location and extent of grasslands versus grassy woodlands in the mid-north of South Australia is uncertain. Hyde (1995, p.1) states that 'true native grasslands were originally rare, and most grassy communities contained at least some shrubs or trees in varying densities'. The detailed original species compositions for areas in this region will probably never be established. Hyde (1995) concludes that the exploitation of the vegetation by early settlers in the mid-north resulted in a rapid and widespread change. By 1879 some weeds outcompeted native plants in the area (Kloot 1980). Today the majority of land is used for cropping and sheep grazing and only remnants of native vegetation remain.

The mid-north region

Geologically, the region originated from uplifts along north-south faults that are now mostly eroded. The landscape thus consists of numerous north-south oriented minor ranges and gently undulating plains, with elevation ranging from sea level to 800 m. Soils are mainly hard alkaline red duplex soils with some hard neutral yellow duplex soils and some calcareous earths (Northcote 1960). Factors such as soil depth, texture or organic matter vary strongly within and between remnants (Chapter 3). The region has a Mediterranean-type climate with cool winters and hot summers. Mean annual rainfall ranges from 350-650 mm (Table 2.1), but annual rainfall can range from 165-880 mm. There is a tendency for more predictable small rain events in the cool season and unpredictable large rain events in the warm season (higher coefficient of variation, Table 2.1). Rainfall amount and seasonality varies highly between years (Figure 2.2) and between sites a few kilometres apart (data not shown, various landholders, 1990-2000).

No accurate information exists about the fire regimes of the mid-north area prior to European settlement or during the early settlement period. Several authors assume that vast areas of vegetation in south-eastern Australia were regularly burned by indigenous people (Flannery 1994; Ryan et al. 1995, in Benson & Redpath 1997; Robertson 1998), which would promote the occurrence of grassland or open grassy woodlands over denser vegetation types. However, Benson (1997) has argued that early settler's notes do not support the evidence of widespread regular burning. Nicholson (1981) summarises a variety of accounts of early settlers and scientists and concludes that fire may have been used to create grasslands mainly in favourable habitats, such as in eastern Victoria, whereas other areas of southern Australia supported grasslands that

remained grasslands in the absence of fire. Scarlett *et al.* (1992, in Davies 1997) also state that grasslands in drier regions of Victoria are similar to the grasslands in South Australia and tend to be self-sustaining in the absence of fire or grazing.

	Mean annual rainfall (mm)	Mean rainfall (mm)		CV rainfall (%)		Mean daily temperature (°C)			
						Minium		Maximum	
		Jan	Jul	Jan	Jul	Jan	Jul	Jan	Jul
Burra (41 yrs)	439	24.8	57.2	161	52	na	na	na	na
Clare (> 140 yrs)	631	25.0	81.0	112	46	13.4	3.1	29.5	13.2
Site 3 (22 yrs)	376	15.7	43.8	116	64	na	na	na	na
Jamestown (123 yrs)	463	20.7	57.0	109	50	na	na	na	na
Mt Bryan (105 yrs)	437	19.3	54.5	125	46	na	na	na	na
Snowtown (> 122 yrs)	407	19.0	49.0	121	49	14.6	5.2	31.2	15.5
Spalding (97 yrs)	437	18.8	53.4	116	46	na	na	na	na
Tarcowie (65 yrs)	416	25.4	48.6	119	49	na	na	na	na
Whyte Yarcowie (123 yrs)	348	20.7	38.4	127	48	na	na	na	na

Table 2.1: Rainfall & temperature statistics for selected locations (Figure 2.3) in the mid-north of South Australia (Bureau of Meteorology; Robin Bruce, pers. com., 2000). CV = Coefficient of variation.

Whether or not fire was a regular occurrence in the region, it has been rare since European settlement. Currently grasslands and grassy woodlands of the region are seldom deliberately burnt (Robertson 1998). Instead grazing, spraying or mowing is used to reduce fuel levels. While fire may still occur in grassland remnants due to burning of nearby stubble paddocks or the occurrence of wildfires, any species that may once have required regular burning probably has already disappeared from unburnt remnants (Robertson 1998).

Since topography, soil properties, climate and fire regime play an important role in the establishment of woody plants in grasslands (Moore 1964; Ripley 1992), I suggest the high underlying variability of these factors at various scales is likely to have corresponded with a similar variability in vegetation types. The result would have been a complex mosaic of both grasslands and grassy woodlands rather than vast expanses of one or the other.

Current status of the mid-north grasslands

Within the mid-north region several communities with different species composition are recognised (Hyde 1995; Robertson 1998), including the once extensive *Lomandra effusa* (Lindley)Ewart grasslands, *Lomandra multiflora* var. *dura* (R. Br.)Britten tussock grassland complex, *Austrostipa eremophila* (Reader) S.W.L.Jacobs & J.Everett/*Austrodanthonia caespitosa* (Gaud.) H.P.Linder grasslands with emergent shrubs, *Triodia scariosa* N. Burb. Hummock Grassland, *Austrostipa blackii* C. E. Hubb. grassland, *Austrostipa nodosa* (S.T.Blake) grassland and *Austrostipa*

nitida Summerh. & CF.E. Hubb./*Gahnia lanigera* (R. Br.)Benth. grassland. Due to their suitability for agricultural purposes these grasslands have been extensively cleared since European settlement. It has been estimated that in Australia overall only 0.77% of the temperate grasslands remain in semi-natural condition, with similar figures quoted for South Australia (Barlow 1999, quoted in Ross 1999). Compared to other vegetation types temperate grasslands are one of the top conservation priorities in South Australia (Davies 1982). The significance of these systems is poorly understood. In at least two cases native grasslands in the mid-north were ripped for tree planting and revegetation (Davies 1997).

Remaining grasslands tend to be fragments, mostly found on steep hillsides, steep or stony areas within cleared paddocks, parklands in towns, cemeteries, rail reserves and roadsides (Ross 1999). Few, if any, of these remnants retain what is thought to be the pre-European understorey. Stock grazing, sporadic ploughing, fertilisers and accidental or deliberate species introduction have resulted in large changes (Robertson 1998). In general, perennial dominated, diverse systems have been replaced with annual dominated systems (Figure 2.4). Recent surveys have shown that in South Australian grasslands or specifically in grasslands and grassy woodlands in the Mount Lofty Region eleven and nine of the twenty most common species respectively are introduced (Hyde 1995; Robertson 1998). The most frequent introduced species in South Australian grasslands in general are *Avena barbata*, followed by *Gynandriris setifolia* and *Salvia verbenaca* (Hyde 1995) and in the mid-north area *A. barbata*, followed by *Vulpia* sp. and *Echium plantagineum* (Robertson 1998).

The invasions have negative effects on native flora and fauna. Living *A. barbata* and its litter, for example, have negative effects on perennial grass growth at the Burra field site (Figure 2.3) (Lenz *et al.* 2003). Litter also decreases the abundance of small-seeded exotics and tends to decrease the abundance of rare small-seeded native species (Lenz *et al.* 2003). By out-competing perennial grasses that provide food or habitat for a variety of animals, including insects (Maxwell 2003) and a bird species (Davies 1997), annual grasses can also impact on native fauna. Overall, they decrease plant diversity (Lenz *et al.* 2003) and change the seasonality of productivity from a more even productivity all year round to a strong peak in productivity over winter and spring. In summer annual grasses senesce and fewer perennial grasses are present to take up available soil moisture. The potential of using native perennial grasses as pasture grasses is increasingly recognised, since they are adapted to local conditions and can take advantage of all year round rainfall and encouraging native perennial grasses is believed to benefit both pastoral and conservation purposes (Lodge 1994; Crosthwait *et al.* 1996; Jones 1996).

Extrapolating other grassland studies to the South Australian mid-north

While the temperate natural and semi-natural grassy ecosystems in south-eastern Australia and other areas are generally grouped together as a vegetation type, they differ considerably in climate. The New England Tableland, for example, has higher rainfall than the mid-north of South Australia and has a summer-dominated rainfall regime (Table 2.2; Figure 2.1). The volcanic plains west of Melbourne are also wetter, considerably less variable and have a more winter-dominated rainfall regime than in the mid-north area. Other areas, such as the drier areas in the Riverine Plains in NSW are slightly more summer-rain dominated than the mid-north area. On the other extreme are the temperate grasslands of the Central Valley in California, USA, with truly Mediterranean winter-dominated rainfall regimes (Table 2.2).

		Mean annual rainfall (mm)	Mean rainfall (mm)		CV rainfall (%)		Mean daily temperature (°C)			
							Minium		Maximum	
			Jan	Jul	Jan	Jul	Jan	Jul	Jan	Jul
New England Tablelands, NSW	Armidale (131 yrs)	780	104	48	56	69	13.8	0.4	26.7	12.7
	Guyra (116 yrs)	884	114	60	57	60	na	na	na	na
	Glen Innes (93 yrs)	848	106	57	58	63	13.5	0.5	24.8	12
Volcanic Plains, VIC	Lismore (84 yrs)	625	37	58	84	40	11.9	4.6	26.8	12.3
	Penshurst (121 yrs)	721	35	79	74	38	na	na	na	na
	Mortlake (120 yrs)	675	35	68	80	40	na	na	na	na
	Melbourne (146 yrs)	655	48	48	75	48	14	5.8	25.8	13.3
Riverine Plains, NSW	Hay (125 yrs)	369	27	31	119	71	17	3.8	32.8	14.7
	Deniliquin (140 yrs)	407	29	35	121	66	15.6	3.4	31.4	13.8
	Tocumwal (105 yrs)	449	33	42	118	60	15.6	3.1	31.7	14
Central Valley, California, US	Stockton (>40 yrs)	347	70	1	69	200	na	na	na	na
	Sacramento (Rain 146 yrs, temperature 30 yrs)	446	91	1	76	300	3.2	14.5	11.5	34
	Fresno (Rain 119 yrs, temperature 30 yrs)	254	47	0	79	-	3	18.4	12.3	37

Table 2.2: Climate statistics for areas containing other temperate grasslands (Clewett *et al.* 2003, http://www.worldweather.org.) CV = Coefficient of variation.

The importance of rainfall regimes to the growth of annual and perennial grasses (Chapter 1), overlaid by potentially different grazing and fire regimes are likely to produce different patterns and results in different ecological processes in different grasslands. Thus management changes that produce desired outcomes in terms of plant species composition in one area may be less or not at all suitable for another area. However, research that assists us to understand the variables driving growth and invasion in the mid-north grasslands will aid management of these grasslands specifically, and potentially of other grasslands in a similar climatic regime.

Figures
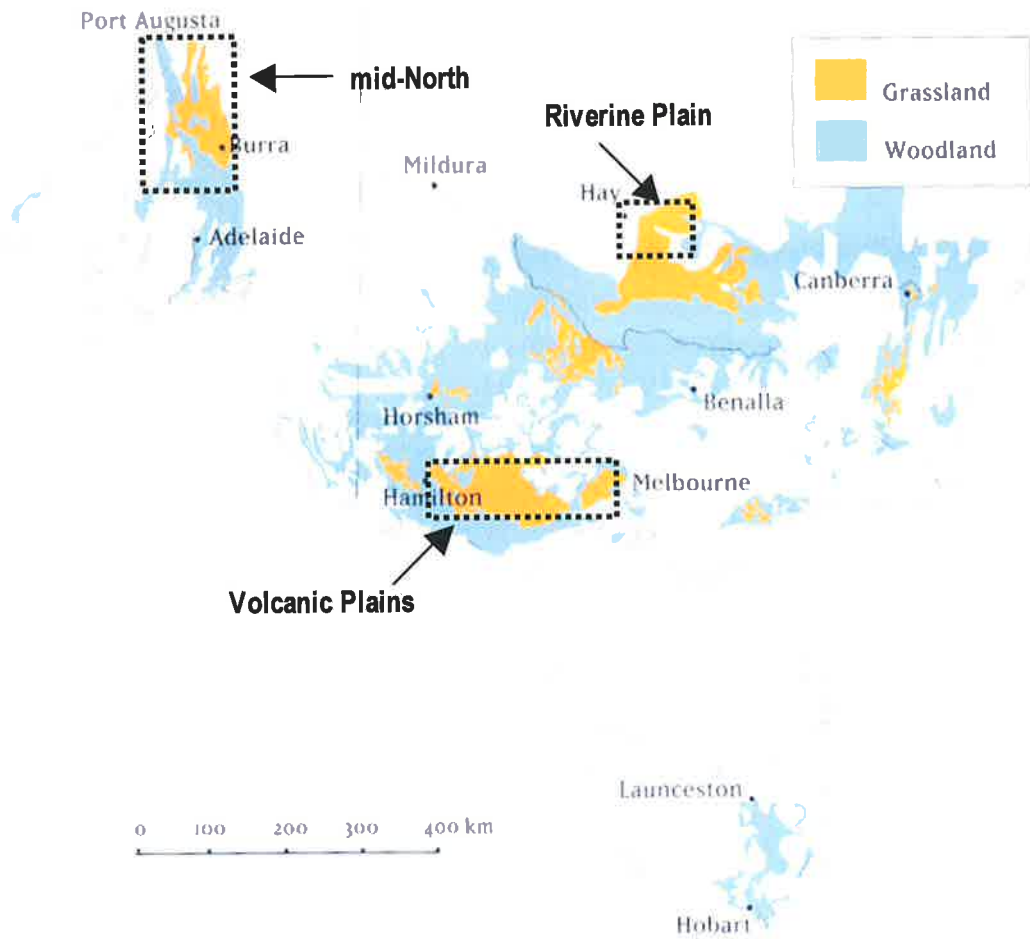
Figure 2.1: Pre-European extent of lowland grasslands and grassy woodlands in south-eastern Australia (Lunt *et al.* 1998). The New England Tableland is located 970 km NE of Canberra at 800-1000 m a.s.l..
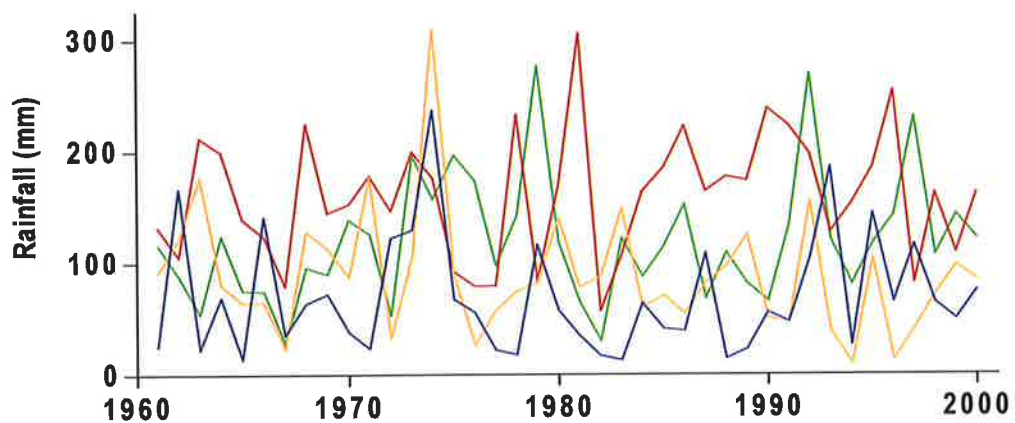
Figure 2.2: Seasonal rainfall statistics (Summer; Autumn; Winter; Spring rainfall of each year) for Burra, South Australia (Bureau of Meteorology, 2000).
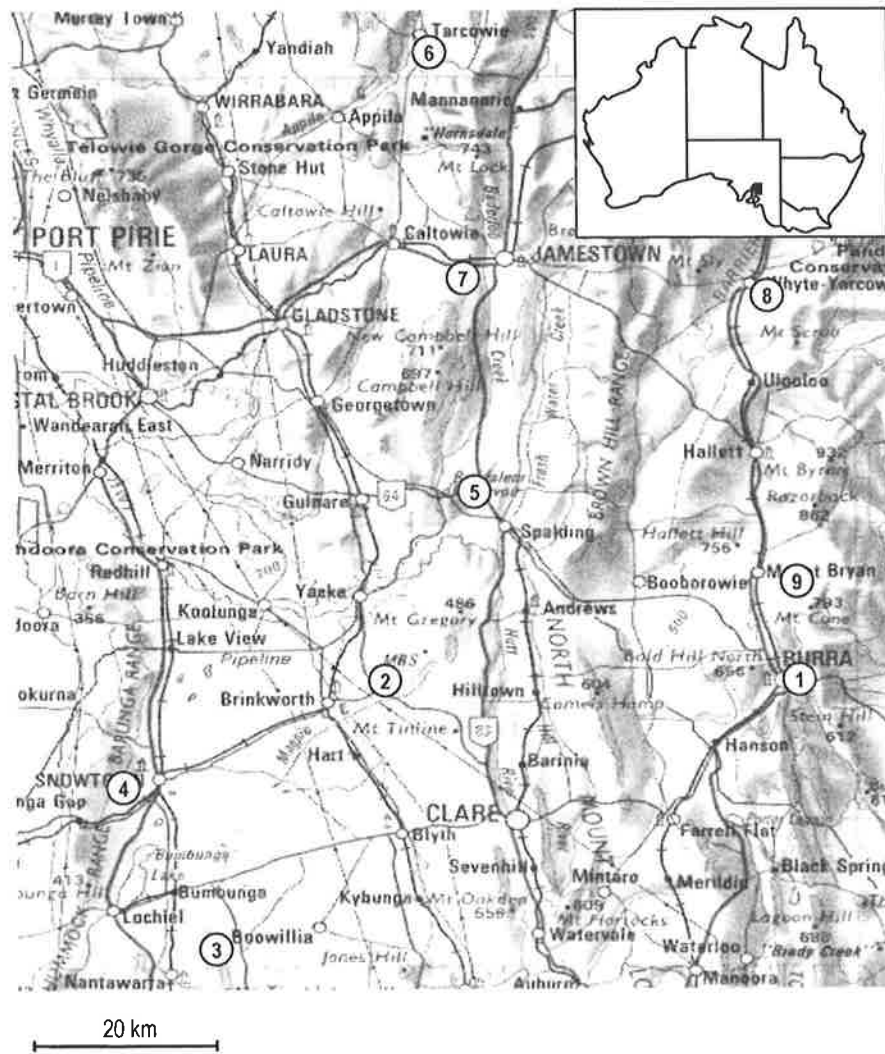
Figure 2.3: Location of the nine study sites. Burra (1); Clare (2); Glen Roburn (3); Snowtown (4); Spalding (5); Tarcowie (6); Caltowie (7); Whyte Yarcowie (8); Mokota (9). Map from Geoscience Australia (2003).

(a)

(b)

Figure 2.4: Site 4). (a) Native perennial grasses and other natives (*Austrodanthonia* sp., *Lomandra* sp., *Scaevola albida*); (b) Invasive annuals (mainly *Avena barbata,* some *Echium plantagineum*).

3. Correlations between environmental factors and grass abundances in the South Australian mid-north

Introduction

A considerable number of studies of semi-arid or temperate grasslands report environmental factors to be at least important as grazing factors (Ayyad & Dix 1964; Kemp & Dowling 1991; McIntyre & Lavorel 1994; O'Connor & Roux 1995; Harrison 1999; Stohlgren *et al.* 1999; Dodd *et al.* 2002). In these studies environmental factors explained more than 50% of the variation in species composition, when grazing regime was not included as an explanatory variable, and explained as much or more variation than grazing regime when grazing regime was included. Burke *et al.* (1998) suggest that soil water availability is the dominant factor controlling species composition in grasslands receiving less than 700 mm annual rainfall. Similarly, the invasion of cool-season Mediterranean annual grasses into temperate grasslands worldwide is associated with rainfall, independent of management history. For example, the species numbers of invasive annual grasses and their abundances decrease with rainfall, while perennial grass species numbers or abundances increase (Bartolome, 1980, in Kemp & Dowling 1991; Heady *et al.* 1992). Furthermore, the invasive annual *Bromus tectorum* is favoured by autumn and spring rainfall, whereas summer rainfall enhances the growth of a native perennial grass (Harris 1967). Similarly, in their native Mediterranean habitat, annual grasses are more abundant in high winter rainfall/low summer rainfall areas (Jackson 1985).

Temperatures and nutrient availability also affect annual and perennial grass growth differently. Independent of photosynthetic pathway, low temperatures decrease perennial grass growth more than annual grass growth (Harris 1967; Harris & Wilson 1970; Jackson & Roy 1986). Similarly, at low nutrient availability the growth rates of perennial and annual grasses are similar, but at high nutrient availability annual grasses have up to four times higher growth rates than perennial grasses (Muller & Garnier 1990; Ernst & Tolsma 1992; Claassen & Marler 1998). Hence, many studies show that the abundance of annual grasses correlates with higher nutrient availability or follow nutrient addition (Lauenroth & Dodd 1978; Huenneke *et al.* 1990; Kotanen 1997; Morgan 1998b; Chiarucci *et al.* 1999; Paschke *et al.* 2000) or that decreasing nutrient availability can reduce annual and increase perennial grass abundance (Paschke *et al.* 2000). These patterns of annual and perennial abundances over large temporal, climatic or edaphic scales do not translate into predictable patterns of annual grass invasion or the re-invasion by perennial grasses at smaller scales. Firstly, temperate grasslands are characterised by large environmental fluctuations such as temperature and soil moisture. Undulating topography, for example, results in various microclimates and soil moisture distributions due to different aspects and slope

positions (Ayyad & Dix 1964; Gurevitch 1986b; Knapp *et al.* 1993; Coronato & Bertiller 1996). Perennial grasses themselves can elevate nutrient levels underneath their tussocks by long-term decomposition processes (Hook *et al.* 1991; Vinton & Burke 1995; Schlesinger *et al.* 1996) and animals in turn can redistribute nutrients (Afzal & Adams 1992; Jaramillo & Detling 1992; Stromberg & Griffin 1996).

Secondly, responses are often species, life stage, or site-specific. Some studies that have correlated grass abundance with environmental factors on smaller scales, such as single sites, indicate, that - like at larger regional scales - annual grasses are more abundant on drier microsites such as exposed aspects and higher slope positions, while perennial grasses are more abundant on sheltered aspects and lower slope positions (McIntosh & Allen 1998; Peco *et al.* 1998; Singh *et al.* 1998). Likewise, increasing soil moisture improved the competitive ability of a perennial grass over annual grass invaders (Hamilton *et al.* 1999). However, this is not always the case. Depending on species and life stage an increase in rainfall or soil moisture can favour perennial grass growth (McIntosh & Allen 1998; Hamilton *et al.* 1999), the growth of some perennial grasses (Ayyad & Dix 1964), or the growth of annual grasses (Hobbs & Mooney 1991; Nicholson & Hui 1993; Hamilton *et al.* 1999). The objectives of this study were thus to gain an understanding of the environmental factors that correlate with exotic annual grass abundance and native perennial grass abundance in the mid-north of South Australia at different spatial scales (site scale and regional scale) and temporal scales (one-off survey versus monitoring over two growing seasons).

Methods

Correlations of grass abundances with environmental factors in space

I conducted the study in nine remnant grasslands in the mid-north of South Australia. The grasslands were chosen using the following criteria: a) the sites included a range of rainfall regimes and soil types; b) no site had been stocked during the current season so not to confound the effect of abiotic factors on current annual grass biomass with recent grazing effects; c) each site included native perennial and exotic annual grasses and little overstorey; (d) there was no evidence of different grazing management within a site, *i.e.* fence-lines or watering points (Table 3.1, Figure 2.3). Subsequently, any mention of locality names refers to field sites, not towns.

Sampling design: Sites 1-5 were sampled 9-20 October 2000 and sites 6-9 were sampled 11-22 October 2001. At each site I sampled 20-30 0.5 × 0.5 m quadrats in a random compass direction and at a random distance from 1-3 central points, depending on the shape of the site. Quadrats were sampled only when they contained mainly grasses as understorey and no overstorey.

Site	Location	Name	Survey area	Annual rain (mm) [1]	Grazing history	Soil type [2]	Overstorey
1	138°55'E, 33°41'S	Burra	120 m × 200 m	439	Medium grazing, fenced 1999	Loam	-
2	138°30'E, 33°42'S	Clare	200 m × 50 m	500	Within stubble-grazed paddock [3]	Sandy clay loam	3 trees
3	138°18'E, 34°00'S	Glen Roburn	200 m × 25 m	375	Corridor, unmanaged for >30 years	Sandy clay loam	Few shrubs
4	138°11'E, 33°47'S	Snow-town	100 m × 50 m	459	Medium grazing, fenced 1999	Sandy clay	-
5	138°37'E, 33°29'S	Spalding	100 m × 200 m	437	Within stubble-grazed paddock, fenced 1997	Sandy clay loam	Few shrubs & trees
6	138°30'E, 32°57'S	Tarcowie	100 m × 50 m	417	Parkland, unmanaged for > 40 years	Sandy loam	Few shrubs
7	138°26'E, 33°10'S	Caltowie	300 m × 40 m	420	Roadside, unmanaged	Sandy clay loam	Few shrubs
8	138°53'E, 33°16'S	Whyte Yarcowie	200 m × 50 m	348	Parkland, unmanaged for >30 years	Sandy loam	Few shrubs
9	138°55'E, 33°35'S	Mokota	100 m × 100 m	440	Light grazing, fenced 1998	Sandy clay loam	Few shrubs

Table 3.1: Details of study sites. [1] Longest-term available annual average of the nearest (0.5-7 km) rain gauge. [2] Based on average sand, silt and clay % of quadrats (Thompson & Troeh 1973). [3] Stocking grain stubble with sheep for a short period after harvest. Sheep have access to any grassland remnants within the paddock but forage mainly in the stubble. Common management practice.

Vegetation sampling: Annual and perennial grass abundance were sampled differently (Appendix I). In each quadrat I harvested the aboveground biomass of all annual grasses rooted in the quadrat. I then recorded the % frequency of each perennial grass species by subdividing the quadrat into 25 10 cm × 10 cm subquadrats and recording the percentage of subquadrats each species was rooted in. I collected voucher specimens of all perennial grass species present per site. Annual grasses were air-dried, sorted to species (in a few cases leaving some unidentifiable vegetative material remaining), identified using Jessop and Toelken (1986), dried to constant weight at 80 °C and weighed. Perennial grasses voucher specimens were identified using Jessop and Toelken (1986) and Walsh (1994). Nomenclature follows Jessop and Toelken (1986) with *Stipa* and *Danthonia* updated to *Austrostipa* and *Austrodanthonia*. Voucher specimens were checked against type specimens of the Adelaide Herbarium. During this process I realised I had not distinguished the different *Austrodanthonia* spp. encountered in the field (*A. caespitosa, A. eriantha, A. racemosa*) consistently and thus grouped them as *Austrodanthonia* spp.. Non-flowering perennial grasses (mainly small plants) were recorded as *e.g.* '*Austrodanthonia* juvenile', if they could be identified to genus or otherwise 'perennial grass'.

Soil sampling: In each quadrat I collected up to three soil samples using a 6 cm auger: one at 0-5 cm depth, and if possible one at 15-20 cm and one at 25-30 cm depth, each in a different

randomly selected 10 cm × 10 cm subquadrat. To estimate soil depth I continued augering in the deepest hole until I hit a solid rock surface or reached a depth of 0.5 m. Soil depth > 0.5 m was arbitrarily assigned the value of 0.6 m for the purpose of numerical analysis.

The soil samples were air-dried for several weeks, crushed in a mortar and pestle and sieved through a 2.36 mm sieve, recording the percentage of gravel weight in each sample. All soil samples were analysed for organic carbon using the Walkley & Black titration method (Allison 1965). In addition, the topsoil sample of each quadrat was analysed for % total nitrogen (Rayment & Higginson 1992, C Soil Method Reference: Method 6B3, Lab Method: LecoCN2000, "SOILLOW", Combustion at 1350 °C), available phosphorus (Rayment & Higginson 1992, Method 9B1), soil texture (Day 1965), pH and electrical conductivity (1 part soil in 5 parts water, shake for 1 h, measure conductivity (EC) using an AthomCDM2d conductivity meter and, after 1 h, the pH of the supernatant using an Activon pH meter).

Topographical measurements: I obtained a measure of the microtopography around the quadrat by averaging the difference in elevation between the quadrat centre and 2 m distance in each of the four compass directions. This measurement is zero if the quadrat is level with its surroundings, negative if the quadrat is elevated and positive if the quadrat is lower compared to its surroundings. In addition, the elevation of each quadrat relative to the highest quadrat was measured with a theodolite and if the quadrat was located on a slope, I recorded its aspect (compass direction to within 45°) and its slope (maximum difference in elevation within the quadrat, converted into degrees). I converted aspect, slope and latitude variables into an estimate of potential direct incident radiation using Equation 2 in McCune & Keon (2002) and rotating the aspect measurements 180°. This rotation swaps north with south, but also east with west. It thus roughly adjusts the equation to the southern hemisphere, since east and west aspects would have more similar radiation loads than north and south aspects.

Grazing and rainfall statistics data: I obtained rainfall data from the nearest landholder or a Bureau of Meteorology weather station, located at distances of 0.5-7 km from the site. All rainfall statistics calculated were adjusted for the survey year (i.e. 2000 or 2001). Detailed grazing statistics such as DSE/ha were not available for most sites due to the nature of the grazing management in the area. I collected basic grazing statistics, consisting of year of destocking and relative grazing pressure before destocking (on a scale from 1 – 5, with 5 being highest for the region as judged by the landholder) from landholders. Grazing pressure over the last 10 years was calculated as = (grazing pressure × number of years stocked in last 10 years). While this estimation of grazing pressure is neither very precise nor accurate, the study was not designed to determine close correlations between grass abundance and grazing management. The grazing estimate was simply added as another possible explanatory variable.

<u>Statistical analysis:</u> Out of 18 variables measured in each of 220 quadrats, I lost four measurements and assume a transcription error in an extremely high silt level of a soil sample. Rather than lowering the number of quadrats for the multivariate analysis I interpolated these values using the linear regression of the missing variable against the environmental variable that had the highest correlation ($0.2 < r^2 < 0.72$) with the missing variable at that site. This procedure may increase the probability of introducing autocorrelation of environmental factors to the dataset (McCune & Grace 2002) and thus could create additional correlations of these factors with grass abundances. I checked the resulting correlation matrices for new significant correlations and found that none occurred.

Data exploration indicated a large number of non-parametric distributions and non-linear correlations. To test correlations between total perennial and annual grass abundances and environmental factors I calculated the nonparametric Spearman's correlation coefficients, using the Bonferroni adjustment for multiple comparisons. For the individual species dataset I used nonmetric multidimensional scaling (NMS) (McCune & Grace 2002) with the Sørensen (Bray-Curtis) index as the distance measure. All analyses were performed in PC-ORD 4.1 (McCune & Mefford 1999), using the "Slow and thorough" Autopilot mode and procedures outlined by McCune & Grace (2002). Initial ordinations results were poor with stress values > 20. There was a high coefficient of variation (CV) between species, both due to highly varying annual grasses abundances and the different abundance measures for perennial and annual grasses. To decrease CV between species I tried two methods: (a) to remove all annual grass species with < 5 g total biomass at each site and perennial grass species with < 8% total frequency. This resulted in acceptable ordinations in some cases but not in others, and (b) to give all species exactly the same weight by relativising each species by the maximum abundance of itself at that site. This resulted in lower stress values in most cases. The ordinations were also visually similar to the first ones and are presented here. I then tested species and quadrats for outliers (defined as >2.3 standard deviations from the grand mean) and investigated the matrix for probable causes of each outlier. Outlying species were removed. When an outlying quadrat turned out to be caused by species of low abundance I also removed the species rather than the quadrat to maintain sample size. I only removed quadrats if this resulted in a significant decrease in the stress value. Overall, I removed only one quadrat each in three site analyses and two quadrats in the overall regional analysis.

Correlations of grass abundances with soil moisture over time

<u>Sampling Design:</u> To monitor soil moisture in areas with different perennial and annual grass abundances, I selected sites 1-3 (Table 3.1; Figure 2.3) with contrasting average rainfall. At Burra, where there was a clear perennial to annual grass gradient down the slope, I established three 72 m transects perpendicular to the direction of the slope, one at the top of the slope where perennial grasses dominated, one halfway within a mixture of annual and perennial grasses and

one at the bottom of the slope where annual grasses dominated. At random distances along each transect I marked out eight 1 m × 1 m quadrats. At Clare and Glen Roburn there was no clear gradient of grass abundance. I visually located six areas, two dominated by annual grasses, two by perennial grasses and two with a mixture of annual and perennial grasses. I established four 1 m × 1 m quadrats in each area a random direction and distance away from the centre.

To measure soil moisture each quadrat was subdivided into 25 subquadrats. For each measurement date I randomly selected a different set of 3-5 subquadrats for all 72 quadrats to take the soil moisture measurements in. I aimed to take five measurements in each quadrat at every measurement date, but equipment problems during dry conditions forced me to decrease the sample size to three at some days. Volumetric soil moisture was measured approximately every 6 weeks between December 2000 and October 2002 in the top 6 cm of soil using a thetaprobe ML2x (Delta-T Devices) and the general mineral soil parameters supplied with the probe. Soil moisture values are not comparable across sites, since sites differ in soil parameters.

Vegetation Monitoring: I estimated perennial and annual grass abundance in all quadrats 21-25 October 2001. In 2002 growing seasons peaked earlier for annual grasses than for perennial grasses. Hence I recorded annual grass abundance 14-16 October and perennial grass abundance 6 November 2002. I estimated perennial grass abundance by recording their percentage frequency in 100 10 cm× 10 cm subquadrats, and identifying the species as described above.

I estimated annual grass aboveground biomass using a variation of the Adelaide technique (Andrew *et al.* 1979). In this method, visual estimates of experimental quadrats are corrected using a regression of visual estimates and real dry weight (DW) of non-experimental plots. I selected eight non-experimental 0.5 m × 0.5 m plots that represented the whole range of above ground biomass at each site on each measurement date. In these I estimated the annual grass aboveground DW to the nearest gram, the first plot using a series of photos of plots with known DW and the remaining seven in relation to the first one. After familiarising myself for some time with estimating the non-experimental plots and other areas, I estimated experimental quadrats, re-visiting non-experimental plots several times to confirm or correct my estimates. I then harvested the non-experimental plots for annual plant aboveground DW (without litter) and used the regression between the estimated and observed dry weights to adjust the estimates of the experimental quadrats. This method corrects for consistent over- or underestimation of biomass and, if non-experimental plots span the range of biomass, no extrapolation is required. The r^2 of regressions between estimated and observed annual grass biomass of the non-experimental plots ranged from 0.64 to 0.97. To be consistent, the experimental 1 m × 1 m quadrats were subdivided into four 0.5 m × 0.5 m quadrats for estimation.

<u>Rainfall and grazing data:</u> Daily rainfall data were obtained from the nearest meteorological station or landholder (within 0.5-3 km of the sites). The paddock surrounding the Clare site was stubble-grazed (see Table 3.1 for explanation) during late summer/autumn 2001. Goats and cattle occasionally entered the Burra paddock from a neighbouring paddock. I observed evidence of kangaroo presence at Glen Roburn, and feral fallow deer (*Dama dama* (L.)) at Clare. However, no significant grazing or trampling damage was ever evident in any of the monitored quadrats.

<u>Statistical analysis:</u> Soil moisture values were averaged for each quadrat on each measurement date. I analysed the correlations between quadrat soil moisture and annual or perennial grasses abundances by calculating Spearman ρ correlation coefficients of the correlation between end-of-growing-season grass abundances and soil moisture for each measurement date and site. These coefficients were plotted against the mean % soil moisture availability at that date and site. I estimated maximum soil moisture availability as the maximum average soil moisture measured at any date at each site and accordingly calculated% mean soil moisture availabilities for other dates.

Results

Correlations of grass abundances with environmental factors in space

Species composition and the relative abundance of perennial and annual grasses varied widely both within and between sites, with total perennial grass frequency ranging from 8.2 % at Glen Roburn to 36.80 % at Burra. Total annual grass biomass ranged from 18.10 g DW 0.25 m^{-2} at Burra to 68.50 g DW 0.25 m^{-2} at Clare (Table 3.2). Overall, twelve perennial grass species or species groups and twelve annual species or species groups were recorded. I will subsequently refer to unique genera by generic name only. *Austrodanthonia* and *Austrostipa* spp. made up the bulk of the perennial grasses encountered, while *Avena* had the highest mean biomass of 22.41 g DW 0.25 m^{-2} followed by *Brachypodium* with a mean of 10.37 g DW 0.25 m^{-2} (Table 3.2).

Annual rainfall ranged from 375-500 mm, with 30-45% falling from October – March. Soils were generally of poor fertility and medium textures, with organic carbon ranging from 0.6-1.8%, total nitrogen from 0.05-0.2% and available phosphorus from 3.5-7.1 ppm (Table 3.3). Soil depths ranged from < 10 cm to > 50 cm and pH ranged from 6.5 to 8.3. Long-term annual rainfall and average levels of organic carbon, total nitrogen and available phosphorus in the topsoil were strongly positively correlated between sites (Table 3.4). Four of the sites had not been directly managed for more than 30 years. Most other sites had been destocked a few years prior to the survey for conservation reasons and none of the sites had experienced recent severe grazing pressure according to the landholders. In particular, stubble-grazing in surrounding paddocks did not result in any visual grazing damage in any grassland remnants.

	Species	Burra (n = 30)	Clare (n = 20)	Glen Roburn (n = 20)	Snowtown (n = 20)	Spalding (n = 25)	Tarcowie (n = 25)	Caltowie (n=25)	W. Yarcowie (n = 25)	Mokota (n = 30)	Overall (n = 220)
(a)	Aristida behriana F. Muell.		0.25 ± 0.25		1.80 ± 1.40	4.64 ± 1.96	1.44 ± 1.00		5.12 ± 1.17	7.47 ± 2.15	2.55 ± 0.47
	Austrodanthonia spp. H.P.Linder	6.28 ± 1.64	6.00 ± 2.16	2.40 ± 1.12	0.80 ± 0.68	7.36 ± 2.12	0.64 ± 0.64	6.08 ± 2.12	0.96 ± 0.42	2.67 ± 0.91	3.76 ± 0.51
	juvenile Austrodanthonia H.P.Linder	3.2 ± 1.04	1.60 ± 0.76	1.40 ± 1.20	0.820 ± 0.48	1.92 ± 0.68	0.16 ± 0.16	5.12 ± 2.51	0.48 ± 0.35	5.20 ± 2.68	2.36 ± 0.52
	Austrostipa blackii (C.E.Hubb.) S.W.L.Jacobs & J.Everett		2.00 ± 0.58	2.00 ± 0.84	0.80 ± 0.48	9.28 ± 2.60	8.16 ± 2.02	0.64 ± 0.64	1.60 ± 0.65		2.67 ± 0.46
	A. eremophila (Reader) S.W.L.Jacobs & J.Everett	24.12 ± 3.96	1.80 ± 0.58	2.00 ± 0.76	4.00 ± 1.80	5.44 ± 2.16		4.32 ± 1.63		1.87 ± 0.81	5.36 ± 0.83
	A. nitida (Summerh. & C.E.Hubb.) S.W.L.Jacobs & J.Everett						0.32 ± 0.32		0.80 ± 0.46		0.13 ± 0.07
	A. nodosa (S.T.Blake) S.W.L.Jacobs & J.Everett	0.92 ± 0.44		0.20 ± 0.20							0.15 ± 0.08
	A. scabra (Lindl.) S.W.L.Jacobs & J.Everett					0.80 ± 0.80					0.09 ± 0.09
	juvenile Austrostipa S.W.L.Jacobs & J.Everett	2.24 ± 0.88	0.60 ± 0.44	0.20 ± 0.20	0.20 ± 0.20	0.64 ± 0.38	5.96 ± 1.56	4.80 ± 1.53	2.40 ± 0.92	10.93 ± 2.64	3.46 ± 0.52
	Enneapogon nigricans (R.Br.)P.Beauv.				4.40 ± 2.28						0.40 ± 0.22
	Themeda triandra Forsskal		0.40 ± 0.04							2.53 ±1.06	0.38 ± 0.16
	Triodia irritans R.Br.						1.60 ± 1.60				0.18 ± 0.18
	Perennial grass		1.60 ± 0.84		0.80 ± 0.48	0.64 ± 0.48	0.16 ± 0.16	3.84 ± 2.48	1.60 ± 1.06	0.13 ± 0.13	0.93 ± 0.33
	Total	36.8 ± 4.8	15.0 ± 3.1	8.2 ± 2.2	14.0 ± 3.2	30.7 ± 5.0	18.3 ± 3.1	24.8 ± 3.3	13.0 ± 1.71	30.8 ± 4.6	22.4 ± 1.4
(b)	Aira caryophyllea* L.					0.001 ± 0.001	1.17 ± 0.39				0.13 ± 0.05
	Avena barbata* (Pott ex Link)	14.56 ± 2.83	13.28 ± 2.06	5.28 ± 0.83	35.11 ± 6.05	18.19 ± 2.82	29.67 ±0.17	2.26 ± 1.32	42.24 ± 3.38	37.00 ± 4.92	22.41 ± 1.49
	Brachypodium distachyon* (L.)P. Beauv.		38.32 ± 3.99	37.51 ± 4.19	17.96 ± 4.64	0.44 ± 0.22		12.50 ± 2.01		2.71 ± 0.75	10.37 ± 1.19
	Bromus diandrus* Roth	1.35 ± 0.92	7.93 ± 2.43	0.12 ± 0.07	4.32 ± 2.30	7.44 ± 2.97	0.17 ± 0.01	0.49 ± 0.31		0.23 ± 0.13	2.26 ± 0.51
	B. hordeaceus* L.	0.04 ± 0.03			0.002 ± 0.002	0.13 ± 0.08		0.002 ± 0.002		0.16 ± 0.07	0.04 ± 0.01
	B. madritensis* L.							0.001 ± 0.001		0.01 ± 0.01	0.001 ± 0.001
	B. rubens* L.	0.58 ± 0.29								0.002 ± 0.002	0.08 ± 0.04
	Hordeum ?leporinum* Link	0.01 ± 0.01									0.002 ± 0.002
	H. vulgare distichon* (L.)Koern					0.03 ± 0.03					0.003 ± 0.003
	Lophochloa cristata* (L.)Hylander	0.003 ± 0.003			0.02 + 0.01			0.001 ± 0.001			0.002 ± 0.001
	Lolium* spp. L.	0.43 ± 0.25	0.88 ± 0.22	0.06 ± 0.04	0.37 ± 0.23	0.29 ± 0.10		0.08 ± 0.03		0.001 ± 0.001	0.22 ± 0.05
	Vulpia myuros* (La.)C.Gmelin	0.50 ± 0.20	0.07 ± 0.07	0.22 ± 0.15	0.19 ± 0.10	1.36 ± 0.55	0.21 ± 0.15	0.05 ± 0.04	0.09 ± 0.02	0.60 ± 0.15	0.39 ± 0.08
	Veg. material	0.63 ± 0.19	8.00 ± 0.81	2.24 ± 0.78	3.65 ± 1.11	2.14 ± 0.58					1.59 ± 0.22
	Total	18.1 ± 3.2	68.5 ± 5.4	45.4 ± 4.7	61.6 ± 7.4	30.0 ± 3.6	31.2 ± 4.0	15.4 ± 3.0	42.3 ± 3.4	40.7 ± 4.7	37.5 ±1.8

Table 3.2: (a) % frequency of perennial grasses & (b) aboveground dry weight of annual grasses (g DW 0.25 m^{-2}) (mean ± 1 SE) at 9 grasslands in the South Australian mid-north. * introduced species.

Environmental variable	Burra (n = 30)	Clare (n = 20)	Glen Roburn (n = 20)	Snowtown (n = 20)	Spalding (n = 25)	Tarcowie (n = 25)	Caltowie (n=25)	W. Yarcowie (n = 25)	Mokota (n = 30)	Overall (n = 220)
Aspect (°)	250.96 ± 7.56	231.00 ± 4.09	238.24 ± 5.13	348.16 ± 9.64	110.00 ± 6.53	-	307.50 ± 52.50	-	182.25 ± 26.62	
Slope (°)	10.98 ± 1.32	5.26 ± 0.90	8.67 ± 1.07	13.17 ± 1.31	7.76 ± 1.15	0.00 ± 0.00	1.71 ± 0.66	0.00 ± 0.00	7.21 ± 1.16	6.02 ± 0.44
Microtopography	-0.33 ± 0.86	0.69 ± 0.31	-3.96 ± 1.31	-0.50 ± 1.20	-0.26 ± 0.84	Near zero	-0.79 ± 1.24	Near zero	0.98 ± 0.71	-0.37 ± 0.29
Potent. direct incident radiation (MJ cm^{-2} yr^{-1})	0.87 ± 0.01	0.86 ± 0.01	0.84 ± 0.01	0.97 ± 0.02	0.87 ± 0.01	0.90 ± 0.00	0.91 ± 0.01	0.90 ± 0.00	0.91 ± 0.01	0.89 ± 0.004
Soil depth (cm)	38.03 ± 2.27	45.90 ± 2.06	29.55 ± 3.06	39.28 ± 3.12	41.54 ± 2.45	> 50 cm	> 50 cm	34.76 ± 2.53	34.22 ± 3.22	40.37 ± 0.90
% gravel (0-5cm)	13.15 ± 2.76	4.26 ± 1.45	2.93 ± 0.45	8.45 ± 2.66	9.50 ± 2.46	3.80 ± 0.53	1.21 ± 0.50	4.41 ± 0.65	10.85 ± 1.80	6.84 ± 0.66
% gravel (15-20cm)	23.79 ± 2.75	14.74 ± 3.29	22.76 ± 8.90	16.07 ± 6.67	17.61 ± 4.66	6.86 ± 1.78	1.31 ± 0.46	8.77 ± 2.00	31.40 ± 6.42	16.32 ± 1.64
% gravel (25-30cm)	28.28 ± 5.01	22.20 ± 5.23	48.79 ± 10.67	35.32 ± 9.95	28.11 ± 7.17	3.58 ± 1.15	1.67 ± 0.55	48.19 ± 9.13	49.22 ± 7.91	29.73 ± 2.57
% clay (0-5cm)	13.35 ± 0.37	32.09 ± 1.17	24.69 ± 1.42	34.44 ± 1.71	19.53 ± 1.05	17.46 ± 0.69	35.05 ± 1.91	13.35 ± 0.25	21.00 ± 0.83	22.68 ± 0.65
% silt (0-5cm)	34.50 ± 1.29	13.25 ± 0.64	14.54 ± 0.58	12.56 ± 0.86	16.40 ± 0.63	16.05 ± 0.59	15.60 ± 0.84	14.03 ± 0.22	18.08 ± 0.79	18.00 ± 0.54
% sand (0-5cm)	52.15 ± 1.43	54.66 ± 1.48	60.78 ± 1.55	53.00 ± 2.27	64.08 ± 1.46	66.49 ± 1.08	49.35 ± 2.09	72.63 ± 0.34	60.92 ± 1.51	59.32 ± 0.71
pH (0-5cm)	7.60 ± 0.16	7.96 ± 0.10	8.30 ± 0.05	7.72 ± 0.14	6.48 ± 0.13	6.53 ± 0.12	8.29 ± 0.04	6.09 ± 0.04	6.57 ± 0.13	7.23 ± 0.07
EC (µS) (0-5cm)	92.10 ± 5.91	114.50 ± 5.04	127.65 ± 5.94	111.75 ± 6.71	55.12 ± 6.06	63.29 ± 5.65	123.04 ± 3.43	38.88 ± 1.76	86.73 ± 8.50	88.53 ± 2.79
% org. C (0-5cm)	1.61 ± 0.06	1.79 ± 0.07	1.41 ± 0.05	1.35 ± 0.08	1.26 ± 0.07	0.88 ± 0.05	0.87 ± 0.06	0.55 ± 0.02	1.18 ± 0.03	1.21 ± 0.03
% org. C (15-20cm)	0.90 ± 0.05	1.25 ± 0.06	0.75 ± 0.09	0.97 ± 0.10	0.69 ± 0.04	0.52 ± 0.03	0.41 ± 0.02	0.37 ± 0.02	0.65 ± 0.07	0.71 ± 0.03
% org. C (25-30cm)	0.65 ± 0.06	0.90 ± 0.06	0.41 ± 0.09	0.66 ± 0.12	0.51 ± 0.05	0.51 ± 0.03	0.36 ± 0.04	0.13 ± 0.03	0.36 ± 0.06	0.49 ± 0.02
Total N (%) (0-5cm)	0.22 ± 0.01	0.24 ± 0.01	0.17 ± 0.01	0.17 ± 0.01	0.13 ± 0.01	0.08 ± 0.01	0.10 ± 0.01	0.05 ± 0.01	0.14 ± 0.01	0.14 ± 0.01
Available P (ppm) (0-5cm)	6.71 ± 0.30	7.15 ± 0.36	4.99 ± 0.38	5.02 ± 0.37	7.24 ± 0.80	4.92 ± 0.66	4.08 ± 0.39	3.48 ± 0.31	6.07 ± 0.65	5.54 ± 0.19

Table 3.3: Environmental factors (mean ± 1 SE) at each of nine grasslands and overall in the mid-north of South Australia.

Regression	SS	F Ratio	P-value	r^2
% organic C (0-5 cm) = -1.44 + 0.0062 × annual rain (mm)	0.62	7.26	0.03	0.51
% organic C (15-20 cm) = -1.11 + 0.0043 × annual rain (mm)	0.30	5.63	0.05	0.45
% organic C (25-30 cm) = -1.00 + 0.0037 × annual rain (mm)	0.21	5.44	0.05	0.44
% total N (0-5 cm) = -0.27 + 0.0010 × annual rain (mm)	0.02	6.65	0.04	0.49
ppm available P (0-5 cm) = -3.74 + 0.0217 × annual rain (mm)	7.52	7.58	0.03	0.52

Table 3.4: Regressions of average soil nutrients against average annual rainfall at grasslands in the mid-north of South Australia (n = 9 sites, 20-30 samples each).

	Burra	Clare	Glen Roburn	Snow-town	Spald-ing	Tar-cowie	Cal-towie	W. Yar-cowie	Mokota	Mean
Grazing pressure prior destocking	3	1	0	3	1	0	0	0	1.5	1.06
Time since destocking (yrs)	2	0.5	>30	2	4	>30	>30	>30	3	14.6
Grazing pressure last 10 years	24	9.5	0	24	6	0	0	0	11.5	8.3
Mean annual rain long term (mm)	439	500	375	460	437	417	420	348	440	426.22
Total rain last 1 yr (mm)	479	595	453	676	485	507	483	450	505	514.78
Total Oct-Mar rain last 1 yr (%)	42	32	39	27	33	26	45	34	34	35.8
Mean rain last 3 yrs (mm)	425	489	418	501	408	365	381	343	456	420.67
Mean Oct-Mar rain last 3 yrs (%)	45	38	40	37	42	41	43	44	36	40.67
Mean rain last 5 yrs (mm)	460	504	412	491	420	368	369	338	461	424.78
Mean Oct-Mar rain last 5 yrs (%)	37	33	41	34	37	46	44	44	36	39.11
Mean rain last 10 yrs (mm)	463	523	408	513	434	399	413	392	478	447.00
Mean Oct-Mar rain last 10 yrs (%)	40	35	40	38	42	43	45	43	39	40.56

Table 3.5: Grazing & rainfall statistics for nine grasslands in the South Australian mid-north. Long-term annual rainfall from 28-125 yrs data. Grazing pressure from 0 (no grazing) to 5 (heavy grazing) compared to other management in the area.

Correlations of grass abundances with environmental factors: At the regional scale total annual grass biomass and total perennial grass frequency showed significant correlations with other factors. The strongest correlation was a negative one between annual and perennial grass abundance (Spearman's correlation coefficient $\rho = -0.59$; Table 3.6; Figure 3.1). In addition annual grass biomass was negatively correlated with the percentage rain falling during October-March in the last year, the last three, five and ten years, and positively correlated with soil clay content at 0-5 cm depth, organic carbon at 15-20 cm and 25-30 cm depth and average rainfall during the last three and five years (Table 3.6; Figure 3.1). There were no significant correlations ($\alpha' = 0.001$) between total perennial grass % frequency with any of the environmental factors measured. The best correlations ($0.18 < \rho < 0.21$; $0.002 < P < 0.008$) were positive correlations with relative elevation, incident radiation and grazing pressure in the last ten years. At the site scale, annual grass and perennial grass abundance were also negatively correlated within six of the

nine sites. The Spearman's correlation coefficient ρ ranged from -0.49 at Spalding to -0.81 at Burra (Figure 2.2). Caltowie tended towards a negative, but highly variable correlation, while Whyte Yarcowie and Glen Roburn did not show any trends.

Variable	Annual grasses (g DW 0.25 m^{-2}) ρ	P-value	Perennial grasses (% frequency) ρ	P-value
Perennial grasses (% frequency)	-0.59	<0.0001		
Aspect (°)	0.10	0.12	<0.0001	0.96
Slope (°)	0.12	0.09	-0.01	0.91
Microtopography	-0.02	0.78	0.13	0.05
Relative elevation	-0.17	0.01	0.18	0.008
Potential direct incident radiation (MJ cm^{-2} yr^{-1})	-0.12	0.09	0.21	0.002
Soil depth (cm)	0.08	0.23	-0.03	0.62
% gravel (0-5cm)	-0.09	0.17	0.13	0.05
% gravel (15-20cm)	-0.09	0.19	0.12	0.09
% gravel (25-30cm)	0.03	0.70	0.02	0.81
% clay (0-5cm)	0.26	<0.0001	-0.19	0.01
% silt (0-5cm)	-0.14	0.04	0.12	0.08
% sand (0-5cm)	-0.04	0.52	0.02	0.79
pH (0-5cm)	0.01	0.84	-0.10	0.16
EC (µS) (0-5cm)	0.09	0.17	-0.10	0.14
% org. C (0-5cm)	0.26	0.0001	-0.05	0.43
% org. C (15-20cm)	0.42	<0.0001	-0.11	0.10
% org. C (25-30cm)	0.26	<0.0001	<0.0001	1.00
Total N (%) (0-5cm)	0.25	0.0002	-0.07	0.32
Available P (ppm) (0-5cm)	0.10	0.14	0.06	0.39
Relative grazing pressure prior to destocking	0.02	0.74	0.20	0.003
Time since destocking (yrs)	-0.18	0.006	-0.12	0.07
Relative grazing pressure last 10 years	0.05	0.49	0.19	0.005
Mean annual rain long term (mm)	0.18	0.007	0.13	0.05
Total rain last 1 yr (mm)	0.25	0.0002	<0.0001	0.95
Total Oct-Mar rain last 1 yr (%)	-0.38	<0.0001	0.18	0.01
Mean rain last 3 yrs (mm)	0.26	<0.0001	0.03	0.68
Mean Oct-Mar rain last 3 yrs (%)	-0.40	<0.0001	0.13	0.06
Mean rain last 5 yrs (mm)	0.25	0.0002	0.07	0.29
Mean Oct-Mar rain last 5 yrs (%)	-0.33	<0.0001	-0.03	0.65
Mean rain last 10 yrs (mm)	0.20	0.003	0.11	0.10
Mean Oct-Mar rain last 10 yrs (%)	-0.39	<0.0001	0.03	0.68

Table 3.6: Correlations between grass abundance & environmental factors at the regional scale in the South Australian mid-north (n = 9 sites) (Spearman's c; Bonferroni adjustment, 63 comparisons; α' = 0.001).

Ordinations: Ordinations were moderately successful. They explained 74-90% of the variation, and stress values ranged from 8.02-14.35 for the site ordinations, with 17.50 for the overall regional ordination (Table 3.7). Stress typically increases with increasing quadrat numbers, thus the regional ordination is not necessarily poorer than the site ordinations. I found no useful ordination (stress < 20) or any strong correlations between grass abundances and environmental factors using the Spearman's ρ correlation coefficients for Whyte Yarcowie (Table 3.8).

	Burra	Clare	Glen Roburn	Snow-town	Spald-ing	Tar-cowie	Cal-towie	Whyte Yarcowie	Mokota	All sites
(a) Axis 1	21	45	37	35	25	20	33		10	28
Axis 2	39	28	10	16	19	42	12		18	22
Axis 3	29	16	43	36	32	27	37		50	25
Total	90	89	90	87	76	89	82		78	74
(b) Stress	10.43	9.80	8.02	10.97	14.35	9.60	10.73	> 20	13.71	17.50

Table 3.7: NMS statistics: (a) % variance explained by an axis (Coefficients of determination for the correlations of ordination distances with distances in the original n-dimensional space, Sørensen/Bray-Curtis index); (b) stress values for ordinations between species abundances and environmental factors within each of nine grasslands and between these grasslands in the mid-north of South Australia.

Variable	Annual grasses (g DW 0.25 m^{-2})		Perennial grasses (% frequency)	
	ρ	P-value	ρ	P-value
Perennial grasses (% frequency)	-0.13	0.53		
Relative elevation	-0.06	0.77	-0.14	0.52
Soil depth (cm)	-0.12	0.56	-0.04	0.86
% gravel (0-5cm)	-0.13	0.53	0.10	0.63
% gravel (15-20cm)	-0.25	0.24	0.19	0.36
% gravel (25-30cm)	0.21	0.32	0.10	0.64
% clay (0-5cm)	-0.45	0.02	0.15	0.47
% silt (0-5cm)	-0.17	0.41	0.42	0.04
% sand (0-5cm)	0.41	0.04	-0.36	0.08
pH (0-5cm)	-0.08	0.70	0.03	0.87
EC (μS) (0-5cm)	0.39	0.05	0.07	0.72
% org. C (0-5cm)	0.19	0.37	-0.43	0.03
% org. C (15-20cm)	0.33	0.10	-0.01	0.96
% org. C (25-30cm)	-0.06	0.79	-0.09	0.66
Total N (%) (0-5cm)	0.29	0.15	-0.18	0.39
Available P (ppm) (0-5cm)	0.05	0.80	-0.04	0.84

Table 3.8: Correlations between grass abundances and environmental factors at Whyte Yarcowie (Spearman's ρ; Bonferroni adjustment, 31 comparisons; α'= 0.0016).

There was no evidence of different behaviours of the sites sampled in 2000 (sites 1-5) and 2001 (sites 6-9). At a regional scale annual and perennial grass species separated clearly along one axis, however no environmental variable was associated with this axis. *Austrostipa eremophila* and *Austrodanthonia* spp. were positively associated with a higher percentage of summer rainfall, *Brachypodium* was positively associated with clay and *Austrodanthonia* seedlings positively associated with EC and pH (Table 3.9, Figure 3.3a). At the site scale annual and perennial grasses were separated clearly or relatively clearly at four sites, twice along elevation or gravel content, once along organic carbon content and once along an axis with no correlation with any of the environmental factors measured (Table 3.9). At most sites some or all annual species were associated with higher nitrogen and organic carbon levels, deeper soils, lower elevation, lower gravel content or finer soils: Burra (Figure 3.3b), Clare (Figure 3.3c), Glen Roburn (Figure 3.3d), Snowtown (Figure 3.3e), Spalding (Figure 3.3f), Tarcowie (Figure 3.3g), Caltowie (Figure 3.3h), Mokota (Figure 3.3i). Exceptions to this were Spalding, where *Bromus hordeaceus* was associated with higher elevation and *Vulpia* and *Brachypodium* with gravel and sand, and at Mokota where *Vulpia* was associated with gravel.

	All sites	Burra	Clare	Glen Roburn	Snow-town	Spalding	Tar-cowie	Caltowie	Mokota
Annuals & perennials separated?	Along ?	Along gravel & elevation	No	No	No	Almost along elevation	Almost along C	No	Almost along ?
Avena	-	N	-	Deep soils, C	High fertility	High fertility	Silt	C, P, silt	Deep soils, C
Brachypodium	Clay	np	C	np	High fertility	Gravel, sand, N	np	C, P, silt	-
Bromus diandrus	-	-	C, N	N	Gravel	Steep slopes	Clay, N	C, P, silt	-
Austrodanthonia spp.	Summer rain	High gravel & elevation	C, N	-	Gravel	High elevation	-	Steep slopes, high elevation, radiation	Gravel
Austrodanthonia juveniles	EC, pH	High gravel & elevation	-	-	High fertility	High elevation	Clay, N	-	Deep soils, C
Austrostipa eremophila	Summer rain	High gravel & elevation	-	-	High fertility	High elevation	np	Steep slopes, high elevation, radiation	Deep soils, C

Table 3.9: Summary of the NMS Ordination results for correlations of the most common species or species groups with environmental factors at the regional scale and at site scale in the mid-north of South Australia. np = not present in significant abundance.

Perennial grasses on the other hand tended to be associated with higher elevation and gravel content and other environmental factors denoting lower soil fertility at Burra (Figure 3.3b), to some extent at Glen Roburn (Figure 3.3d), to some extent at Snowtown (Figure 3.3e), at Spalding (Figure 3.3f), Caltowie (Figure 3.3h), and for some species at Mokota (Figure 3.3i).

Exceptions to this were Snowtown, where *Austrodanthonia* juveniles and *Austrostipa eremophila* were associated with 'high' fertility', Tarcowie, where *Austrostipa nitida* and *Austrodanthonia* juveniles were associated with clay and nitrogen and Mokota, where *Austrodanthonia* juveniles and *Austrostipa eremophila* were associated with deeper soils and organic carbon. The associations of *Austrostipa* juveniles, *Austrodanthonia* spp. and *Austrodanthonia* juveniles with clay at Glen Roburn were not supported by raw data or due to outliers (*Austrostipa* juveniles = 0.8 - 0.02 clay, r^2 = 0.03, P = 0.46; *Austrodanthonia* spp. without outlier = 5.8 - 0.2 clay, r^2 = 0.08, P = 0.25; *Austrodanthonia* juveniles without outlier = 0.7 - 0.02 clay, r^2 = 0.01, P = 0.70).

Correlations of grass abundances with soil moisture over time

Rainfall varied considerably from site to site and between the two growing seasons with rainfall being slightly above average in 2001 and 68% of the average in 2002 (Table 3.10). Annual grass biomass was positively correlated with rainfall between sites and years, but there was no correlation between rainfall and perennial grass frequency (Figure 3.4).

Site	Year	Annual grass DW estimate (g m^{-2})	Perennial grass (% frequency)	Annual Rainfall (mm)	Mean soil moisture (% vol.)
Burra	2001	112.34 ± 21.92	22.63 ± 4.05	444.20	12.78 ± 0.24
	2002	88.46 ± 8.17	13.75 ± 2.50	293.10	8.27 ± 0.19
Clare	2001	210.31 ± 14.76	8.13 ± 1.31	576.83	20.00 ± 0.30
	2002	64.42 ± 4.12	6.50 ± 1.04	341.70	15.83 ± 0.37
Glen Roburn	2001	160.54 ± 10.41	6.71 ± 1.43	465.25	15.29 ± 0.18
	2002	29.99 ± 2.09	8.08 ± 1.74	255.00	10.20 ± 0.16

Table 3.10: End-of growing-season grass abundances rainfall & soil moisture statistics (mean ± 1 SE) at three grasslands in the mid-north of South Australia.

The correlations of grass abundances at the end of the season with soil moisture during the season varied from strongly negative to strongly positive. Thus, there were no correlations between the average seasonal quadrat soil moisture and grass abundances, with the exception of a strong negative correlation between average quadrat soil moisture and perennial grass frequency at Clare. (Table 3.11, Figure 3.5). However, the correlations between the soil moisture and grass abundance at the end of the growing season in each quadrat followed a seasonal pattern throughout both growing seasons for annual grasses at all sites and for perennial grasses at Burra and Glen Roburn. During the cool and wet season, annual grasses tended towards positive correlations and perennial grasses towards negative correlations, and vice versa for the warm and dry seasons (Table 3.12; Figure 3.6; Figure 3.7). When relating these correlations to relative soil moisture availability, annual grasses tended to have positive correlations at high soil moisture availability, suggesting that the more soil moisture quadrats received or retained after rain the higher their end-of-growing-season annual grass biomass (Figure 3.8). Perennial grasses, in

contrast, tended to have negative correlations with soil moisture immediately after rainfall, suggesting that the less soil moisture quadrats received or retained after rain the higher their end-of-growing-season perennial grass frequency (Figure 3.8). At Clare correlations were consistently negative; independent of rainfall, quadrats with the lowest soil moisture always had the highest end-of-growing-season perennial grass frequency.

	Annual grass r^2		Perennial grass r^2	
Site	2001	2002	2001	2002
Burra	0.14ns	0.12 ns	0.04 ns	0.01 ns
Clare	0.05 ns	0.08 ns	0.56***	0.47***
Glen Roburn	0.02 ns	0.002 ns	0.04 ns	0.02 ns

Table 3.11: Correlation coefficients of average quadrat soil moisture with end-of-growing-season grass abundances in three grasslands in the mid-north of South Australia 2001-2002.

	Burra		Clare		Glen Roburn	
Date	Annual	Perennial	Annual	Perennial	Annual	Perennial
9 Mar 01	-0.70	0.53	-0.14	-0.36	-0.03	-0.24
20 Apr 01	-0.28	0.20	0.08	-0.15	-0.22	0.28
11 May 01	-0.61	0.46	-0.27	-0.47	-0.06	-0.18
2 Jun 01	0.07	0.01	0.21	-0.53	0.23	-0.07
5 Jul 01	0.41	-0.32	-0.01	-0.52	0.03	0.03
14 Aug 01	0.59	-0.50	0.29	-0.49	0.14	-0.13
26 Sep 01	0.71	-0.43	0.33	-0.57	0.43	-0.33
22 Nov 01	-0.71	0.53	-0.11	-0.01	-0.18	-0.16
17 Jan 02	-0.72	0.81	0.05	-0.54	-0.05	-0.14
30 Apr 02	-0.59	0.62	-0.22	-0.28	-0.07	-0.04
14 Jun 02	0.34	0.07	-0.06	-0.31	0.43	-0.25
24 Jul 02	0.64	-0.72	0.34	-0.61	0.41	-0.09
5 Sep 02	0.17	-0.12	0.15	-0.22	0.08	0.23
28 Sep 02	0.44	-0.15	-	-	-	-
17 Oct 02	-0.41	0.62	-0.14	-0.22	-0.29	0.26

Table 3.12: Correlation between quadrat soil moisture and end-of-growing-season grass abundances at each measurement date in three grasslands in the South Australian mid-north (Spearman's ρ).

Discussion

The study did not detect any consistent environmental factors that correlated with total or species-specific perennial grass abundance in the area. However, it detected strong correlations of environmental factors with annual grass abundance; a strong negative correlation between annual

and perennial grass abundance and concurs with previous studies on floristic composition and abundance.

In terms of grass species abundances the sites in this study were representative of the temperate grassy systems in the Mount Lofty Block Bioregion, where *Avena barbata* has the highest abundance, followed by the *Austrodanthonia caespitosa* group, *Vulpia* spp., *Bromus rubens* and *B. diandrus* (Robertson 1998). The results also provide evidence to support observations by Hyde (1995), who states that in temperate grasslands of South Australia annual grass invasion is more frequent on sites with higher rainfall (p.33) or deeper soils (p.33, 42). While high exotic annual plant abundance can occur on the drier and shallower soils of ridges and higher slope positions in some areas (Hyde *et al.* 2000, p26), this is usually due to the presence of sheep camps (elevated, heavily disturbed, areas regularly occupied by sheep), which I avoided during sampling. No positive association between annual grasses and higher elevation was obvious in my study.

The abundance of perennial grasses showed few clear correlations with environmental data. Depending on site and species they were correlated with factors associated with either low or high productivity. Much unexplained variation remained, suggesting the presence of other controlling factors not included in the survey, such as past grazing regimes or different initial plant species composition, although limitation in the survey design cannot be ruled out.

The driving variables of annual grass abundance

In this study annual grass abundance correlated positively with soil moisture and rainfall, in contrast to the negative correlations between annual grass abundance and rainfall observed in their original Mediterranean habitat in an annual rainfall range between 300-1000 mm (Jackson 1985; Jackson & Roy 1986) and in central NSW between 500-1100 mm annual rainfall (Kemp & Dowling 1991). Similarly, an observed decrease in annual grass abundance and documented decrease in annual grass species numbers occurred in California between an annual rainfall gradient of 160-1600 mm (Bartolome *et al.* 1980). In California, increasing soil moisture improved the competitive ability of a perennial grass over invasive annual grasses at 500 mm annual rainfall (Hamilton *et al.* 1999). The results of this study are not consistent with an increased competitive ability of perennial over annual grasses at high soil moisture. Competitive interactions between annual and perennial grasses in this system are discussed in Chapter 6.

The abundance of annual grasses was generally positively correlated with higher soil fertility as found in other Australian studies (Morgan 1998b; Pettit *et al.* 1998; Prober *et al.* 2002), however cause–effect relationships between these correlations were not established. Soil moisture and nutrient availability are often auto-correlated, making it difficult to distinguish between the relevance of either factor. At regional scales, increases in mean annual rainfall are correlated with

increases in soil nutrients (Quilchano *et al.* 1995; Austin & Sala 2002; Feral *et al.* 2003). At smaller scales, nutrient availability increases with soil moisture due to increases in mass flow and diffusion of minerals (Marschner 1995). Availability of phosphorus and nitrogen released through litter decomposition and soil microbiotical activity may be positively correlated to soil moisture in some systems (Cui & Caldwell 1997), but this is not generally the case (Whitford *et al.*; Reynolds *et al.* 1997; Farley & Fitter 1999; Barrett *et al.* 2002). While the data indicate that soil moisture and nutrient availability are positively correlated on a large scale, and possibly positively correlated on a small scale, further studies are needed to determine the relative importance of moisture and nutrient availability in this system.

Correlations of annual grasses with soil moisture (or nutrient availability) were also apparent on small scales. Although the results do not prove the cause-effect relationship between soil moisture and grass abundance, it is evident that quadrats dominated by annual grasses received and or retained the most soil moisture after rain. The following discussion assumes differences in soil moisture distribution after rain causes different end-of growing-season grass abundances. On the other hand, quadrats dominated by annual grasses are the driest after dry periods. At this end of the scale it is more likely that differential soil moisture uptake of quadrats dominated by different grasses causes this pattern. *Avena barbata* has significantly higher absolute water uptake rates than perennial grasses in this system (Chapter 5).

A large and complex combination of environmental variables determines soil moisture distribution over space and time. Many of these factors are correlated, feed back onto each other, and change greatly over space and time in some systems (Famiglietti *et al.* 1998; Singh *et al.* 1998; Descroix *et al.* 2002). Assuming equal rainfall, soil moisture run-on generally decreases with relative elevation, slope and decreasing contributing area (Ayyad & Dix 1964; Gurevitch 1986a; Knapp *et al.* 1993; Enoki *et al.* 1996). Overall, soil moisture also increases with clay content (Williams *et al.* 1983; Famiglietti *et al.* 1998), absence of physical or biological crust (Maestre *et al.* 2002) as well as soil chemical properties such as organic carbon content (Williams *et al.* 1983). Another important feature influencing soil moisture distribution is vegetation density and type. Plants modify soil and soil surfaces properties within the spread of their canopy and root system, which can lead to feedback processes between soil properties and vegetation (Archer *et al.* 2002). The exact nature of any correlations of environmental factors and soil moisture dynamics in these systems are currently being investigated. However, so far the results consistently show that annual grass abundance increases with soil moisture, as well as average rainfall, organic carbon and clay, all of which can increase soil moisture.

Differences in the correlations between sites could be related to factors such as the different rainfall regimes and general soil properties between the sites. For example, the level of accuracy

of volumetric soil moisture measurements decreases with increasing clay content due to the volume changes of clay. Thus, the measurement accuracy was highest at Burra and lowest at Clare, where the measurements may have underestimated moisture in wet soils and overestimated moisture in dry soils.

The driving variables of perennial grass abundance

I detected no clear correlations between perennial grass frequency and environmental factors. There was a trend for positive correlations with elevation, radiation, % summer rainfall and grazing pressure prior to destocking. Perennial grass abundance was higher in quadrats that received and/or retained the least soil moisture after rainfall. At two sites, areas with relatively higher soil moisture after dry periods correlated with increasing abundance of perennial grasses, while at the third site relatively higher soil moisture was always correlated with decreased perennial grass abundance. While these correlations were weaker for perennial grasses, again survey and monitoring results agree: perennial grasses tended to decrease with soil moisture, as well as increase with elevation, radiation, gravel, October to March rainfall, and slope factors, which all tend to be negatively correlated with soil moisture.

The lower degree of correlation for perennial grasses could be real or could be due to measuring errors. I used % frequency to measure their abundance, which is considerably less accurate and precise than destructive sampling of perennial grass biomass (to which some landholders were averse). During a pilot study at the Burra site % frequency appeared appropriate to measure perennial grass abundance (Appendix I). At other sites, though, tussock sizes varied greatly and the frequency values were likely to have a much smaller range than the actual biomass. I have since found that measuring two orthogonal basal diameters and tussock height, although more time-consuming, results in accurate and precise biomass estimates.

Perennial grasses also show inconsistent or few correlations with specific environmental factors in other Australian studies. In grasslands in south-eastern Australia, for example, the most acidic and depleted top soils were dominated by several perennial grasses species, including *Austrodanthonia* spp. and *Austrostipa scabra*, while the least compacted and most nutrient-rich soils were dominated by annual exotics (Prober *et al.* 2002). Similarly, soils sustaining *Austrodanthonia caespitosa* grasslands in NSW were deficient in nitrogen and phosphorus (Hunter & Williams, undated, in Williams 1961), whereas *Austrodanthonia* spp. in 'improved' pastures in NSW were associated with increased fertiliser addition and soil phosphorus levels (Garden *et al.* 2001). In the NSW New England tablelands *Austrodanthonia* spp. occurred over a wide variety of soils, but they were generally associated with sites that had never been cultivated or at least not for a long time (Scott & Whalley 1982). Of the species that I grouped into *Austrodanthonia* spp. in this study, *A. racemosa* in the NSW tablelands had a slight preference for undisturbed sites (Scott & Whalley

1982) or higher pH soils (Dowling *et al.* 1996), while *Austrodanthonia eriantha* and *A. caespitosa* were too infrequent to conclude on their distribution (Scott & Whalley 1982) or *A. caespitosa* was associated with higher pH soils and *A. eriantha* with lower pH soils (Dowling *et al.* 1996). In this study the *Austrodanthonia* juveniles tended to be associated with higher pH soil between sites.

The tendency for perennial grass abundance to increase with grazing pressure prior to destocking must be viewed with caution. In central NSW, increased stocking rates have been associated with decreases in some perennial grasses (Garden *et al.* 2001) and while certain grazing regimes can be more advantageous to perennial grasses than complete destocking, rare native plants such as lilies, legumes, daisies and orchids (Stuwe & Parsons 1977; McIntyre 1995, quote in Davies 2000) decrease with grazing. Too little is known about past management practices and exact stocking rates at the sites surveyed to infer clear cause-effect relationships.

Correlations between perennial grass abundance and rainfall in southern Australia have to my knowledge only been investigated in central NSW, which has a different rainfall regime of 500-900mm annual rainfall with relatively even monthly distribution (Bureau of Meteorology). Unlike in the mid-north of South Australia, perennial grass species in central NSW occur from 600 mm annual rainfall onwards and increase with rain, exceeding annual grass abundance at 900 mm annual rainfall or at high elevation (Kemp & Dowling 1991).

Little published information exists on any correlation of southern Australian perennial grasses to rainfall seasonality. Unlike related Californian perennial grasses (Laude 1953, in Williams 1961), most Australian perennial grass species are able to respond to summer rainfall (Williams 1961; Davies 1997), which would explain the slight association of perennial grasses with percentage October-March rain found in this study. In the Riverine Plain of NSW (annual rainfall 400 mm), *Austrodanthonia* and *Austrostipa* species continued to grow as long as soil water was available; summer irrigation in these areas resulted in dense perennial grass tussocks that prevented invasion by exotic annuals (Williams 1961). Winter-growing annuals including grasses, on the other hand, were unable to extend their lifecycle independent of rainfall during the flowering period (Williams 1961).

If further confirmation of the low degree of correlation between perennial grasses and the environmental factors used in this study is found, future studies should include more environmental factors or life stages, such as recruitment phases. In addition, perennial grasses may respond better to soil moisture at deeper soil depths, and this should also be considered. Other additional environmental factors could include soil infiltration rates, which I observed to be higher in annual dominated areas than in perennial dominated areas or the occurrence of extreme rainfall events such as consecutive years with high summer rainfall. Overall, though, the strongest correlation of perennial grass abundance with any other variable, however, was the

negative correlation with annual grass abundance, as observed in grazed pastures in central NSW (Kemp & Dowling 1991), but unlike general trends on a larger scale in NSW (Garden *et al.* 2001). Consequently, some environmental factors that are strongly positively correlated with annual grass abundance in this study are negatively correlated with perennial grass abundance and vice versa, such as clay content, summer rain of the previous year and partially soil moisture. Another possible explanation, though, for the lack of correlations of perennial grasses with environmental factors, but negative correlations with annual grasses in this survey is the presence of negative interactions between the two groups. In the absence of annual grasses, native perennial grasses may be able to exist in a range of environments in these grasslands. Exotic annual grasses, however, have strong competitive effects on perennial grass growth and fecundity (Harris 1967; Melgoza *et al.* 1990; Claassen & Marler 1998; Dyer & Rice 1999; Hamilton *et al.* 1999; Hoopes & Hall 2002; Kolb *et al.* 2002; Lenz *et al.* 2003). In areas where abiotic factors favour annual grass growth, perennial grass abundance may thus decrease. Since such areas change with spatial and temporal rainfall regime and management, the outcome would be a multi-scale mosaic of perennial and annual grass abundance, with a negative correlation with each other, but with environmental factors mainly correlated to annual grass abundance.

Conclusions

The species compositions, levels of annual grass invasion and influences of different environmental factors in remnant grasslands in the mid-north region of South Australia are highly variable. In addition, past management practices and original species composition of remnants are generally unknown, probably leading to further unexplained variation in the data. At the present time, however, it is evident that rainfall regimes and soil properties are important variables driving the abundance of annual grasses.

The complex study design with two spatial scales and extended temporal scales successfully indicated various correlations on each scale. Thus, any conclusions or predictions on the correlation between environmental variables and grass abundances depend on the spatial and temporal scale of the system in question. The positive correlations of annual grasses with soil moisture and rainfall occurred over most temporal and spatial scales measured, with exceptions during the dry seasons, and are contrary to studies in other temperate grasslands. Perennial grass abundance, on the other hand, tended to be negatively associated with or independent of rainfall or soil moisture, with exceptions at all temporal and spatial scales. The controlling variables of perennial grass abundance were less clear and require further research.

Figures
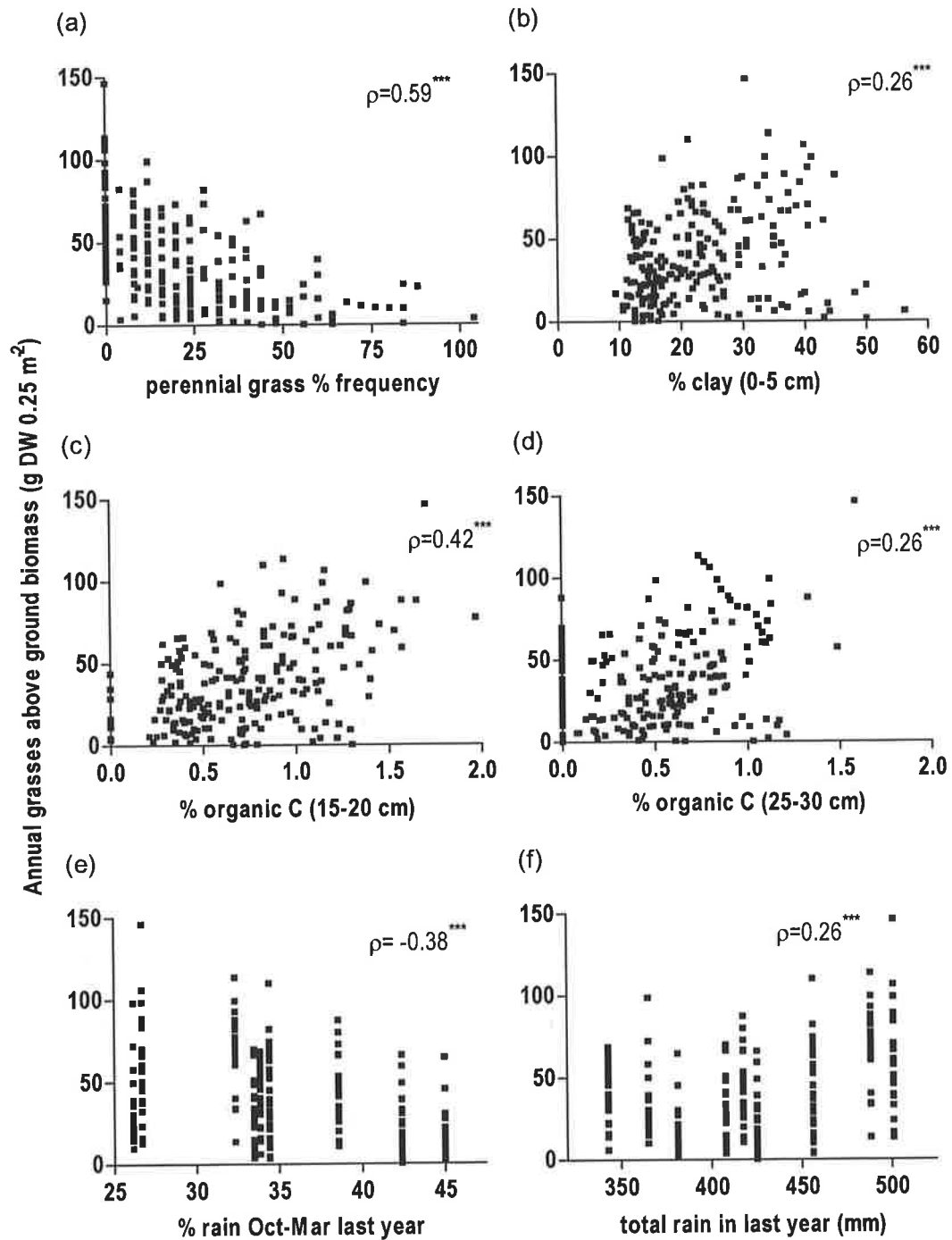
Figure 3.1: Significant correlations between total annual grass abundance with environmental factors, grazing and rainfall statistics (α= <0.001) between nine grasslands in the mid-north of South Australia.
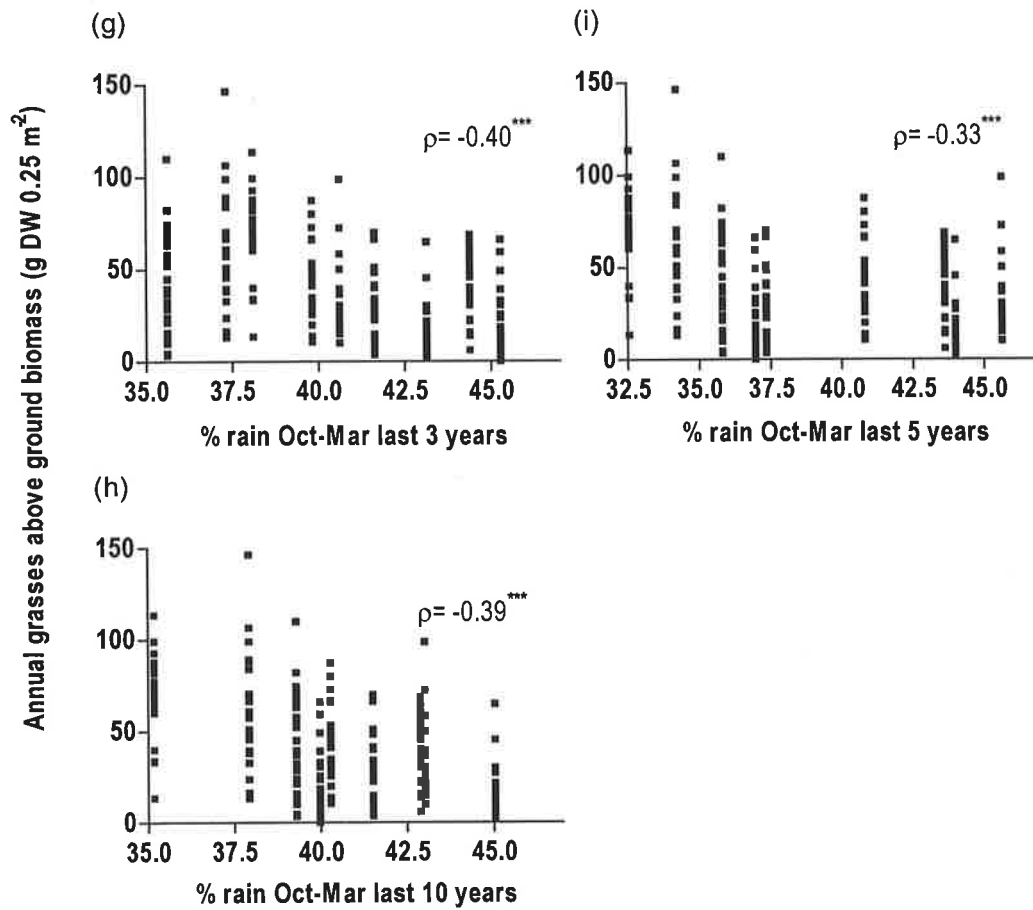
Figure 3.1 continued: Significant correlations between total annual grass abundance with environmental factors, grazing and rainfall statistics (α= <0.001) between nine grasslands in the mid-north of South Australia.
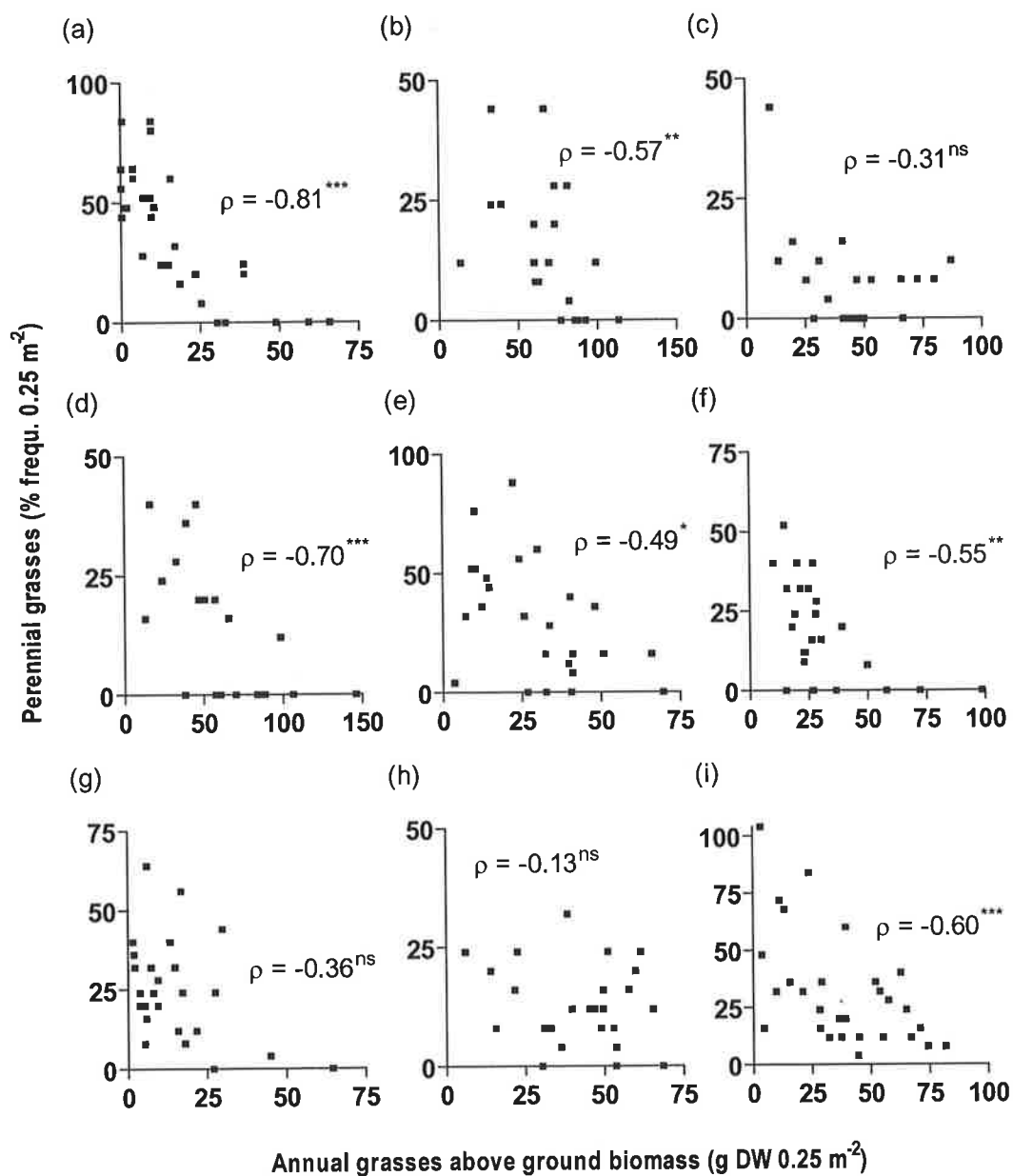
Figure 3.2: Correlations between annual grass biomass and perennial grass frequency at nine grasslands in the mid-north of South Australia: (a) Burra; (b) Clare; (c) Glen Roburn; (d) Snowtown; (e) Spalding; (f) Tarcowie; (g) Caltowie; (h) Whyte Yarcowie; (i) Mokota.
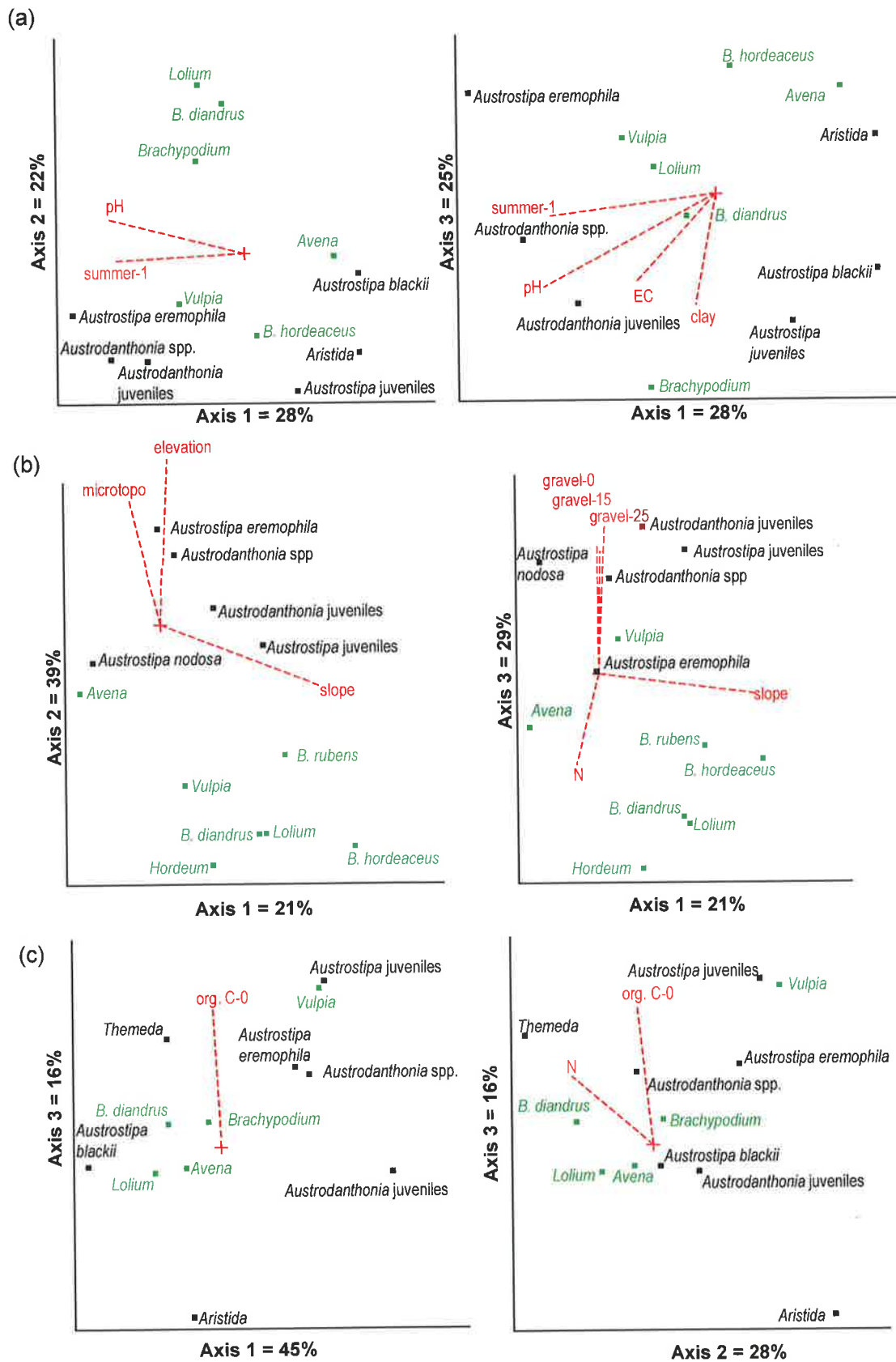
Figure 3.3: NMS ordination of correlations between environmental factors and grass species abundance (perennial grasses, annual grasses) for (a) between nine grasslands in the South Australian mid-north and (b)–(c) within grasslands: (b) Burra; (c) Clare. Vectors represent environmental factors with vector length indicating the relative strength of the correlation ($r^2 > 0.2$) and vector direction the direction of increase of the variable.
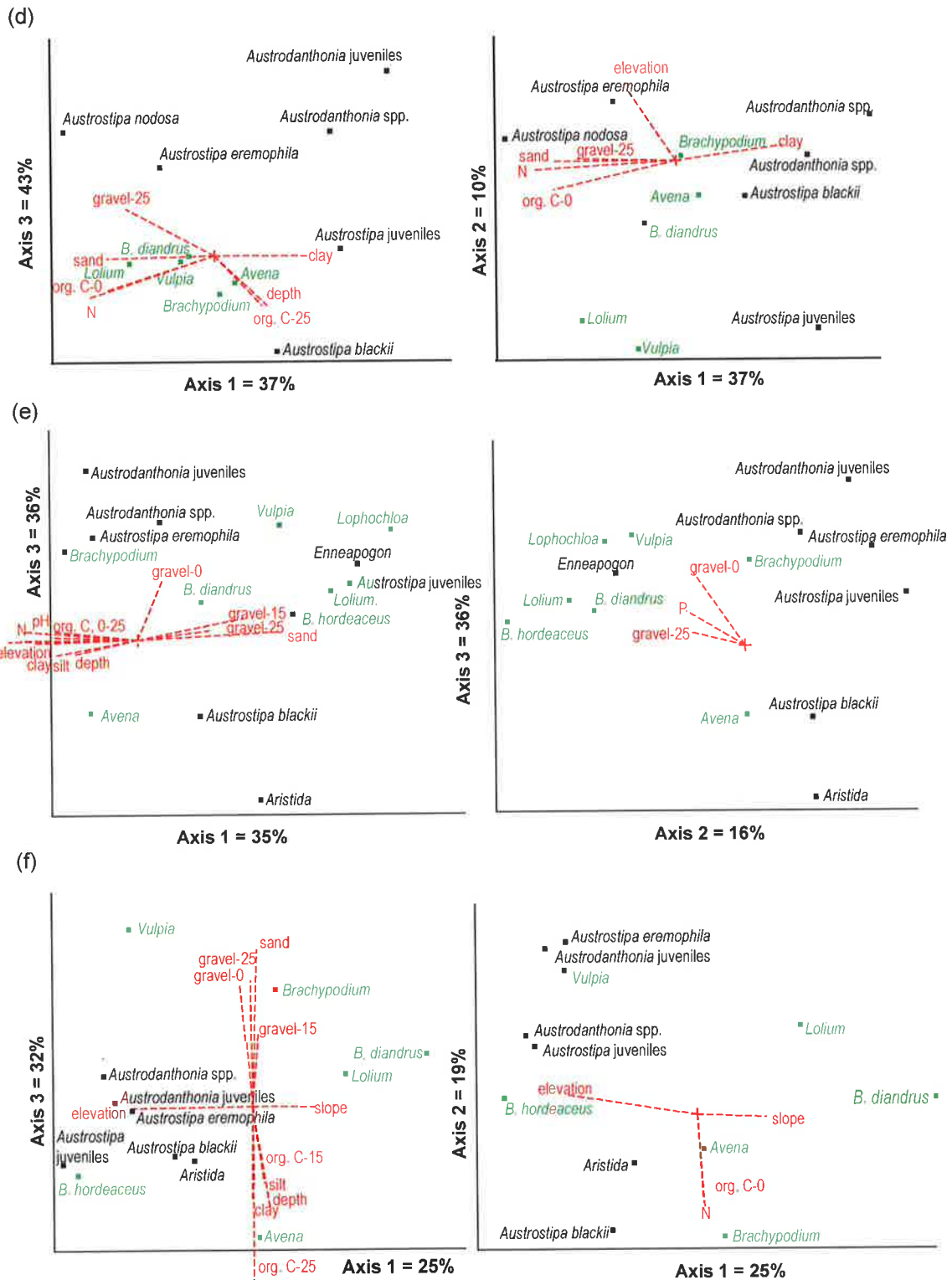
Figure 3.3 continued: NMS ordination of correlations between environmental factors and grass species abundance (perennial grasses, annual grasses) within grasslands in the South Australian mid-north: (d) Glen Roburn; (e) Snowtown; (f) Spalding. Vectors represent environmental factors with vector length indicating the relative strength of the correlation ($r^2 > 0.2$) and vector direction the direction of increase of the variable.
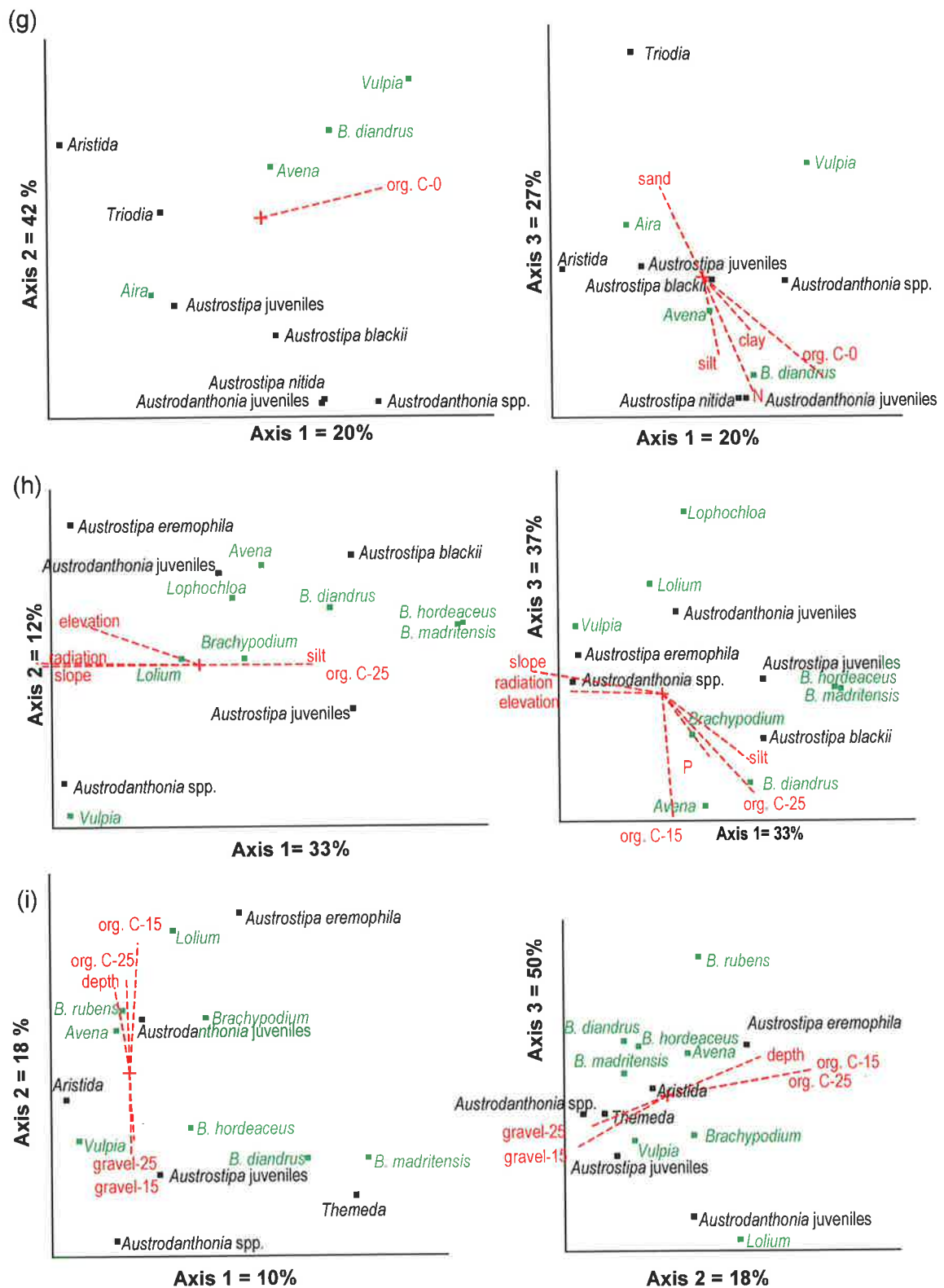
Figure 3.3 continued: NMS ordination of correlations between environmental factors and grass species abundance (perennial grasses, annual grasses) for within grasslands in the South Australian mid-north: (g) Tarcowie; (h) Caltowie; (i) Mokota. Vectors represent environmental factors with vector length indicating the relative strength of the correlation ($r^2 > 0.2$) and vector direction the direction of increase of the variable.
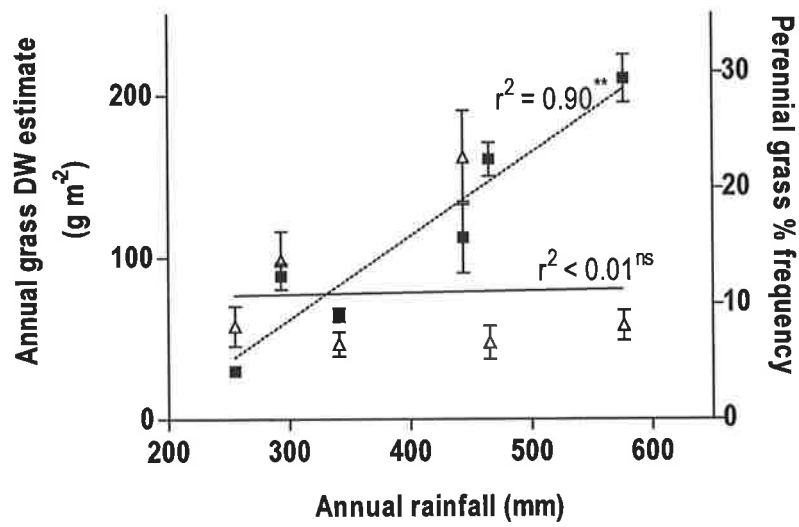
Figure 3.4: End of the season DW estimate of annual grasses (··■··) and end of season % frequency of perennial grasses (△) plotted against season's rainfall for three grasslands in the 2001 and 2002 growing seasons in the mid-north of South Australia.
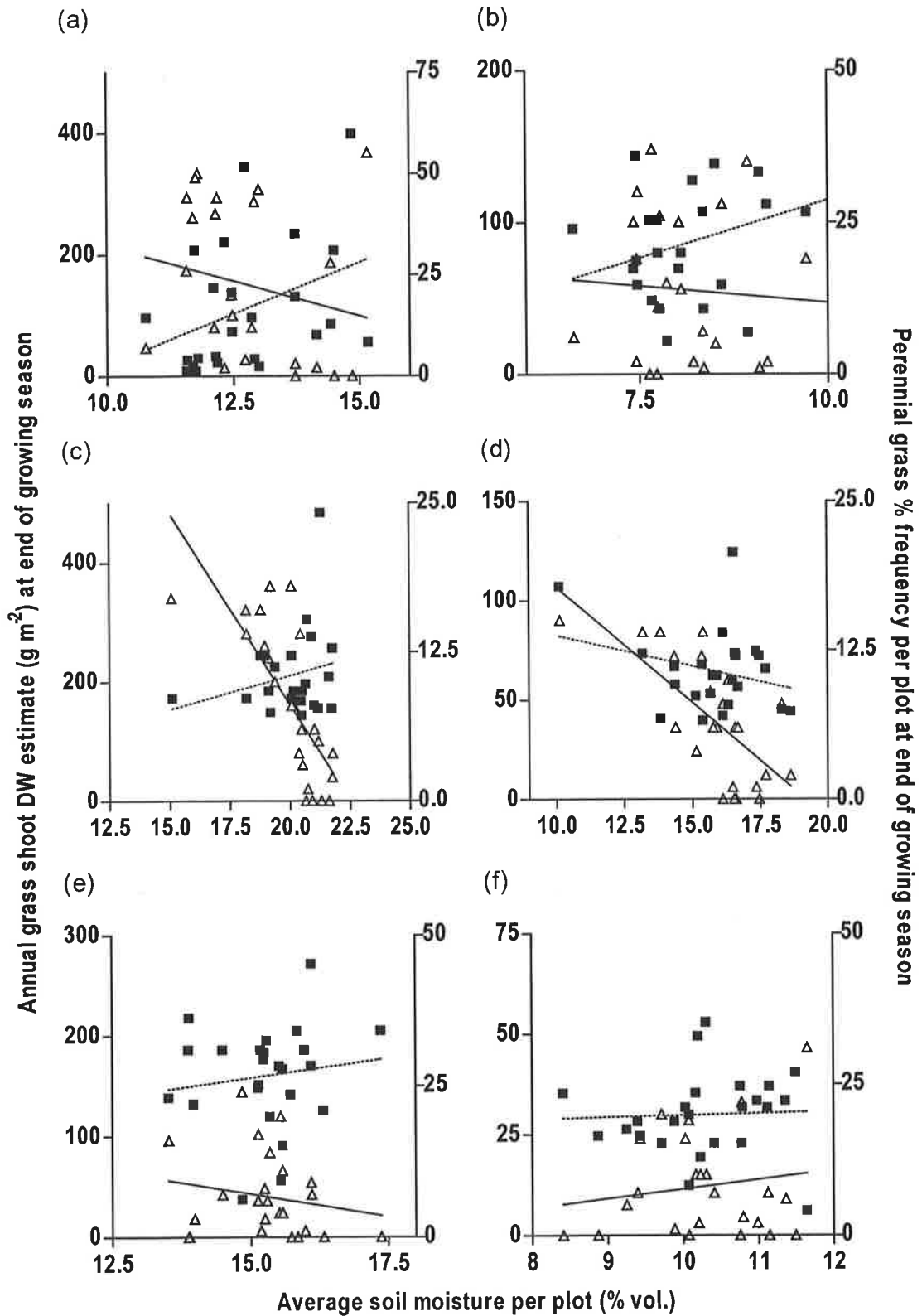
Figure 3.5: End-of-growing-season DW estimate of annual grasses (··■··) and % frequency of perennial

grasses (△) plotted against the average soil moisture throughout the season at three grasslands in the mid-north

of South Australia: (a) Burra 2001; (b) Burra 2002; (c) Clare 2001; (d) Clare 2002; (e) Glen Roburn 2001; (f) Glen

Roburn 2002.
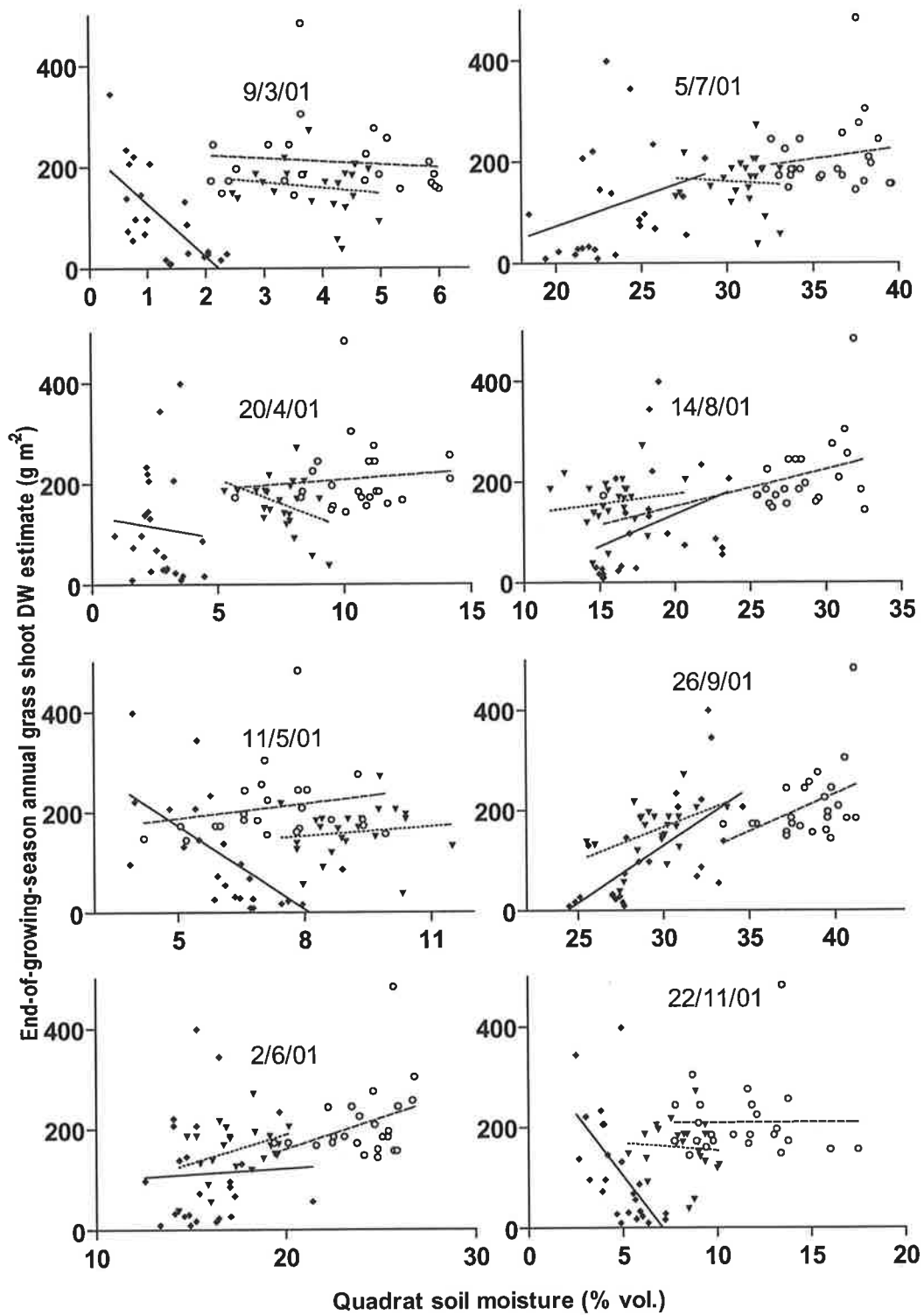
Figure 3.6: Correlations of quadrat soil moisture at various dates with end-of-growing-season annual grass DW in three grasslands (Burra (◆); Clare (○); Glen Roburn (▼)) in the mid-north of South Australia.
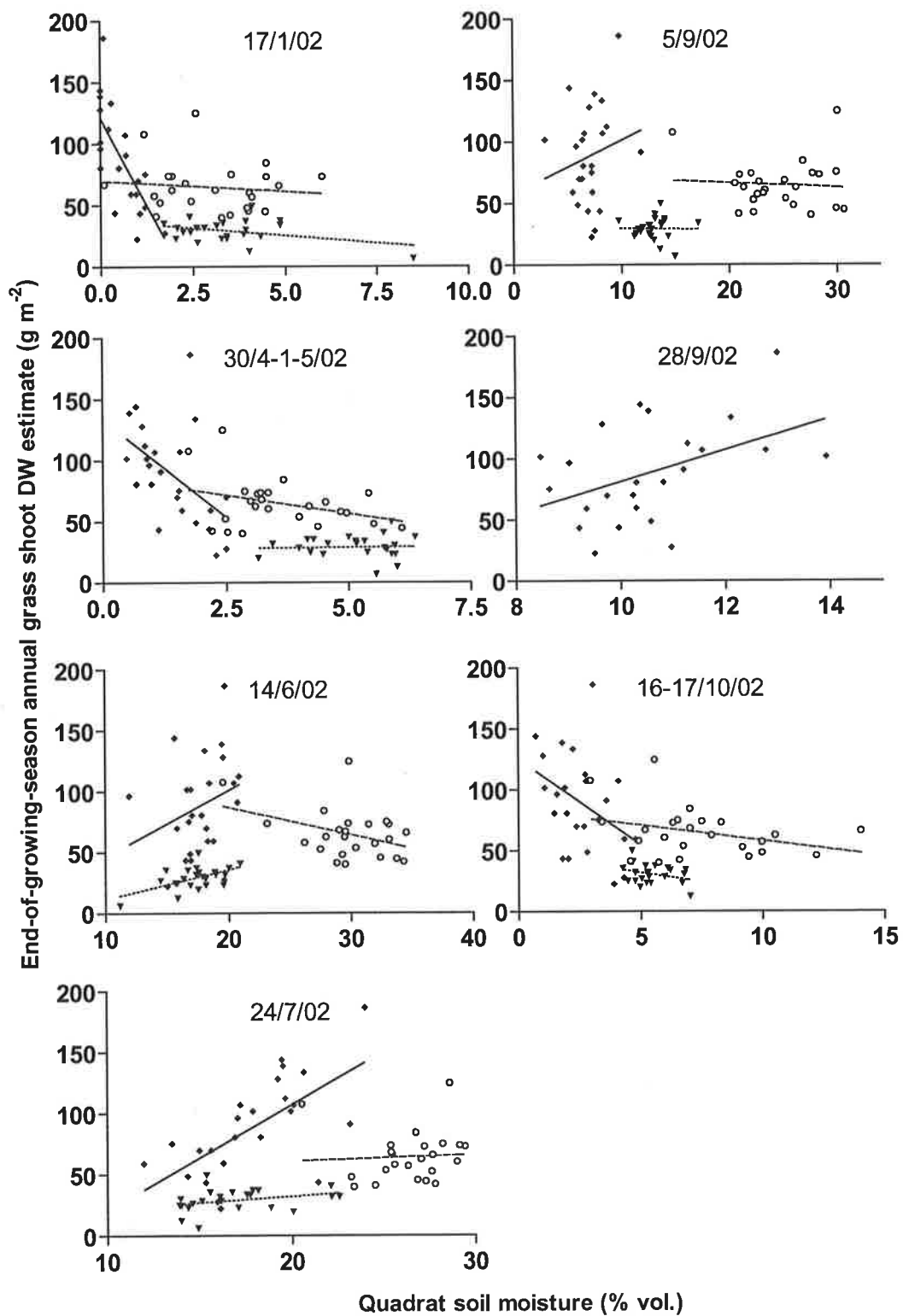
Figure 3.6 continued: Correlations of quadrat soil moisture at various dates with end-of-growing-season annual grass DW in three grasslands (Burra (◆); Clare (○); Glen Roburn (▼)) in the mid-north of South Australia.
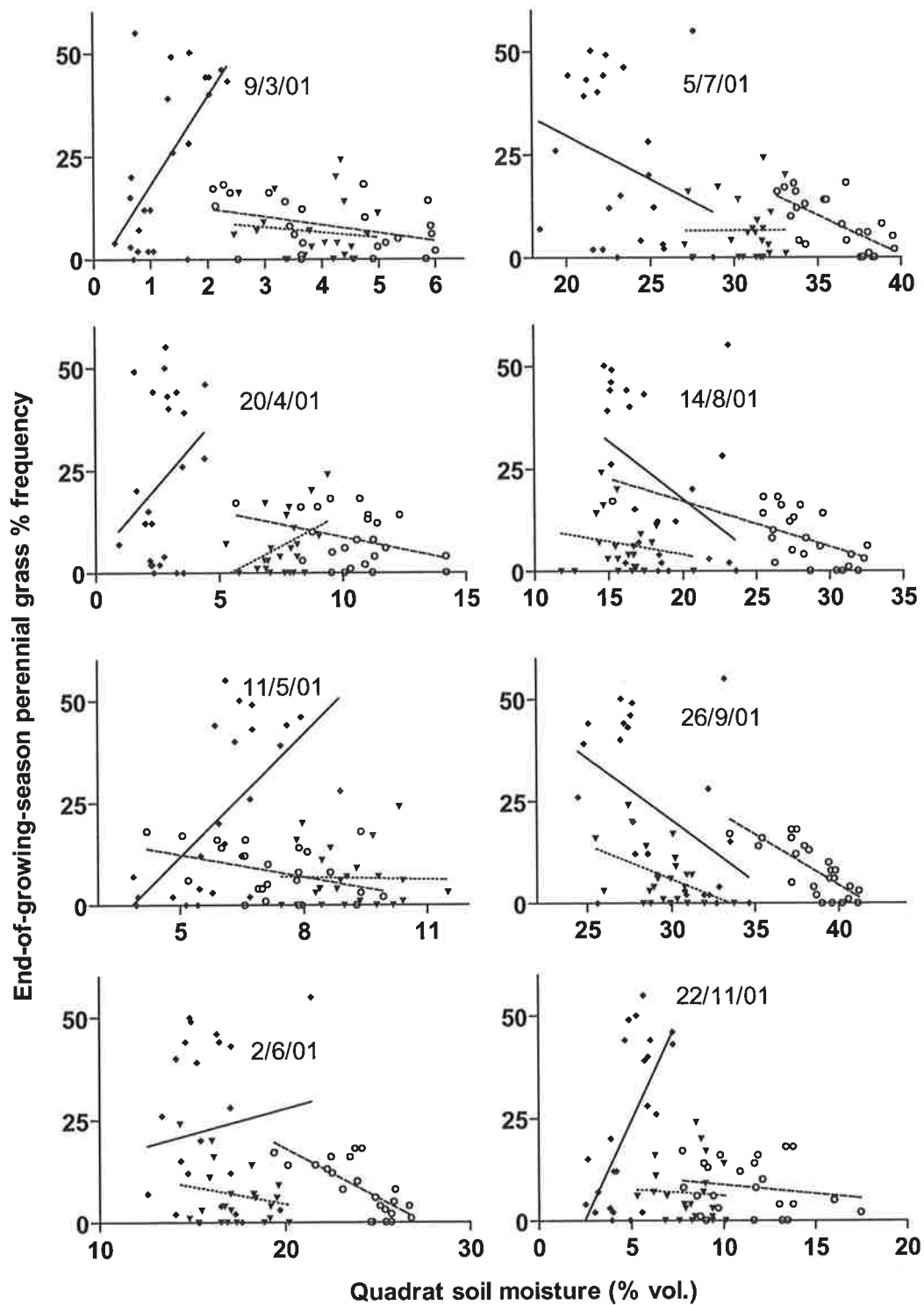
Figure 3.7: Correlations of quadrat soil moisture at various dates with end-of-growing-season perennial grass % frequency in three grasslands (Burra (♦); Clare (○); Glen Roburn (▼)) in the mid-north of South Australia.
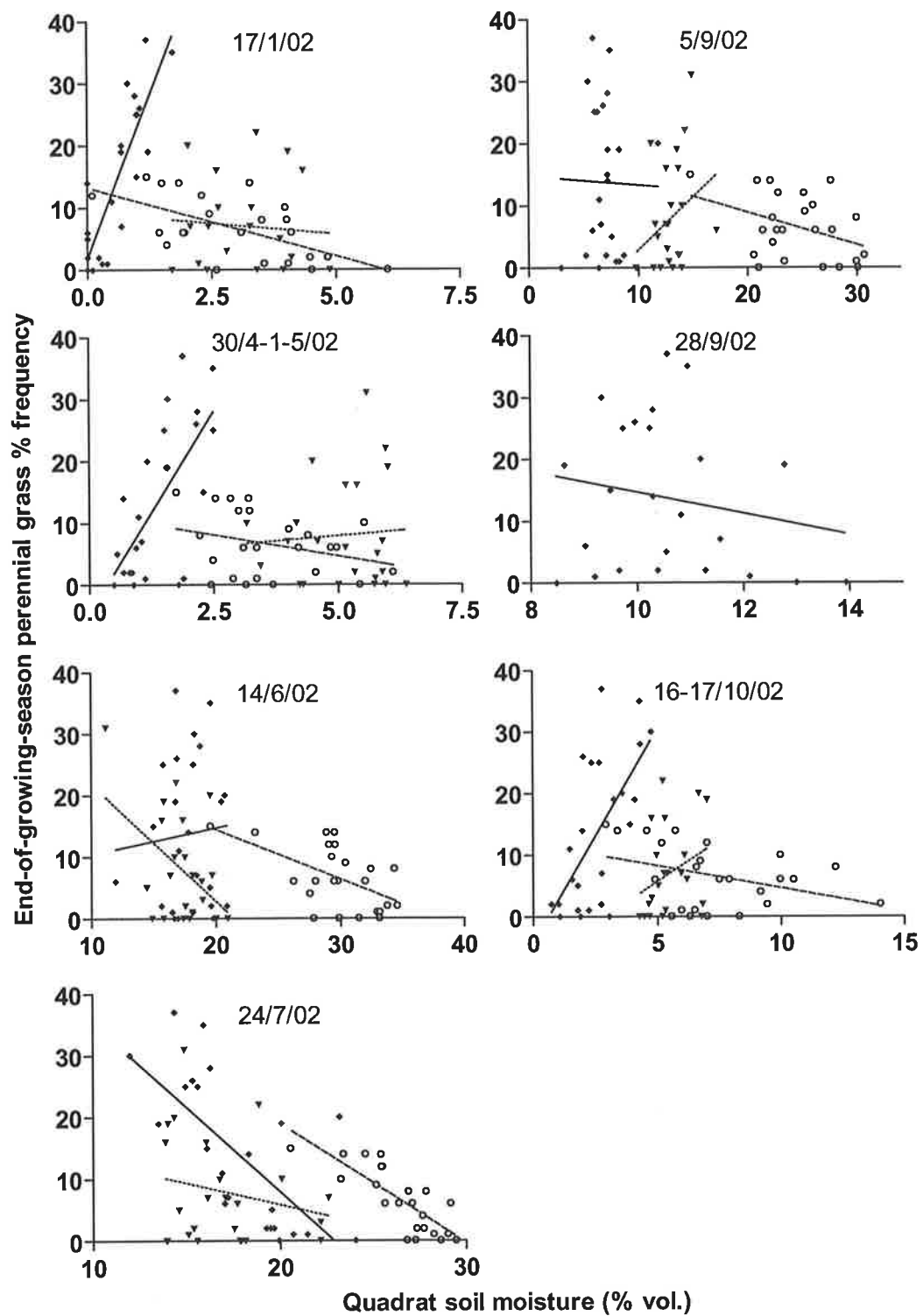
Figure 3.7 continued: Correlations of quadrat soil moisture at various dates with end-of-growing-season perennial grass % frequency in three grasslands (Burra (◆); Clare (○); Glen Roburn (▼)) in the mid-north of South Australia.
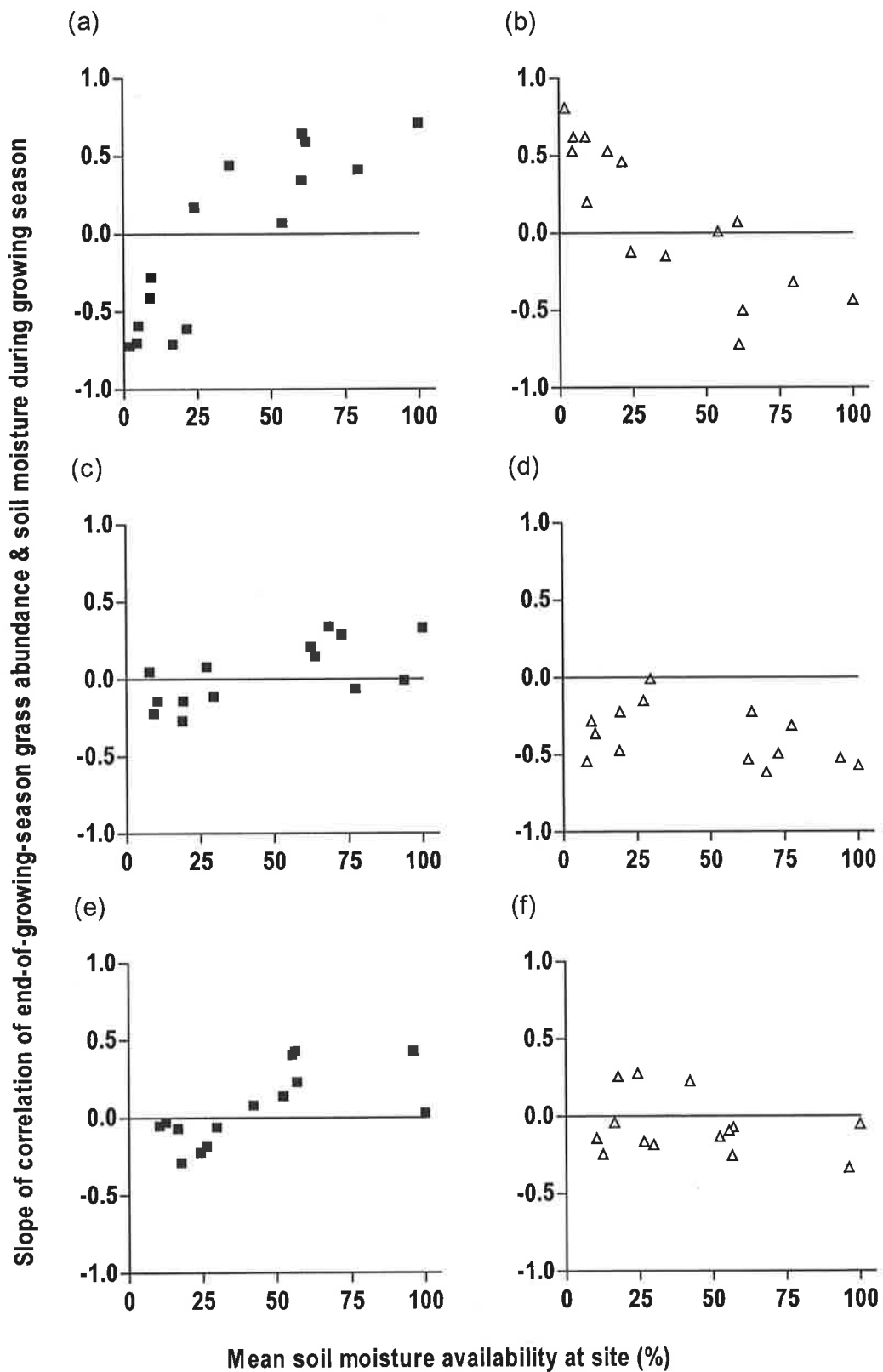
Figure 3.8: Correlations of % soil moisture availability with soil moisture regime for annual grasses (■) and perennial grasses (△) at three grasslands in the South Australian mid-north: (a)+ (b) Burra; (c) + (d) Clare; (e) + (f) Glen Roburn.

4. The role of seed limitation and resource availability in the recruitment of exotic annuals among native perennial grasses and vice versa in a South Australian mid-north grassland

Introduction

The initial stage of invasion of a system by a new plant species is the emergence, survival and successful recruitment of newly arrived propagules. In the absence of significant herbivory, such as in the case of destocked or unmanaged South Australian grasslands, these recruitment dynamics of temperate grasslands will be driven by propagule availability (dispersal and seed bank dynamics), abiotic conditions, direct resource competition or interference via litter accumulation. Previous research has shown that the degree of control that each of those factors exert on recruitment dynamics varies with species and in space and time as abiotic conditions change. Species-specific and provenance-specific properties, environmental fluctuations and microclimates are responsible for the high variability in the recruitment of many grassland species (Maze *et al.* 1993; Peco *et al.* 1998; Hamilton *et al.* 1999; Zobel *et al.* 2000; Buckland *et al.* 2001; Morgan 2001; Reynolds *et al.* 2001; Thompson *et al.* 2001; Pywell *et al.* 2003).

In grassy ecosystems both invasive and native species are generally more limited by propagule availability than other factors (Milchunas *et al.* 1992; Foster & Gross 1998; Hamilton *et al.* 1999; Bischoff 2002; Seabloom *et al.* 2003) and most manipulative studies that research recruitment or invasion in grassy ecosystems begin with the addition of propagules (Fowler 1988; Milchunas *et al.* 1992; Foster & Gross 1998; Morgan 1998a; Foster 1999; Hamilton *et al.* 1999; Buckland *et al.* 2001; Thompson *et al.* 2001; Foster 2002; Warren *et al.* 2002). Local seed bank limitation is an important factor, especially in unmanaged or overgrown grasslands (Kalamees & Zobel 1998; Zobel *et al.* 2000; Kalamees & Zobel 2002). In particular, the proportion of perennial species and the total species richness is often lower in the seed bank than in the standing vegetation (Peco *et al.* 1998). Doubling seed rain density over three years increased species richness and abundance in unproductive perennial semi-natural grassland in northern Europe (Zobel *et al.* 2000). Similarly, restoration efforts in European grasslands are as much hampered by the lack of propagules as by unsuitable abiotic conditions (Bakker & Berendse 1999) and restoration can be achieved in California grasslands by seed addition (Seabloom *et al.* 2003).

When propagules are not limiting, abiotic conditions (Hamilton *et al.* 1999; Buckland *et al.* 2001; Thompson *et al.* 2001), the competitive environment (Gurevitch 1986a; Milchunas *et al.* 1992; Foster & Gross 1998; Morgan 1998a; Foster 1999; Buckland *et al.* 2001) and their interaction (Fowler 1988; Foster 2002) control recruitment dynamics of invasive and native

species in grasslands. In general, small-seed species are more likely to benefit from gaps in the vegetation than large-seeded species (Burke & Grime 1996; Kalamees & Zobel 2002). Overall, however, invasion often follows changes in resource dynamics via resource addition or disturbances (Huenneke *et al.* 1990; Pérez-Fernández *et al.* 2000; Buckland *et al.* 2001; Thompson *et al.* 2001).

The theory of fluctuating resource availability predicts that the invasibility of system increases with the amount of unused resources (due to increased supply or decreased demand), assuming propagules are present and the species is suited to the habitat (Davis *et al.* 2000). In temperate grasslands of the South Australian mid-north, areas with higher soil moisture and nutrient availability are associated with higher biomass of invasive annual grasses, whereas perennial grasses are associated with areas of lower soil moisture and productivity (Chapter 3). To explore the future potential of further invasion by exotic annuals or re-invasion by perennial grasses, I aimed to determine the importance of increased resource and propagule availability for the recruitment of annual exotic species in perennial grass stands and perennial grasses into annual grass stands. Resource supply was increased directly by watering and indirectly by preventing the growth of resident vegetation through regular clipping. I applied different experimental treatments over two seasons and measured resulting recruitment. While not closely monitoring resource levels or competitive interactions as necessary to test for the predictions of non-equilibrium theories of plant invasion, this study serves as a pilot study of the factors that require further research.

Methods

Field emergence and survival

The experiments were carried out in a grassland located on a hillside 1 km north of Burra, South Australia (138° 55' E, 33° 41' S, 500 m a.s.l., Figure 2.3). Burra has a Mediterranean climate with hot summers and mild winters and an average annual rainfall of 439 mm (Bureau of Meteorology). Rainfall in 2001 was 413 mm. In January 1999 stock (mainly sheep) were excluded from two hectares of a southeast facing hillside paddock. Past grazing pressure has been estimated between medium to heavy for the region (J. Agnew, R. Williams, pers. com). No evidence of any vertebrate grazing (grazing damage, pellets) was observed during the course of the field experiment. The soil is a sandy loam and varies between skeletal to more than 0.5m depth (Chapter 3).

The pre-settlement vegetation of the study site is unknown. A grassland 1 km west that has been unstocked for more than 30 years is a *Lomandra multiflora* (R. Br.)Britten tussock complex (Hyde 1995). A few *Lomandra* individuals occur at the study site. However, exotic annual species (*Avena*

barbata (Pott ex Link), *Bromus diandrus* Roth, *B. hordeaceus* L., *B. rubens* L., *Echium plantagineum* L., *Gynandriris setifolia* (L.f.)Foster, *Romulea* spp Maratti, *Salvia verbenaca* L.) dominate the base of the hillside. The upper part of the hillside is dominated by native perennial grasses (*Austrodanthonia caespitosa* (Gaud.) H.P.Linder, *Austrodanthonia eriantha* (Lindl.) H.P.Linder, *Austrostipa eremophila* (Reader) S.W.L.Jacobs & J.Everett, *Austrostipa nodosa* (S.T.Blake) S.W.L.Jacobs & J.Everett) with some exotics in the interstitial spaces. In general the exotic annuals have larger, and presumably heavier propagules than the native grasses (Table 4.1).

Species	Seed size or weight
*Avena barbata**	12–20 mm long lemma [b]
*Bromus diandrus**	25-28 mm long lemma [a]
*B. hordeaceus**	8-9 mm × 4 mm lemma [a]
*B. rubens**	14-17 mm × 2-2.5 mm lemma [a]
*Echium plantagineum**	3.0 ±\ 0.5 mg / seed [c]
*Gynandriris setifolia**	1-1.5 mm long seed [a]
Romulea sp.*	1mm diameter seed [a]
Austrodanthonia caespitosa	3-6 mm long lemma [a], < 0.001 g /caryopsis [b]
A. eriantha	3.5-4 mm long lemma [a]
Austrostipa eremophila	6-9.5 mm long lemma [a]
A. nodosa	4-7 mm long floret [a]

Table 4.1: Available propagule size or weight for the dominant introduced (*) and native species at the study site. [a] Jessop and Toelken (1986); [b] T. Lenz (unpublished data, 2003); [c] Sheppard (2001).

Experimental design: To test for the effects of seed availability and changes in resource uptake and resource supply on the recruitment of annual exotics into perennial stands and perennial grasses into annual stands I set up two blocked three-way experiments. I ran a 75 m transect in both the annual stand at the base of the slope (80-100% annual grass cover) and the perennial-grass stand at the top of the slope (40-60% perennial grass cover, plus lichens, rocks and bare ground) perpendicular to the slope. On each site of each transect I established fifteen 4 m × 2 m blocks with 1 m spacing between each. I randomly selected ten blocks for the experiment and in each block established eight 0.5 m × 0.5 m quadrats, with 0.5 m spacing between each. These were randomly allocated to the eight factorial combinations of the factors: seed addition (seed addition versus control), decreased resource uptake (removal of standing biomass versus control), and increase resource availability (watering versus control).

Seed addition: I used *Avena barbata* (study site provenance) as a potential invader for the perennial-grass stand, and *Austrodanthonia caespitosa* (Auburn provenance; 138°41' E, 34°1' S) as a potential invader for the annual stand. Subsequently I will refer to both species by their generic

name. To check for seasonal differences, I planted seeds twice, once at the start of autumn (6-10 March 2001) and once at the start of winter (30 May -6 June 2001).

I hammered a 0.22 m × 0.22 m board with protruding nails in a 7 × 7 grid, each 3 cm apart, into an area in both control quadrats and seed addition quadrats to create 1 cm deep holes. In the seed addition quadrats I planted one floret in each hole using pre-prepared batches of seemingly viable florets of each species. To assess seed viability I also randomly selected three pre-prepared seed batches of each species, placed them at ambient laboratory temperature in Petri dishes containing moist filter paper and recorded the number of seeds with an emerging radicle daily.

Reduced resource uptake: Based on the positive relationship between plant size and soil moisture uptake in both *Avena* and *Austrodanthonia* (Chapter 5), I assumed that clipping reduces moisture uptake in both species. I thus treated 'reduced uptake' quadrats initially by clipping alive and dead standing biomass just above ground level and removing clippings from the quadrats. To estimate the initial standing biomass, I collected clippings from the same two treatments in each block, dried them at 80 °C for 72 h and weighed them. Significantly less biomass was removed in the annual stand (45.29 g ± 16.11 SD) than in the perennial-grass stand (61.50 g ± 21.00 SD) (ANOVA: F = 7.51; df = 1; P = 0.009). Once the growth period started, I re-clipped quadrats approximately fortnightly (25 April, 9 May, 30 May, 14 June, 26 June and 13 July).

Increased resource supply: I watered all 'increased resource supply' quadrats fortnightly if the soil water content of any quadrat was below field capacity by sprinkling the equivalent of 10 mm of water slowly over the quadrats. I had previously determined field capacity by flooding three 0.25 m × 0.25 m quadrats with 3 litres each in the centre and on each side of each transect and measuring volumetric soil moisture with a thetaprobe ML2x (Delta-T Devices) early the next morning. The field capacity was 14.33 ± 1.99 and 12.53 ± 1.70 % volumetric moisture (mean ± SE) in the perennial-grass stand and the annual stand transect respectively.

Harvest: I harvested exotic annuals in the perennial-grass stand quadrats on 30 May and 31 August by clipping the 0.22 m × 0.22 m inner quadrats at ground level and discarding native plant material and litter. Exotic plant material (mostly annual grasses, *Gynandriris setifolia*, and *Medicago* spp.) was dried at 80 °C for 72 h and weighed. After log-transformation, data conformed to assumptions of normality (Shapiro-Wilk W, JMP 3.1.4) and homoscedasticity (Brown-Forsythe, JMP 3.1.4) at P ≤ 0.05. I analysed the data using repeated-measure MANOVA, followed by separate ANOVAs on the two harvests and Tukey-Kramer Honestly Significant Difference (HSD) multiple comparison tests (JMP 3.1.4). The conservative Tukey-Kramer HSD test differed in both cases from the ANOVA. To increase its power I repeated the test after pooling factors that were not significant in the ANOVA.

I examined the quadrats within the annual-dominated stand for the presence of perennial grass seedlings (defined as those with basal diameter < 1 cm) on both dates but found no obvious seedling within the dense cover of live annuals and *Poa bulbosa*. I re-examined all 40 quadrats on 31 March 2002, after the annual vegetation had died back, intensively within five replicate blocks and briefly within the remaining five blocks.

Glasshouse emergence and survival

Due to the lack of perennial grass recruitment in the field I ran a glasshouse experiment to determine the effect of competition by annual grasses, soil moisture and nutrient availability on the emergence and then survival during a drought of *Austrodanthonia* under controlled conditions. The experiment included eight factorial combinations of the following factors: *Avena* competition (24 viable *Avena* seed per tray, Snowtown provenance, 138° 11' E, 33° 47' S, versus no *Avena*), soil moisture (watered to field capacity three times a week versus misting the top layer (30 squirts with hand mister) three times a week) and nutrient availability (15 squirts with hand mister containing 1g l⁻¹ Hortico Aquasol ™ (23% N, 4% P, 18% K + trace elements) in tap water versus 15 squirts tap water fortnightly). Each combination was applied to eight replicates of 1 litre plastic trays (9-11 cm wide, 14.2-16.5 cm long, 6 cm deep, 6 drainage holes), that contained Nu-Erth™ Special Native Plant mix (20% sand, 80% composted pine bark, trace elements) and were planted with 0.1 g (± 0.0005) cleaned *Austrodanthonia* seed (Monarto provenance: 139°8'E; 35°1'S) on 2 May 2003. I counted seedlings numbers of both species per tray weekly and weeded any dicot seedlings. After eight weeks, when little further recruitment was recorded, I discontinued watering and nutrient addition and terminated the experiments ten weeks later, when no more recruits survived. I also assessed initial seed viability by germinating three batches of both species in Petri dishes as described above.

The majority of data distributions, where more than one tray contained living seedlings (*i.e.* > 1 replicate ≠ 0) were normal, but variances were unequal. Departures from homoscedasticity have little effect on F-ratios and associated probabilities if samples sizes are equal and the experiment has more than five treatments and six replicates (Underwood 1997, p. 193). I thus performed repeated-measures MANOVAs, followed by ANOVAS on each period.

Results

Field recruitment

Rainfall (daily readings 1 km west of field site; Bureau of Meteorology) was 58.6 mm during autumn (March - May) and 154.6 mm during winter (June - August). The watering plots received an additional 20 mm during each autumn and winter (25 April, 9 May, 30 May & 26 June).

<u>Recruitment of exotic annuals:</u> Under laboratory conditions 70.89 ± 3.15% (mean ± SE) *Avena* seeds of the autumn run germinated and 80.25 ± 4.23% (mean ± SE) of the winter run. In the field the mean dry weight of exotic annuals harvested was 0.34 ± 0.02 g (mean ± SE) at the end of autumn and 1.87 ± 0.07 g at the end of winter. Treatment effects differed with season. Watering strongly increased exotic annual dry weight during autumn and seed addition slightly increased exotic annual dry weight during winter (Table 4.2; Figure 4.1). However, the significant effect of block in both periods suggests further small-scale factors, such as soil properties, have a strong effect on the recruitment of exotic annuals. Plotting the initial quadrat biomass harvested against final harvest of exotic annuals of the same quadrat showed a trend towards positive correlations (log autumn harvest = -5.5 + 1.0 × log initial biomass, $r^2 = 0.31$, P = 0.09; log winter harvest = -2.7 + 0.8 × log initial biomass, $r^2 = 0.40$, P = 0.05), suggesting that the recruitment of exotic annuals may be more likely in higher productivity sites. Quadrat moisture or nutrient availability was not monitored.

Factor	Repeated-measures MANOVA			ANOVA Autumn (r^2=0.63)			ANOVA Winter (r^2=0.76)		
	Numerator DF	F	P-value	DF	F	P-value	DF	F	P-value
Seed addition (S)	1	3.71	0.06	1	1.74	0.19	1	6.62	0.01
Clipping (C)	1	0.59	0.45	1	0.14	0.71	1	2.03	0.16
Watering (W)	1	11.44	0.001	1	14.72	0.001	1	0.27	0.60
Block (B)	9	3.53	0.001	9	2.33	0.03	9	7.23	<0.0001
Time (T)	1	836.30	<0.0001						
T × S	1	0.15	0.70						
T × C	1	0.03	0.85						
T × W	1	16.30	0.0001						
T × B	9	2.12	0.04						
S × C				1	0.42	0.52	1	0.13	0.72
S × W				1	0.07	0.79	1	1.68	0.20
S × B				9	0.66	0.74	9	1.72	0.12
C × W				1	0.14	0.71	1	0.01	0.94
C × B				9	0.95	0.49	9	1.41	0.22
W × B				9	1.23	0.31	9	1.53	0.17

Table 4.2: Effects of seed addition, clipping & watering on log-transformed exotic annual biomass during autumn & winter 2001 in a grassland in the South Australian mid-north. Higher interactions not significant at P ≤ 0.05. Denominator DF = 67 for MANOVA.

<u>Native perennial grass recruitment:</u> Under laboratory conditions 40.52 ± 4.90% (mean ± SE) *Austrodanthonia* seeds of the autumn run germinated. I also tested winter run viability but data

were lost. The same batch of seed was used for both runs and I assume seed viability to be similar in the second run.

There was no evidence of perennial grass recruitment in the field. I could not locate any perennial grass seedlings in the experimental quadrats at any time after planting, including the planned censuses in May & August 2001 and the later census of March 2002. During other extended fieldwork at this site I occasionally noticed what appeared to be perennial grass seedlings (1-3 leaves), but never located an obvious larger juvenile perennial grass (*i.e.* not a tiller from a nearby plant or a plant re-shooting after dormancy) in areas dominated by annual grasses. In comparison, I located 0.38 ± 0.18 (mean $\pm$ SE, n = 8) apparent *Austrostipa* juveniles per square metre in an area co-dominated by both annual and perennial grasses and 1.00 ± 0.38. apparent *Austrostipa* juveniles per square metre in a perennial-grass-dominated area (T. Lenz, 2002, unpublished data).

Glasshouse recruitment

The 0.1 g *Austrodanthonia* seed added to each experimental replicate contained 418 ± 7.7 seed (mean $\pm$ SE). Under controlled conditions $62.1 \pm 0.9\%$ (mean $\pm$ SE) of the *Austrodanthonia* seeds that did not decay with fungal disease (60-80 seed per dish) germinated. *Avena* germination was 100%.

Neither nutrient addition nor its interactions with other treatments had any effect on *Austrodanthonia* in the repeated-measures MANOVA model of the complete dataset (data not shown), thus I removed the nutrient addition factor from the analysis. The resulting MANOVA (Table 4.3) showed a highly significant three-way interaction between watering level, *Avena* presence and time, indicating strong and complex changes of the different factors over time.

Source	Test	Exact F	Num DF	Den DF	P-value
All between	F	109.56	3	60	<0.0001
Water (W)	F	315.68	1	60	<0.0001
Avena (A)	F	10.15	1	60	<0.01
W × A	F	2.84	1	60	0.10
All within	Wilks' λ	15.89	54	128.94	<0.0001
T (Time)	F	128.75	18	43	<0.0001
T × W	F	123.59	18	43	<0.0001
T × A	F	7.50	18	43	<0.0001
T × W × A	F	4.26	18	43	<0.0001

Table 4.3: Effects of water availability and *Avena barbata* on *Austrodanthonia caespitosa* seedling numbers (Repeated-measures MANOVA; Num = numerator; den = denominator).

In the high watering treatments 80-100 *Austrodanthonia* seedlings emerged in the first two weeks, while in the low watering treatments 10-20 *Austrodanthonia* emerged over seven weeks (Figure 4.2a). While the presence of *Avena* seedlings appeared to decrease *Austrodanthonia* seedling numbers in both watering treatments, *Avena* had a larger relative negative effect in the low watering treatment, where it halved the number of seedlings compared to a 10% decrease in the high watering treatment. *Avena* emerged a lot faster, especially in the low watering treatment. Furthermore, the difference between the number of seeds emerging in the low versus the high watering treatment was much smaller in Avena than in *Austrodanthonia* (Figure 4.2a; Figure 4.2b). In both watering treatments *Avena* decreased the survival of *Austrodanthonia* seedlings by 2–3 weeks after water and nutrient addition ceased in Week 8.

To investigate the differences in the experimental effects in further detail, I analysed the high watering and low watering treatments separately. In the low watering treatments, the number of *Austrodanthonia* seedlings tended to be reduced by nutrients and by the presence of *Avena* between Week 6 to Week 13 (Table 4.4). In the high watering treatments, neither nutrient nor any of its interactions had any effect on *Austrodanthonia* emergence and survival (data not shown). With the nutrient factor removed from the analysis, the effect of *Avena* changed over time (Table 4.5). Initially *Avena* had no effect on *Austrodanthonia* numbers, but from Week 11 on *Avena* increasingly decreased the number of *Austrodanthonia* seedlings.

(a) Source	Test	Exact F	Numerator DF	Denominator DF	P-value
All Between	F	5.77	3	28	<0.01
Nutrients (N)	F	5.63	1	28	0.02
Avena (A)	F	11.45	1	28	<0.01
N × A	F	0.24	1	28	0.63
All Within	Wilks' λ	1.10	54	33.59	0.39
Time (T)	F	3.16	18	11	0.03
T × N	F	0.69	18	11	0.76
T × A	F	2.31	18	11	0.08
T × N × A	F	0.70	18	11	0.75

(b)	Nutrients		Avena	
Period	F	P-value	F	P-value
0-1	<0.01	1.00	2.24	0.15
1-2	<0.01	1.00	2.24	0.15
2-3	0.01	0.94	0.26	0.61
3-4	<0.01	0.95	1.01	0.33
4-5	0.38	0.54	0.74	0.40
5-6	2.00	0.17	0.84	0.37
6-7	8.22	0.01	4.17	0.05
7-8	8.27	0.01	7.07	0.01
8-9	7.02	0.01	7.20	0.01
9-10	5.99	0.02	6.32	0.02
10-11	6.68	0.02	12.76	<0.01
11-12	3.80	0.06	43.93	<0.0001
12-13	0.85	0.37	24.95	<0.0001
13-14	0.16	0.69	6.60	0.02
14-15	1.10	0.30	5.33	0.03
15-16	1.00	0.33	1.00	0.33

Table 4.4: Effects of nutrient addition & *Avena barbata* on *Austrodanthonia caespitosa* seedling numbers in low watering treatments ((a) Repeated-measures MANOVA; (b) effect of nutrient addition & *Avena barbata* in ANOVAs (No interactions significant at $\alpha = 0.05$; numerator DF = 1, denominator DF = 28)).

(a)	Source	F	Numerator DF	Denominator DF	P-value
	Avena	6.28	1	30	0.02
	Time	86.77	18	13	<0.0001
	Time × *Avena*	5.16	18	13	<0.01

(b)	Period	F	P-value		Period	F	P-value
	0-1	1.40	0.25		9-10	0.94	0.34
	1-2	1.22	0.28		10-11	2.15	0.15
	2-3	1.52	0.23		11-12	8.28	0.01
	3-4	1.92	0.18		12-13	21.59	<0.0001
	4-5	1.85	0.18		13-14	55.77	<0.0001
	5-6	1.03	0.32		14-15	16.79	<0.01
	6-7	1.28	0.27		15-16	11.51	<0.01
	7-8	1.65	0.21		16-17	3.46	0.07
	8-9	1.35	0.25		17-18	Too few data	

Table 4.5: Effects of *Avena barbata* on *Austrodanthonia caespitosa* seedling numbers in high watering treatments ((a) Repeated-measures MANOVA; (b) ANOVAs (Numerator DF = 1, denominator DF = 30)).

Discussion

Recruitment of exotic annuals

Exotic annual species were able to recruit in all experimental plots, and their biomass was considerably increased by watering in autumn, and slightly increased by seed addition in winter. Although soil water content in all plots fell below field capacity in winter and received as much additional water as during autumn, soil moisture was not as limiting as seed availability. Using the same plot for two seasons may also have resulted in reduced seed availability for the second run and this confounding effect cannot be excluded. Originally, I had planned to use new blocks for subsequent seasons but time and resource limitations prevented this. Thus, overall, the recruitment of exotic annuals was not strongly affected by any of the experimental treatments during winter. This suggests that propagules of exotic annuals are present and that exotic annuals can recruit well in areas still dominated by perennial grasses. Their recruitment is mainly limited by the supply of soil moisture through rainfall or run-on rather than strong resource uptake by perennial grasses. The large effect of block on the results suggests that site-specific properties are a further important aspect in the recruitment of annual exotics and requires further research. The trend towards a positive correlation of initial biomass of the quadrats and harvested biomass suggests that differences in productivity, for example due to soil properties, are the most likely cause of this variation.

Not only does the germination, recruitment and growth of *Avena* strongly increase with soil moisture (Pérez-Fernández *et al.* 2000, Chapter 5), but also it is relatively drought tolerant as a seedling. Its drought tolerance during the recruitment phase is shown here by its ability to survive almost as long during a drought as *Austrodanthonia*. Due to their need for yearly seed production (Young & Evans 1989) annual grasses like *Avena* tend to be adapted to the driest possible conditions rather than average conditions (Jackson & Roy 1986). Within a few hundred years of arriving in California different *Avena* populations have adapted to specific local climates (Jain & Rai 1980; Jain 1982). *Avena* seed are also unaffected by drying out during germination (Pérez-Fernández *et al.* 2000). Overall, it is thus unlikely that annual grasses decrease significantly in density compared to perennial grasses during periods of drought.

Recruitment of native perennial grasses

Given suitable moisture and temperature conditions provided during at least the winter period, perennial grass seeds from both the natural seedbank, if any, and experimental seedbank should have been able to germinate. The lack of evidence of the survival of any perennial grass seedlings could be due to several reasons. Firstly, the recruitment of native grasses from seed may be naturally rare. Perennial grass species are adapted to long-term survival rather than high recruitment, and the increase in resources or seeds may have been of an insufficient magnitude or with inappropriate timing to allow the survival of any perennial grass seedlings that emerged. Secondly, the exotic annual vegetation may have changed the biotic and abiotic environment to such a degree that perennial grass seedlings are not suited to this habitat any more. Events of an extreme magnitude, such as a severe grazing event to reduce standing biomass and litter, followed by high summer rainfalls may be required to encourage perennial grass recruitment. Thirdly, the planting density of perennial grasses may have to be considerable higher for a successful recruitment event.

Without further research none of these possibilities can be negated or confirmed. The results are consistent with findings from studies in most other temperate grasslands that perennial grass recruitment from seed is relatively rare. In Victorian grasslands in south-eastern Australia the recruitment of native species is rare, especially in unmanaged sites (Morgan 2001). In California grasslands the recruitment of one native perennial grass species is strongly moisture and seed limited, with moisture limitation due to the high water uptake by invasive annuals (Hamilton *et al.* 1999). In the northern tablelands of New South Wales, south-eastern Australia, where annual grasses are less abundant and rainfall is evenly distributed throughout the year, rainfall events over 40 mm in spring and summer drive the emergence of other native perennial grasses (Huxtable & Whalley 1999). *Austrodanthonia,* in particular, germinates over a broad range of

temperatures, but requires high soil moisture (Maze *et al.* 1993), as confirmed by the glasshouse experiment.

A factor that can lead to recruitment limitation in perennial grasses is seed predation by ants. While viable seed was added to half the quadrats, predation of both annual and perennial grass seeds by ants is an important factor in other grasslands (Capon & O'Connor 1990; O'Connor 1991; Heady *et al.* 1992; Haase *et al.* 1995; Veenendaal *et al.* 1996; Vila & Lloret 2000; Mayor *et al.* 2003). I observed some seed predation by ants during extended fieldwork at the site. Heavy predation within a short period after seed production may be all that is required to remove significant amounts of seed from the seed bank. However, the glasshouse results also indicate that even low levels of annual grass presence have a negative effect on the emergence and survival of *Austrodanthonia* seedlings, especially at low soil moisture or at times of decreasing soil moisture. Even the short, but dense, cover of annual grasses and *Poa bulbosa* that still remained in the field quadrats after fortnightly clipping could have had a strong negative effect on any perennial grass seedlings that emerged, especially in the plots where soil moisture was amended. Although soil moisture availability was the main factor that controlled seedling numbers in the glasshouse, the presence of a short, but dense, cover of actively growing vegetation would have had a strong effect on available soil moisture. Neither *Avena* nor *Austrodanthonia* are strongly affected by temperature during germination (Maze *et al.* 1993; Reynolds *et al.* 2001). Thus, assuming the initiation of germination in both grass types after heavy rainfalls, annual grasses tend to germinate faster and at higher rates than many perennial grasses, which may have dormancy periods or lower seed viability (Harris & Wilson 1970; Reynolds *et al.* 2001). The wetter winter season may have been more suitable for perennial grass survival under annual grass competition, however experimental treatments were discontinued at the end of winter and annual grasses did regrow to some extent. Longer continuation of the experimental treatments and higher planting density may have been required to allow the survival of any perennial grasses that emerged.

Conclusions

Overall, I suggest that the successful recruitment of perennial grasses in unmanaged areas dominated by annuals in the mid-north is either unlikely due to permanent changes to environmental conditions produced by annual grass invasion and/or dependent on an extended warm-season-dominant rainfall regime and specific grazing events. Although soil moisture appears to drive the recruitment of annual exotics and will be important to the recruitment of native perennial grasses, their responses to, and their effects on, soil moisture are very different. During the cool season the relatively low soil moisture uptake of perennial grasses (Chapter 5) may create unused resources enabling annuals to recruit, while the rapid water uptake by annuals

(Chapter 5) may create few windows of opportunity for perennial grasses to recruit amongst them. During high warm-season rainfall or after low cool-season rainfall the invasibility of annual stands by perennial grasses may increase, however to what extent still remains to be determined. The extent of recruitment limitation for the native perennial grasses in this system also remains unknown, but cannot be excluded as a major factor.

These results stand in stark contrast to recent findings by Seabloom *et al.* (2003), who were able to restore a field site in California with native perennial grasses through ploughing and heavy seed addition. After introducing seeds of annual exotics and imposing a range of experimental treatments over several seasons, they found that the resident perennial grasses were strong competitors in all instances. The abundance of exotic annuals tended to increase with disturbance, but annual species were unable to resisted invasion by native perennials under any circumstances. They concluded that the persistent dominance of California grasslands by annual exotics was mostly due to their strong recruitment, and dispersal limitation of perennial grasses, and only partially due to environmental factors.

In my study a more extreme disturbance, such as ploughing, heavier seed addition or a longer experimental period may well have led to the recruitment of perennial grasses in the field. However, unlike in Seabloom *et al.* (2003), annual grasses in the South Australian mid-north grassland are able to recruit in stands dominated by perennial grasses and as adults strongly compete with perennial grasses (Chapter 6). Species-specific or environmental differences may be responsible for this difference between the invasion process in these two quite similar systems and between similar species groups. This lends further indirect evidence to the recent conclusions by several authors that invasion events are not a result of predictable habitat or species characteristics but depend on the outcome of specific interactions between invader and invaded system in terms of resource availability, species traits and seed availability (Leishman 1999; Buckland *et al.* 2001; Thompson *et al.* 2001; Milbau *et al.* 2003; Pywell *et al.* 2003).

Figures

(a)

(b)
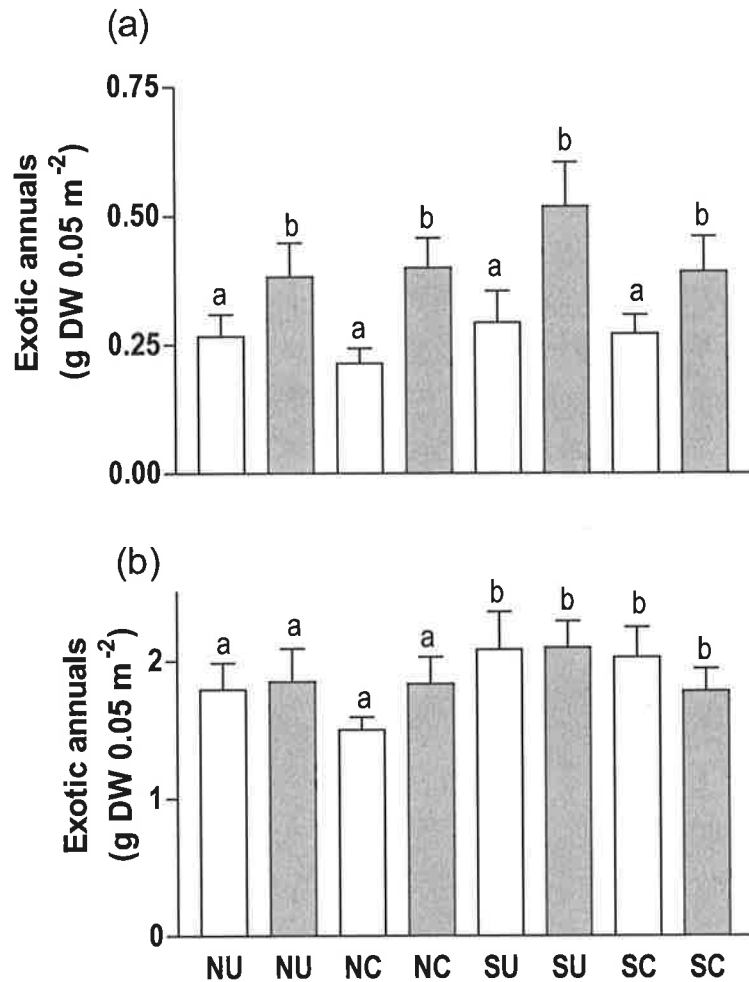
Figure 4.1: Aboveground biomass of exotic annuals after three months under different environmental conditions (not irrigated (□); irrigated (▨); no seed added (N); seed added (S); unclipped (U); clipped (C)) at (a) the end of autumn 2001 and (b) the end of winter 2001 in a grassland in the mid-north of South Australia. Different letters show significant differences at $\alpha = 0.05$ (Tukey-Kramer HSD test on significant treatment effects only). Note different scales for both graphs.
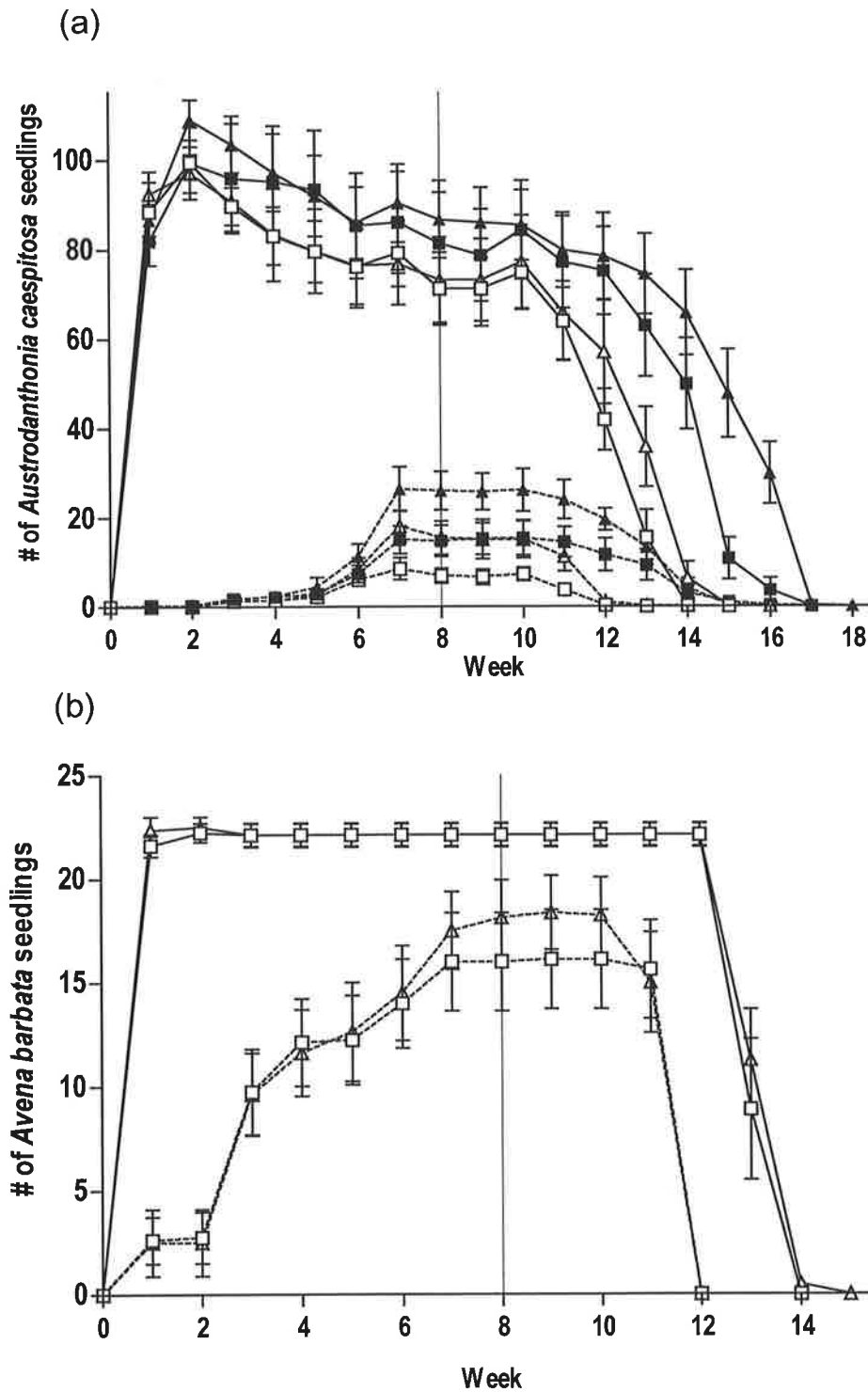
Figure 4.2: Effect of water availability (low (···); high (—)) and nutrient availability (low (△or ▲); high (■ or □)) on (a) number of *Austrodanthonia caespitosa* seedlings without (■ or ▲) or with (△ or □) *Avena barbata* as competitors and (b) number of *Avena barbata* seedlings acting as competitors. Grey lines indicate final water and nutrient addition. Note different scales for both graphs.

5. Effects of spatial and temporal soil moisture gradients on growth of four common South Australian grasses

Introduction

The theoretical framework of the process of plant invasion has changed from models examining characteristics of invasive plants (Baker 1965) or invaded habitats (Fox & Fox 1986; Orians 1986; Hobbs 1989; review in Levine & D'Antonio 1999) to models that include non-equilibrium conditions, stochastic events and neighbourhood interactions, regardless of whether these processes are driven by productivity, diversity, disturbance regimes or species characteristics (Johnstone 1986; Hengeveld 1988). Several recent experimental studies have directly supported the importance of interactions between resource fluctuations, propagule availability and neighbourhood interactions to invasions or have implied the importance of these interactions via the lack of other explaining factors (Buckland *et al.* 2001; Davis & Pelsor 2001; Thompson *et al.* 2001; Troumbis *et al.* 2002). The 'fluctuating resource availability theory', in particular, states that *'a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources'*, when propagules are of the invasive species are present and the species characteristics are suitable for the habitat (Davis *et al.* 2000).

According to the fluctuating resource availability theory, environments in which resource availability fluctuates due to changes in their rate of supply or uptake should be more susceptible to invasions than environments in which resource availability tends to be constant. Similarly, species that tolerate a range of conditions or resources are predicted to be more likely to become invasive than species that tolerate only narrow ranges of conditions and resources. Beyond these general predictions, a detailed understanding of resource fluctuations and species biology is required to predict the outcome of introducing a particular species into a particular system at a particular time. Considering the large number of actual and potential invasions it is not viable to monitor all systems for all resource fluctuations and to test the response of possible invaders to these fluctuations. However, with an understanding of the dynamics of the main resources that control a system and how they affect focal species, it should be possible to identify combinations of resources and conditions that favour the abundance of potential invaders and resident species.

Some growth response parameters of a species may be indicative of its overall abundance and competitive ability, such as the level of and plasticity in growth rates and root/shoot ratios. Plants with higher root/shoot ratios and/or higher growth rates or final biomass tend to have higher abundances or better competitive ability in high resource conditions (Roush & Radosevich 1985; Aerts *et al.* 1991; Goldberg & Landa 1991; Theodose *et al.* 1996; Cahill & Casper 1999; Wardle *et*

al. 1999). However, in many cases species vary root/shoot ratios or growth rates with resource levels, presence and identity of competitor or even pot size (Goldberg & Fleetwood 1987; Gurevitch *et al.* 1990; Wilson & Tilman 1995; Dietz *et al.* 1998; Bakker & Wilson 2001). In general, plants shift biomass allocation towards the resource that is limiting growth (Poorter & Nagel 2000) and many studies find a decrease in root/shoot ratios with increasing belowground resource availabilities and vice versa (Aerts *et al.* 1991; Wilson & Tilman 1995; Reynolds & D'Antonio 1996; Poorter & Nagel 2000; Levang-Brilz & Biondini 2002). Furthermore, plasticity in response to environmental factors can change competitive outcomes (McGraw & Chapin 1989). Levels of plasticity vary between species; for instance, rapidly growing species from high nutrient habitats show considerable more phenotypic plasticity in root/shoot ratios than species from low nutrient habitats (Chapin 1980). Plasticity can eliminate any tight correlation of competitive ability with growth parameters that are measured at one level of resource availability (McGraw & Chapin 1989). Instead, the competitive ability is determined by the interactions between the environment and species-specific parameters in response to the environment.

In the grasslands of the South Australian mid-north, increasing annual grass abundance is associated with higher levels of soil moisture or rainfall, whereas native perennial grass abundance and soil moisture show few direct associations with environmental factors (Chapter 3). This study aims to establish growth rates, root/shoot ratios and long-term water uptake parameters of a common annual and three common perennial grasses to spatial and temporal soil moisture gradients to determine the abiotic conditions that favour one species over another in this system. The aim was not to simulate soil moisture fluctuations exactly as they occur in the field but to determine the differential responses of the species to possible soil moisture gradients. I predict that along a soil moisture gradient the growth rates of the four grass species increase and their root/shoot ratios decrease. The possibility of a trade-off between maximum growth rates and tolerance to low resource availability (Chapin 1980) and the typically higher growth rates of annual grasses at high resource availability (Muller & Garnier 1990; Ernst & Tolsma 1992; Claassen & Marler 1998) suggest that the perennial grasses should be more tolerant to low resource availability (Figure 5.1). These differences between the species should allow predictions on the competitive outcomes at different resource availabilities in the field. Whether these predictions agree with competitive interactions in the field will be tested in Chapter 6.

Methods

Species selection and description

I chose three native perennial grasses (*Austrodanthonia caespitosa, Austrostipa eremophila* and *Enneapogon nigricans*) and one exotic annual grass (*Avena barbata*) that occur in the mid-north of

South Australia as well as other areas in Australia. They occur in a range of abundances in the mid-north and include various growing seasons (Table 5.1). Little information exists on growth parameters for the perennial grasses and both published and unpublished parameters are highly variable (Table 5.1). Subsequently I will refer to the species by generic name.

Attribute	Austrodanthonia caespitosa	Austrostipa eremophila	Avena barbata*	Enneapogon nigricans
Life form [a]	Perennial	Perennial	Annual	Perennial
Australian distribution [a]	Widespread except NT, QLD	Southern SA, WA, NSW, VIC	SA, WA, NSW, VIC, (orig. Mediterranean)	Mainland states except WA
Lofty Block Bioregion % occurrence (513 quadrats [b])	62#	26	63	13
Mid-north mean % frequency (220 quadrats [c])	30	27	90	2
Growing season [d]	Cool & warm (C_3)	Cool & warm (C_3)	Cool (C_3)	Warm (C_4)
Pot growth (g shoot DW day^{-1}), various conditions	0.004-0.02 [j]; 0.003-0.03 [k]; 0.003-0.02 [l] ($\downarrow$ w/ latitude) [l]	0.02–0.18 [f]	0.04-0.18 [f]; 0.008-0.02 [g]; 0.002-0.02 [i]	0-0.07 [f]
Field growth (g shoot DW day^{-1}), various conditions	-0.02-0.04 [e]	0.004-0.2 [f]	0-0.03 [f]; 0.13 [h]	-0.003-0.003 [e]
Root/shoot ratio	1.5-6.0 [j], 0.5-0.1 [l] ($\downarrow$ w/ temperature) [l]			
Provenance of experimental plants	Auburn (138°42' E, 34°1' S)	Burra (138°55' E, 33°41' S)	Burra (138°55' E, 33°41' S)	Blyth (138°32' E, 33°49' S)

Table 5.1: Species attributes. [a] Jessop (1986); [b] Robertson (1998); [c] Ch. 3 (this study); [d] Williams (1961); Davies (1997), Ch. 6 (this study), Watson (1980); [e] Ch. 6 (this study); [f] Williams (2003); [g] Callaway (2003); [h] Jackson (1986); [i] Marshall (1969); [j] Williamson (2002); [k] Quinn & Hodgkinson (1983); [l] Hodkginson & Quinn (1976); # includes *A. eriantha* and *A. laevis*.

Effects of spatial and temporal soil moisture gradients on root/shoot ratios and growth rates

For the two soil moisture regime experiments I planted one individual of similar sized 2-3-month-old perennial grass seedlings or one-week-old annual grass seedlings into 130 mm diameter pots filled with 740 g of Nu-Erth™ Special Native Plant mix (20% sand, 80% composted pine bark, trace elements) and 7 g of Osmocote Plus™ (16% N, 3.5% P, 10% K, trace elements). To aid establishment, pots were misted with water for 5 min. daily for a week. On 13 June 2001 I randomly allocated individuals to the treatments of the two experiments:

1) 'Spatial gradients': To determine the growth response of the species to different levels of soil moisture in different areas, I randomly allocated four individuals of each species to each of eight levels of gravimetric soil moisture (5, 10, 15, 20, 30, 40, 50 and 60% gravimetric soil moisture, with 60% equivalent to field capacity). Soil moistures were maintained as constant as possible throughout the experiment.

2) 'Temporal gradients': I randomly allocated five individuals of each species to each of three treatments: permanent medium gravimetric soil moisture level (30%), early high soil moisture level (60%, later 10%) or late high soil moisture level (10%, later 60%). These treatments were meant to represent different seasonal rainfall regimes (even rainfall throughout winter and spring; wet winter, dry spring; dry winter, wet spring). I changed soil moisture levels ten weeks into the experiment. At fourteen weeks roots became strongly pot-bound and plants had to be harvested. Thus the time frame for the 'second season' had to be cut short.

I watered all pots three times a week by slowly pouring water on the pot until the correct weight was reached. In addition, pots to be kept at 60% were placed under an irrigation system that sprayed daily for 3 min. Due to highly variable growth rates and fresh weight/dry weight ratios between species and treatment I could not estimate the plants weights accurately enough to adjust the watering weights for growth of the plants. Judging from the harvest weights, the amount of soil moisture in pots with heavier plants was 75-98% that of lighter plants.

Biomass estimates: I estimated biomass of each plant at the start of the experiment by calculating the cone volume of each plant using the following measurements: average orthogonal basal diameters (BD, n = 2) to the nearest 0.05 mm and height (H, extension of the longest leaf or culm to the nearest mm) (1). This volume was converted into a total dry weight estimate, using regressions determined from non-experimental plants of the same volume range and species, but grown under optimal conditions (Table 5.2).

$$\text{Cone volume} = \frac{1}{2} * \left(\frac{BD}{4} \right)^2 * \pi * H \qquad (1)$$

Species	Spatial		Temporal		Water uptake	
	r^2	n	r^2	n	r^2	n
Austrodanthonia	0.86	6	0.92	7	0.81	4
Austrostipa	0.96	8	0.97	9	0.96	8
Avena	> 0.99	4	0.94	5	>0.99	3
Enneapogon	0.90	11	0.56	6	0.93	21

Table 5.2: Statistics of regressions used to estimate the dry weight of the study species.

Harvest: I harvested all plants in the 'temporal gradients' experiment for shoot and root biomass after 14 weeks, when roots became pot-bound. 'Spatial gradients' pots were also harvested as species became pot-bound: *Avena* after 11 weeks, *Austrostipa* and *Austrodanthonia* after 13 weeks and *Enneapogon* after 17 weeks. I washed the potting mix through a 300 μm sieve, drying the remaining roots and potting mix and separating the roots from potting mix by hand. Roots and shoots were dried at 80 °C for 72 h and weighed.

Analyses: Using the initial biomass estimates and harvest data I calculated the growth rates. Relative growth rate was not calculated since it is extremely sensitive to initial weight, which was only estimated. I tested all data distributions for normality (Shapiro-Wilk W, JMP 3.1.4 software) and homoscedasticity (Brown-Forsythe, JMP 3.1.4) at $\alpha = 0.05$. Most of the twelve growth rate and root/shoot ratio distributions of the 'temporal gradients' experiment conformed to assumptions of normality. Root/shoot ratio distributions also conformed to assumptions of homoscedasticity, while growth rate distributions did not. However, departures from homoscedasticity have little effect on F-ratios if sample sizes are equal and there are more than five treatments and six replicates (Underwood 1997, p. 193). This experiment had only five replicates, however, I decided to analyse growth rates and root/shoot ratios using an Identity MANOVA, followed by ANOVAs and Tukey–Kramer HSD multiple comparison tests. This may have slightly increased the probability of a Type I error.

Most 'spatial gradients' growth rate and root/shoot ratio distributions conformed to the assumption of normality but not heteroscedasticity and it was not possible to use ANCOVA to compare the curves of the species. Rank-transformation resulted in the loss of crucial non-linear differences within the species and the multiple comparison tests on rank-transformed data produced complex significant differences between the 32 treatment combinations, resulting in lettering such as 'cdefgh' versus 'jklmnop'. No software was available to run other non-parametric non-linear regressions. I thus tested first for differences between the species and then analysed the response to soil moisture within each species separately. To reduce variances I log-transformed the distributions, resulting in root/shoot ratio distributions that conformed to the assumption of homoscedasticity and less heteroscedastic growth rate distributions ($P = 0.01$ compared to < 0.0001). I then tested for differences between species using a MANOVA on both response variables followed by an ANOVA and a Tukey-Kramer HSD test on each response variable. To test for the effect of soil moisture on the growth rate and root/shoot ratio within each species I ran linear regressions on the log-transformed data. While this analysis pathway is not strictly suitable to the experimental design, the differences between the species are evident.

Long-term water uptake

To estimate relative differences in long-term water uptake rates of the four species, I prepared 30 pots with equal amounts of potting mix as described above. I randomly assigned ten pots to controls and planted 20 pots with five individuals of each of the four species and measured their cone volumes. After thoroughly watering all pots to field capacity, I randomly selected five control pots and measured their gravimetric soil moisture. The remaining control pots and the treatment pots were randomly distributed on a glasshouse bench without irrigation. I harvested all pots for shoot and root biomass (drying at 80 °C to constant weight) after 23 days when some

plants started to wilt. In addition I measured the wet and dry weight of the potting mix of each treatment and control pot. Using these measurements I was able to estimate the DW gain of each individual plant, the initial soil moisture and the evaporation in the control pots. From these estimates I was able to estimate absolute daily water uptake, daily water uptake per average g DW biomass and water use efficiency (WUE), i.e. dry weight increase per gram water uptake for *Austrodanthonia, Austrostipa and Avena*. The estimates for *Enneapogon* were extremely variable and were excluded from the analyses. Overall its water uptake was very low (with 0.1-5 g day^{-1}).

Analyses: All data distributions of water uptake and WUE conformed to assumptions of normality (Shapiro-Wilk W, JMP 3.1.4 software) and homoscedasticity (Brown-Forsythe, JMP 3.1.4) at $\alpha < 0.05$. I analysed the two response variables using an Identity MANOVA, followed by ANOVAs and by Tukey–Kramer HSD multiple comparison tests on all treatment combinations.

Results

Effects of spatial and temporal soil moisture gradients on root/shoot ratios and growth rates

Soil moisture treatment accuracy: The large differences in water uptake of the four species (see below) not only resulted in large differences between the amounts of water that had to be added to maintain the same soil moisture level, but also resulted in differences between the actual period the moisture treatments were imposed. Depending on species and soil moisture level, the growing medium took between four to ten weeks to dry out to the lower soil moisture levels, diminishing the treatment effects.

'Spatial gradients': Increasing soil moisture increased growth rates in all four species (Table 5.3; Figure 5.2), but the responses differed between species. Overall, *Avena* had the highest growth rates, ranging from 0.03 to 0.32 g DW day^{-1} and the strongest correlation with soil moisture, *i.e.* the most plastic response to soil moisture. Its growth rate showed no signs of saturation at the higher soil moisture levels; on the contrary, it increased sharply between 50% and 60% soil moisture. Although 60% soil moisture represented field capacity, the watering frequency was presumably too low to saturate water uptake in this species. *Austrodanthonia* and *Austrostipa* had generally lower growth rates, ranging from 0.02 - 0.13 g DW day^{-1}. Whereas *Austrodanthonia* showed lower increases in growth rate with increasing soil moisture and approached saturation level from 40% onwards, *Austrostipa*, like *Avena* showed a large increase in growth rate between 50% and 60% soil moisture, where it reached the growth rate levels of *Austrodanthonia*. *Enneapogon* had much lower overall growth rates, ranging from 0.002 - 0.05 g DW day^{-1} and also did not appear to reach moisture saturation. Its correlation with soil moisture was overall the weakest.

| Species | Growth rate (g DW day^{-1}) | | Root/shoot | |
	Regression	R^2	Regression	R^2
Austrodanthonia	Log (GR) = -3.86 + 0.04 × moisture [ab]	0.75[***]	Log (R/S) = -0.88 - 0.02 × moisture [c]	0.56[***]
Austrostipa	Log (GR) = -4.43 + 0.04 × moisture [b]	0.69[***]	Log (R/S) = 0.15 - 0.03 × moisture [a]	0.77[***]
Avena	Log (GR) = -3.97 + 0.05 × moisture [a]	0.95[***]	Log (R/S) = -1.17 + 0.003 × moisture [b]	0.04[ns]
Enneapogon	Log (GR) = -6.17 + 0.05 × moisture [c]	0.59[***]	Log (R/S) = -0.13 - 0.02 × moisture [ab]	0.44[***]

Table 5.3: Effects of soil moisture on *Austrodanthonia*, *Austrostipa*, *Avena* and *Enneapogon* growth rates and root/shoot ratios. Different letters denote significant differences between species at $\alpha = 0.05$ (Identity MANOVA; ANOVAs, Tukey-Kramer HSD on log-transformed data). [***] Regression slope significantly ≠zero ($P < 0.0001$); [ns] slope not significantly ≠ zero at $\alpha = 0.05$.

Overall, *Enneapogon* and *Austrostipa* had the highest and most variable root/shoot ratios ranging between 0.15 – 1, followed by *Avena* with a root/shoot ratio range of 0.25 - 0.5 and *Austrodanthonia* with a root/shoot ratio range of 0.10 - 0.35 (Figure 5.2b). The three perennial species showed a decrease in their root/shoot ratio with increasing soil moisture, whereas soil moisture had no consistent effect on root/shoot ratio in *Avena*.

'Temporal gradients': There was a highly significant interaction between the effect of species and temporal gradients in soil moisture on the growth rate and root/shoot ratio of the four species (Identity MANOVA: Wilks $\lambda = 0.24$; F ≈ 8.18, Numerator DF = 12, Denominator DF = 94, P < 0.0001; ANOVA: Table 5.4). Overall, temporal variability in soil moisture had little effect on the growth rates of *Austrodanthonia* and *Austrostipa* (Figure 5.3). *Avena*, on the other hand, had higher growth rates with varying temporal watering regimes than with the constant intermediate soil moisture. *Enneapogon*, a C4 species, surprisingly did better with constant intermediate soil moisture or early high soil moisture than with the late high soil moisture, although ambient temperatures increased with time.

| Factor | DF | Growth rate (g DW day^{-1}) ($r^2 = 0.94$) | | | Root/shoot ratio ($r^2 = 0.82$) | | |
		SS	F- ratio	P-value	SS	F- ratio	P-value
Whole Model	11	0.31	66.57	< 0.0001	1.16	20.31	< 0.0001
Species	3	0.28	214.72	< 0.0001	0.59	38.06	< 0.0001
Soil moisture	2	0.01	10.91	0.0001	0.38	36.57	< 0.0001
Species × soil moisture	6	0.03	11.05	< 0.0001	0.19	6.02	< 0.0001
Error	48	0.02			0.25		
Total	59	0.33			1.41		

Table 5.4: Effects of temporal variability in gravimetric soil moisture on *Austrodanthonia*, *Austrostipa*, *Avena* and *Enneapogon* growth rate and root/shoot ratio (ANOVAs).

Root/shoot ratios tended to be quite similar between temporal variability treatments (Figure 5.3) and did not differ between watering regimes in *Austrodanthonia* and *Enneapogon*. In *Avena* they were higher in the early high soil moisture treatments than in the other treatments. *Austrostipa* also had higher root/shoot ratios in the early high soil moisture treatment and in the medium constant soil moisture treatment than in the early low soil moisture treatment.

Long-term water uptake

Avena differed significantly from *Austrodanthonia* and *Austrostipa* in some water uptake parameters (Table 5.5; Figure 5.4). *Avena* had the highest absolute water uptake of 8 g day^{-1}, compared to < 4 g day^{-1} for *Austrodanthonia* and *Austrostipa*. This was due to the larger sizes of the *Avena* plants, since the relative water uptake to per gram of average biomass throughout the experimental period was equal (between 8-17 g day^{-1} DW^{-1}) for all species. However, the water use efficiency was almost twice as high in *Avena*, 0.008 g DW g^{-1} H$_2$O compared to 0.004 g DW g^{-1} H$_2$O in *Austrodanthonia* and *Austrostipa*. The power of the test was low (Power = 0.54; effect size = 0.0018) and this difference was only marginally statistically significant (Table 5.5; Figure 5.4). Further research is required to confirm water use parameters in more detail, however, the subsequent discussion will assume that *Avena* is at least slightly more water use efficient than the perennial grasses.

Factor	DF	Absolute water uptake (r^2 = 0.77)			Relative water uptake (r^2 = 0.19)			WUE (r^2 = 0.37)		
		SS	F Ratio	P-value	SS	F Ratio	P-value	SS	F Ratio	P-value
Species	2	118.50	19.80	<0.01	380.89	1.45	0.27	0.00005	3.48	0.06
Error	12	35.91			1581.42			0.00009		
Total	14	154.41			1962.31			0.00015		

Table 5.5: Absolute and relative water uptake estimates and WUE estimates of *Austrodanthonia, Austrostipa* and *Avena* (Identity MANOVA on all response variables: Wilks λ = 0.06, F $\approx$ 9.90; Numerator DF = 6; Denominator DF = 20, P < 0.0001; ANOVAs).

Discussion

Austrodanthonia caespitosa, Austrostipa eremophila, Avena barbata and *Enneapogon nigricans* exhibited different responses to different soil moisture regimes. The three perennial grasses responded little to increasing soil moisture and reached their maximum growth rates at intermediate soil moisture levels, while the shape of the growth rate curve of *Avena* suggests that even at the highest soil moisture level the growth rate was not at its maximum. Overall, the growth rate of *Avena* was at least as high or higher than the growth rates of the three perennial grasses at any soil moisture. This result is contrary to the expected trade-off between maximum growth rates and tolerance to resource availability (Figure 5.1). A similar lack of trade-offs has been found in other grasses

(Fernández & Reynolds 2000). Alternatively, the trade-off may occur at even lower resource levels and be expressed in survivorship rather than in growth.

Of the perennial grasses, *Austrodanthonia* had the highest overall growth rates and the highest plasticity. Below 40% gravimetric soil moisture its growth rates were similar to the rates of *Avena* and similarly to *Avena* it had a low root/shoot ratio. Perennial grasses responded little to the different temporal soil moisture regimes, while *Avena* performed best in temporal soil moisture regimes that included at least some period of high soil moisture, regardless of timing or the soil moisture in other periods.

The growth rates determined are similar to other estimates available (Table 5.1), with the exception of *Avena*, where I found higher growth rates. The low growth rate of *Enneapogon* is most likely due to its C_4 pathway combined with low temperatures during the experimental period. Other parameter estimates are available only for *Austrodanthonia*, a highly variable species across a large latitudinal range (Quinn & Hodgkinson 1983, 1984; Maze *et al.* 1993). Plants from the same provenance have a once-off measured water use efficiency of 0.007 g C g^{-1} H$_2$O transpired (Williamson 2002), compared to 0.004 g DW g^{-1} H$_2$O taken up in this study. Given the differences in units these estimates are comparable. Root/shoot ratios of *Austrodanthonia* vary highly, including the range found in this study. In other studies they decreased with increasing temperature when grown at optimal belowground resource availability (Hodgkinson & Quinn 1976), while root/shoot ratios of plants with a 300-400 mm annual rainfall provenance under very low belowground resource availability were much higher (Williamson 2002).

Whereas perennial grasses responded to decreasing soil moisture by increasing their root/shoot ratio, the root/shoot ratio of *Avena* remained unchanged. Plant species with high 'competitive ability' and growth rates tend to have high root/shoot ratios (Roush & Radosevich 1985; Aerts *et al.* 1991; Goldberg & Landa 1991; Theodose *et al.* 1996; Cahill & Casper 1999; Wardle *et al.* 1999), but *Avena* exceeded the root/shoot ratio of the other three species only at the highest soil moisture level. Several explanations are possible for relatively low root/shoot ratios in *Avena*. For example, the range of soil moisture levels may not have been large enough to affect biomass allocation, or growth was limited by factors that did not influence biomass allocation. However, growth rates of *Avena* responded strongly to the range of soil moisture levels and it is thus unlikely that other factors were strongly limiting growth. Comparing overall root/shoot ratios and species abundance (Figure 5.2; Table 5.1) indicates that the two species with the highest abundance have overall the lowest root/shoot ratios. Generalisations between growth rates or other traits with competitive ability are generally limited (McGraw & Chapin 1989). It is thus possible that in this system lower root/shoot ratios, possibly together with faster growth rate and higher WUE correspond to a better 'competitive ability'.

Implications for invasion processes

In terms of growth, *Avena* has a clear advantage over perennial grasses at high soil moisture levels. Years with wet winters and springs could provide good opportunities for annual grass populations to expand. Their high growth rate and high water uptake while maintaining a relatively low root/shoot ratio is likely to lead to reduced above- and belowground resource availability for plants that are not able to respond quickly to soil moisture. Furthermore it is possible that their high water uptake in the top soil layer decreases infiltration into deeper soil layers, which may negatively affect perennial grasses later in the season, after annual grasses have died off. Competitive effects of annual grasses on perennial grasses should thus be greatest when soil moisture levels are highest, but may continue into the dry season.

Further factors that may assist the invasion of annual grasses are disturbances such as grazing, which can change soil infiltration rates or decrease soil moisture uptake by perennial grasses. Since water uptake is related to plant biomass, grazed perennial grasses will take up less soil water. In addition, hard-hoofed stock tends to destroy any soil lichen crust (Andrew & Lange 1986; Hiernaux *et al.* 1999), which affects soil moisture dynamics, either decreasing or increasing infiltration rates depending on the system (DeFalco *et al.* 2001; Maestre *et al.* 2002). In the mid-north of South Australia, lichen crusts are developed at some sites and are associated with lower infiltration rates and higher perennial grass abundances than at sites without lichen crusts (pers. obs., 2000-2002). It is possible that the destruction of these crusts may have increased soil moisture availability and thus promoted annual grass invasion.

In addition to rainfall amount, its frequency and event size and site-specific edaphic factors will also play a major role. Heavy, prolonged rain in areas that experience run-on are likely to recharge soil moisture to full field capacity more frequently than intermittent rainfall in areas that experience run-off. Annual grasses will have a growth advantage in areas where soil moisture in the top soil is more frequently recharged to full field capacity, independent of rainfall.

Overall, *Avena* performed best at high soil moisture availability, both compared to low soil moisture availability and compared to the perennial grasses. With decreasing soil moisture availability the perennial grasses decreased less in growth than *Avena*, but never performed better than *Avena* in absolute terms – contrary to predictions by trade-off hypotheses. Thus, during the shared growing season no opportunities exists for established perennial grasses to outgrow *Avena*. Overall the growth response to soil moisture is limited in the perennial grasses. This suggests that opportunities for perennial grasses to increase in abundance in areas where annual grasses have invaded exist only in terms of recruitment and growth in the remaining growing season or possibly through survival in drought conditions (Chapter 6). These results partially reflect the differences between the life forms of the four species. Perennial grass recruitment appears to be

limited in this system (Chapter 4), rather it appears that perennial grasses have adapted for survival between years than regular recruitment to maintain population levels. They use water conservatively and increase their root/shoot ratio during drier periods to continue to access available soil moisture. *Avena*, on the other hand, has a high water uptake and water use efficiency, since its strategy relies on yearly seed production. Whether or not these glasshouse observations agree with competitive interactions in the field will be investigated in Chapter 6.

Practicality of approach

Customarily, ecological experiments use two to three levels of a resource gradient (*i.e.* high versus intermediate versus low), allowing predictions of the behaviour of a system at different resource availabilities. However, non-linear and variable growth responses of different species to a resource that is highly patchy will result in predictions of low accuracy, especially for specific sites and specific seasons. By determining the response curves in more detail, I was able to compare the relative performances of the perennial species and *Avena* at more levels and to document the most and least favourable conditions for the species. However, the experimental soil moisture levels cannot be directly translated into specific gravimetric soil moisture levels, since it was difficult to attain and maintain the specified gravimetric soil moisture levels with the approach taken here. Thus, further research is necessary to test how these changes in growth with soil moisture translate to soil moisture levels in the field and furthermore whether the observed differences in growth actually result in different competitive outcomes in the field. However, traditional experiments with two – three levels have the same caveats.

Neither nutrients nor water at the highest soil moisture level were supplied *ad libitum*, and the maximum growth rates found in this study may not reflect the true maximum growth rates or the true range of root/shoot ratios and other parameters in these species. Thus it must be remembered that the results are based on relative comparisons only. Interactions of soil moisture availability and nutrient availability, which would change the relative shape of the response curves at different nutrient availability cannot, however, be excluded. Although soil moisture has been found to influence competitive interactions between grasses (Harris & Wilson 1970; Melgoza *et al.* 1990; Nernberg & Dale 1997; Dyer & Rice 1999; Hamilton *et al.* 1999), nutrient availability has been implicated in other studies (Bakker & Wilson 2001; Kolb *et al.* 2002). Generally, nutrient availability increases with soil moisture due to increased mass flow and diffusion of minerals (Marschner 1995). However, while phosphorus and nitrogen availability may be positively correlated to soil moisture in some systems (Cui & Caldwell 1997), this is not generally the case (Whitford *et al.*; Reynolds *et al.* 1997; Farley & Fitter 1999; Barrett *et al.* 2002). Studies to determine the correlation between soil moisture regime and nutrient availability have commenced at three sites.

Figures
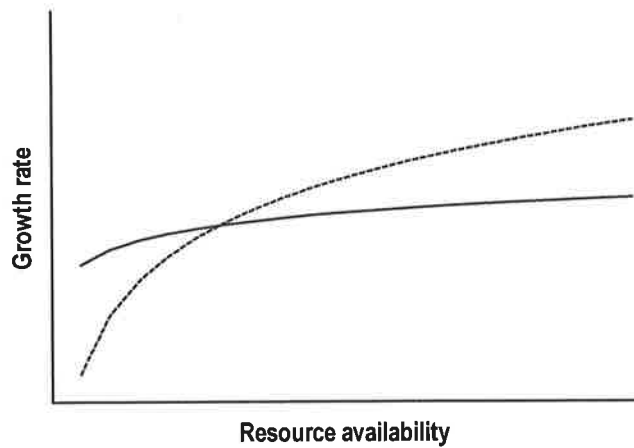
Figure 5.1: Potential trade-off between maximum growth rate and tolerance for low resource availability: expected effect of resource availability on growth rates in annual (---) and perennial (—) grasses.
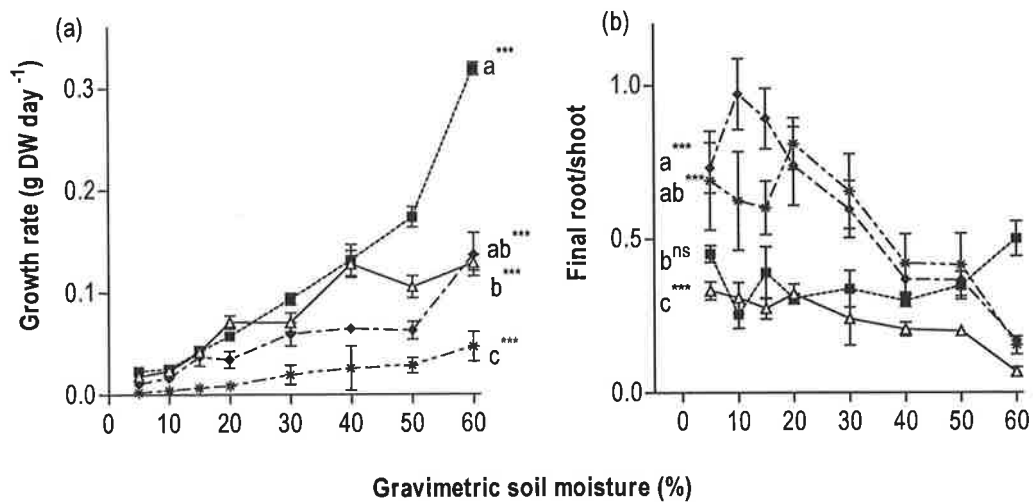
Figure 5.2: Effects of soil moisture on (a) growth rate and (b) root/shoot ratio of *Austrodanthonia* (△); *Austrostipa* (—·◆·—); *Avena* (···■···); *Enneapogon* (···✳···). Error bars represent ± 1 SE. Different letters denote significant differences between species at $\alpha = 0.05$. *** regression slope significantly $\neq$ zero (P < 0.0001); ns not significantly $\neq$ zero at $\alpha = 0.05$.
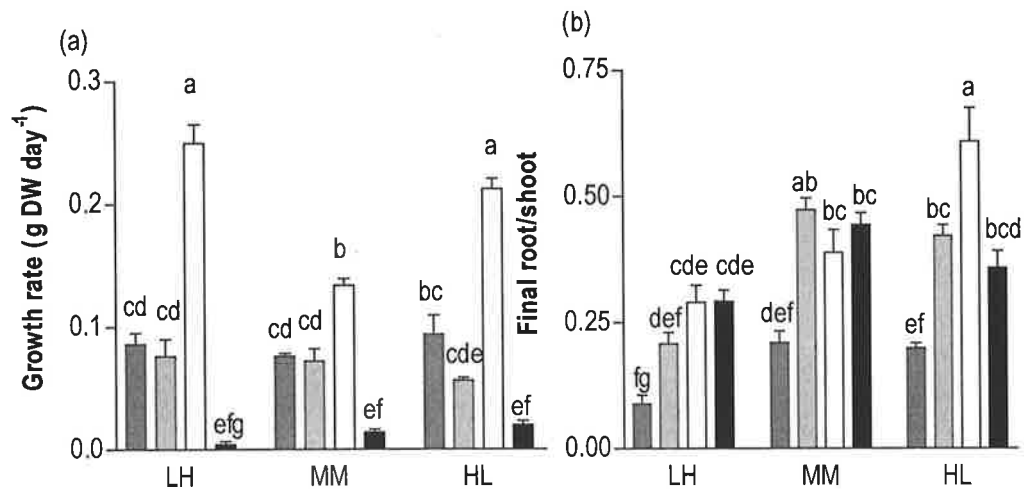
Figure 5.3: Effects of temporal variability in gravimetric soil moisture (soil moisture first 10%, then 60% (LH); soil moisture always 30% (MM); soil moisture first 60%, then 10% (HL)) on (a) growth rate and (b) root/shoot of *Austrodanthonia* (■); *Austrostipa* (▨); *Avena* (□) and *Enneapogon* (■). Error bars represent 1 SE. Different letters denote significant differences at α = 0.05.
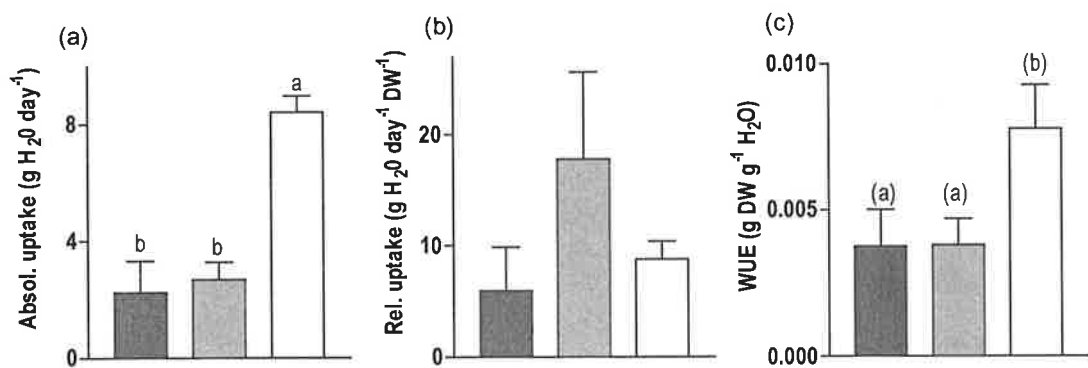
Figure 5.4: Water use estimates of *Austrodanthonia* (■); *Austrostipa* (▨) and *Avena* (□). Error bars represent 1 SE. Different letters denote significant differences at α = 0.05 in (a) and at α = 0.10 in (c) (Identity MANOVA; ANOVAs; Tukey-Kramer HSD tests; Table 5.5).

6. Effects of soil moisture on competitive interactions of exotic annuals and native perennial grasses in a South Australian mid-north grassland

Introduction

While some invasions occur only after disturbances release resources that become available for exotic plants (Hobbs 1989), other invaders are able to establish in undisturbed vegetation (Hobbs 1989; Huenneke & Vitousek 1990) and alter the community composition by out-competing native species (Hamilton *et al.* 1999; Callaway & Aschehoug 2000; Bakker & Wilson 2001; Davis & Pelsor 2001; Blicker *et al.* 2002; Hoopes & Hall 2002; Lenz *et al.* 2003). Understanding these competitive interactions between native plants and invaders is vital for predicting the effects of an invasion, the environmental factors regulating invasions and the timing and hot spots of future invasions (Davis *et al.* 2000).

Competitive interactions between plants have long been central to the study of community and population ecology. While this research has provided us with various theoretical models (Tilman 1977; Grime 1979; Tilman 1982; Goldberg & Novoplansky 1997; Arii & Turkington 2001), experimental designs (Goldberg 1994; Gibson *et al.* 1999; Connolly *et al.* 2001; Inouye 2001; Cahill 2002), various competition indices and analysis strategies (Austin 1982; Goldberg 1996; Markham & Chanway 1996; Freckleton & Watkinson 1997a; Goldberg *et al.* 1999; Inouye 2001; Navas *et al.* 2002), hundreds of experiments have shown that competitive interactions are highly complex and not readily predictable. Care has to be taken to compare like with like in terms of response variables (Welden & Slauson 1986), scale (Garrett & Dixon 1997), type of productivity gradient (Carson & Pickett 1990; Goldberg & Novoplansky 1997), productivity level (Gurevitch 1986a; Connolly *et al.* 1990; Flores-Martínez *et al.* 1998; Dyer & Rice 1999; Foster 2002; Jurjavcic *et al.* 2002), life stage or size of organism (Goldberg 1990; Hamilton *et al.* 1999; Connolly *et al.* 2001; Foster 2002), density (Freckleton & Watkinson 1997b), timing of factors or responses (Goldberg & Novoplansky 1997) as well as taking into account non-linear responses (Miller & Werner 1987; Foster 1999), interactions between root and shoot competition (Cahill 1999), resource transport rates (Huston & DeAngelis 1994) and other processes that affect competitive interactions (Hartnett & Wilson 1999; Suding & Goldberg 2001; Callaway *et al.* 2003).

In conclusion, there is no evidence to support notions that competitive hierarchies between organisms, the type of limiting resource, levels of productivity and importance of competition in a system are fixed in time and space. Moreover, indices of intensity of competition are not

generally useful to predict species abundances in the field, especially under different environmental conditions (Goldberg 1996). Indices based on plant physiological performance have been developed and appear highly suitable to investigating and predicting changes in competitive interactions under changing environmental conditions, especially at higher levels of resource availability (Austin 1982; Navas *et al.* 2002; Groves *et al.* 2003). They include the species-specific properties necessary to compare neighbourhood interactions between different species and thus not only offer opportunities for developing and testing new theoretical models, but also have important practical implications. If competitive interactions play an important role in invasions, an improved understanding or predictability of the competitive interactions under different environmental conditions will allow better weed management efficiency by manipulating competitive interactions to advantage native species and/or disadvantage invaders.

In grasslands, annual exotic grasses compete with native perennial grasses and other grassland species for soil moisture and nutrients (Harris 1967; Harris & Wilson 1970; Melgoza *et al.* 1990; Claassen & Marler 1998; Dyer & Rice 1999; Hamilton *et al.* 1999; Kolb *et al.* 2002) and this interaction can be affected by the presence of mycorrhizal fungi (Hartnett & Wilson 1999; Callaway *et al.* 2003). In general, annual grasses have higher growth rates than perennial grasses under high soil moisture and nutrient availability (Harris 1967; Harris & Wilson 1970; Muller & Garnier 1990; Ernst & Tolsma 1992). They tend to outcompete perennial grasses at high nutrient availability (Hoopes & Hall 2002; Kolb *et al.* 2002; Groves *et al.* 2003) or high soil moisture availability (Melgoza *et al.* 1990; Dyer & Rice 1999), although irrigation during winter and spring can improve the competitive ability of a perennial grass in competition with annual grasses (Hamilton *et al.* 1999). Under conditions of low resource availability the growth rate of annual grasses is equal to or still better than perennial grass growth rates (Muller & Garnier 1990; Claassen & Marler 1998; Kolb *et al.* 2002). Perennial grasses may have an absolute competitive advantage, if they are seeded earlier than the annual grasses. They will then perform better at any nutrient availability (Claassen & Marler 1998) or only at low nutrient availability (Kolb *et al.* 2002). Perennial grasses can also have higher survivorship than annual grasses at low resource availability (Hamilton *et al.* 1999).

While the general trend of competitive interactions over environmental gradients between annual and perennial grasses is predictable, the competitive advantage of one life form over another is species-specific and system-specific. In an ungrazed grassland in the South Australian mid-north perennial grasses experience competition from annual grasses and the intensity of competitive interactions appears to change with slope position (probably because of different resource dynamics) on a small spatial and short temporal scale (Lenz *et al.* 2003). In this chapter I aim to determine the effect of soil moisture dynamics on the performance of annual grasses (represented by *Avena barbata*) and selected established native perennial grasses (*Austrodanthonia*

caespitosa and *Enneapogon nigricans*) in above- and belowground competition. *Avena barbata* is the dominant annual exotic grass in the area (Robertson 1998, Chapter 3). I chose *Austrodanthonia caespitosa* as a representative native perennial grass due to its high abundance (Robertson 1998, Chapter 3), its similar growth rate relative to *Avena barbata* (Chapter 5) and as a representative C_3 species and *Enneapogon nigricans* as a representative C_4 species.

Short-term experimental data indicate that the growth rates of *Avena* are equal to perennial grass growth rates at low soil moisture and higher than perennial grass growth rates at high soil moisture. It also has a higher water uptake and higher water use efficiency the perennial grasses (Chapter 5). Comparing these growth parameters suggests that perennial grasses are unlikely to outcompete *Avena* in any environmental conditions during their shared growing season in terms of growth. To investigate whether this is the case I grew annual and perennial grasses in the field in areas with different soil moisture dynamics and compared their competitive interactions over two growing seasons. I also compared their water use, root/shoot ratios and competitive responses with and without competitors under controlled conditions in the glasshouse to investigate the differences in growth parameters in plants with and without competitors.

Methods

Field Experiment

The field experiments were run at the Burra field site (see Chapter 4 for description) in 2001-2002. Rainfall was 413 and 293 mm in 2001 and 2002 respectively, with a dry autumn and a particularly dry spring in 2002. During autumn/winter 2002 goats entered the site on several occasions and cattle once. I removed any droppings from experimental quadrats at the next visit and noted grazing damage to experimental plants. Most of the outliers in the data were due to this grazing.

Experimental design: I set up three transects perpendicular to the main direction of the slope along the base, middle and top of the slope ('slope position'), representing three different soil moisture dynamics. While average soil moisture availability is similar in all slope positions, soil moisture decreases with increasing slope position during wet seasons and increases with increasing slope position during dry seasons (Figure 6.1). Every 4-5 m along each transect I located the nearest patch with high annual grass abundance (= 24 blocks/transect). Each block was randomly assigned to target taxa (*Austrodanthonia caespitosa, Enneapogon nigricans,* annual grasses (mainly *Avena barbata*)), creating eight replicated blocks of each target taxa per transect. Subsequently I will refer to the species by their generic name. Each block contained three 0.5 m × 0.5 m quadrats that were randomly assigned to a competition treatment (no, partial, or full competition).

Perennial grasses had to be added as competitors or targets, since low perennial grass abundance in the lowest slope position prevented the standard practice of removing competitors close to established targets. In the blocks allocated to *Austrodanthonia* and *Enneapogon*, I planted a 5-month-old *Austrodanthonia* or *Enneapogon* individual in the centre of each quadrat on the 1-2 June 2001. To aid establishment I watered each individual on 27 June and 6 July, after a dry spell, with 0.125 L, corresponding to a 12 mm rainfall event. I manipulated annual grass density by clipping the aboveground biomass in the remainder of the quadrat, half the remainder or none of the remainder (Figure 6.2a) every three weeks during the growing season, April - October, and every six weeks during the remainder of the year until the harvest of the aboveground biomass of both target species and competitors on 23-24 October 2002.

In the blocks allocated to annual grasses as target plants, I manipulated perennial grass density by planting *Austrodanthonia* in different densities (nil, four or eight individuals per quadrat) (Figure 6.2b). I clipped other perennial grasses once initially to improve transplant survival. A large number of perennial grasses (both target and competitor individuals) did not survive the experimental period. Between April and November I replaced dead individuals with individuals of similar size, recorded their biomass estimates and watered them with 0.125 L, taking care to water only around the plant, not other areas of the quadrat. I did not replace plants that died after November until the following April due to low survival chances during summer.

Biomass estimates: I estimated changes in above ground perennial grass biomass every six weeks all year round and annual grass biomass every six weeks from April to November and noted the presence of flowers, when more than one inflorescence of the target species was present in a quadrat. To estimate annual grass biomass I used an adaptation of the Adelaide technique (Andrew *et al.* 1979, see Chapter 3). The r^2 values between observed and estimated biomasses ranged from 0.76 - 0.99. I tested this method once by using the technique prior to harvesting the experimental plants and found good correlations between estimated and harvested DW ($r^2 = 0.67$ for annual grasses as competitors; $r^2 = 0.71$ for annual grasses as target species).

I estimated perennial grass biomass by converting their cone volumes (see Chapter 5) into an estimate of total plant dry weight using pre-determined regressions based on potted plants of a wide range of sizes (*Austrodanthonia* DW: $= 0.0084 \times$ cone volume $^{0.6985}$, n $= 61$, $r^2 = 0.94$; *Enneapogon* DW $= 0.0061 \times$ cone volume $^{0.6816}$, n $= 53$, $r^2 = 0.93$). Again, this method was tested once for *Austrodanthonia* by measuring cone volumes prior to harvesting the experimental plants. The r^2 values for the regressions between estimated and observed DW were 0.83 and 0.87 for *Austrodanthonia* as competitors and as target species respectively. Harvest data reflected growth rate data and are not further presented. Due to high mortality in *Enneapogon* I could not test the method for that species.

Glasshouse experiment

Set-up: To determine competitive interactions between *Avena* and *Austrodanthonia* in relation to water use I set up a factorial experiment with one individual of the target species per pot (*Avena* or *Austrodanthonia*), different numbers of interspecific competitors (nil or two individuals per pot), different watering treatments (5, 30, 60% gravimetric soil moisture) and eight replicates per treatment combination. I washed the growing medium of the roots of several-month-old *Austrodanthonia* individuals (Freeling provenance, 138°49' E, 34°27'S), clipped their leave blades to 50 mm to reduce transplantation shock and planted them into 130 mm diameter pots filled with 740 g of Nu-Erth™ Special Native plant mix and 7 g of Osmocote Plus™ on 19 June 2002, Five-day-old *Avena* (Burra Provenance, 138°55' E, 33°41' S) seedlings were planted on 24 June. I watered each pot with 100 ml every 2-3 days until the start of the experiment.

Biomass estimates and replacement of dead plants: Prior to the start of the experiment I estimated the biomass of all individuals by converting their cone volume into a total dry weight estimate using regressions determined from non-experimental plants of the same volume range and species (see Chapter 5) (*Austrodanthonia:* $r^2 = 0.84$, n = 38, *Avena:* $r^2 = 0.81$, n = 4). I also replaced individual plants that had died during the first four weeks of the experiment (two *Avena* and one *Austrodanthonia*) with spare plants and watered each with 10 ml. I measured each of the replaced individuals and corrected the number of days when calculating growth rates.

Soil moisture levels: On 1 July I randomly allocated each pot to one of three watering levels (5, 30, 60% gravimetric soil moisture), with eight replicates for each combination of target species, competitor density and watering level. All pots were watered three times a week to the correct weight by pouring tap water slowly around the experimental plants. Water that drained immediately was slowly replaced until the correct amount of water was absorbed. To estimate the amount of evapotranspiration (hence 'water use') during the experimental period I measured the amount of water each pot received by recording the pot weight before every watering event to an accuracy of 1 g. I also misted all pots with a hand mister after each watering event to improve relative humidity, shuffled pots at every watering event and completely re-randomised pot placement twice during the experimental period.

I watered all pots in the 5% soil moisture treatment out of turn twice; on 29 July with 15 ml each and on 5 August with 5 ml each. Many pots had not dried out sufficiently to be watered, but the topsoil where roots were concentrated was dry and plants were highly stressed.

Harvest: I harvested all plants after 14 weeks and measured individual shoot and root DW in the control pots and individual shoot DW and total pot root DW in the competition pots. Since roots could not be separated by species in the competition pots I used the average root/shoot ratio of the non-competition plants of the same soil moisture level and species to calculate the

expected root biomass in the competition treatments. Expected root biomass added up to the observed total pot root biomass with some exceptions. Not all roots may have been retrieved and root/shoot ratios were not completely constant. I adjusted expected results by correcting the expected root biomass of each plant by its share of the observed error by shoot weight. Each individual plant was also scored for survival (presence of green meristems or shoot apexes) and flowering (exserted inflorescences present). However, changes in DW were measured regardless of whether plants were alive or dead at the end of the experimental period.

Statistical analysis

None of the competition indices suited the data distributions due to negative values and non-linearities. Consequently, I compared absolute and relative performance of perennial and annual grasses under different environmental conditions and densities and correlated these with patterns of water use under controlled conditions. I tested all data distributions for normality (Shapiro-Wilk W, JMP 3.1.4) and homoscedasticity (Brown-Forsythe, JMP 3.1.4) at $P \leq 0.05$.

In the field experiment I analysed growth rates between measurement periods ((DW at end of measurement period – DW at start of measurement period)/ # days) and growth rate per DW competitor ((DW at end of measurement period – DW at start of measurement period)/ (# days * DW of competitor at the end of the measurement period)) as response variables for all target groups plus the total number of transplant deaths per quadrat for the two perennial grass species. While competition level was already an independent variable in the analysis, it accounted only for the reduction in ambient competitor biomass within each block, but not between blocks or slope positions. To determine the effect of these different competitor densities between blocks or slope positions I used growth rates per DW competitor as the response variable. To calculate the annual grass growth rate per DW perennial competitor I excluded quadrats without perennial grasses. To calculate the perennial growth rate per DW annual grass competitor I set the competitor biomass in quadrats with fully clipped annual grasses to 0.46 g 0.25 m^{-2}, just below the minimum annual biomass in unclipped quadrats during the experimental period. This accounts for some growth that occurred between clippings.

I used absolute growth rate as the response variable, since using changes in plant size between measurement periods relies on low mortality and relative growth rates are highly sensitive to initial size, which was only estimated. They also do not show the absolute comparisons necessary to judge whether or when the different species are able to outgrow each other and thus to judge competitive interactions outcomes.

Most of the mortality distributions conformed to the assumption of homoscedasticity but not normality. Log transformation improved distributions a little for *Austrodanthonia*, but not

Enneapogon. The majority of growth rate distributions conformed to assumptions of normality and homoscedasticity. Most of the growth rate per DW competitor distributions of all three species did not conform to the assumption of normality, but conformed to the assumption of homoscedasticity. ANOVA is robust to departures from normality (Underwood 1981) and thus the data were analysed using analysis of variance techniques. I analysed the response variables using ANOVA for the mortality response variable and repeated-measures MANOVA for the growth rates and growth rates per DW competitor response variables. When the sphericity assumption was not met in repeated-measures MANOVAs, the Greenhouse–Geisser epsilon adjustment (G–G ε) was used to test the effect of time and the interaction of time with treatments (von Ende 1993).

In the glasshouse experiment I analysed growth rates, final root/shoot ratios, water use and growth rates per DW competitor between treatments as response variables. In addition I regressed growth rates over competitor biomass within each competition treatment to determine competitive response within treatments. In all response variables the majority of the data distributions were normal, but in some variables variances were strongly unequal. However, sample sizes were equal, with eight replicates in each of the 12 treatment combinations and I proceeded with ANOVA (Underwood 1997, p. 193). I ran separate ANOVAs on each response variable, followed by Tukey-Kramer HSD multiple comparison tests (JMP 3.1.4.). No software was available to run non-parametric multiple regressions.

Results

Field experiment

Mortality of perennial grass transplants was differently affected by slope position and annual grass competition. In *Austrodanthonia* there was a marginally significant effect of slope position and a trend towards slope position interacting with competition (Table 6.1; Figure 6.3). Whereas competition levels had no effect on mortality in the two lower slope positions, increasing competition levels appeared to increase *Austrodanthonia* mortality in the highest slope position. Mortality of *Enneapogon* was considerably higher than mortality of *Austrodanthonia* and at the end of the first season almost 100% of *Enneapogon* individuals died. Due to drought I could not establish *Enneapogon* during the next season, thus there are no results for 2002.

Growth of the three target species or groups was also affected differently by slope position and interspecific competition. Annual grasses were unaffected by interspecific competition with the planted perennial grasses, and the effect of slope position changed strongly over time (Table 6.2a; Figure 6.4a). They grew equally well in all slope positions at the start of the season, but later in the season grew substantially better in the two lower slope position in the first year, and

somewhat better in the second year, with small differences only between the two lower slope positions. The lack of a competitive effect of the perennial grasses is not surprising, since the perennial grasses planted as competitors did not perform well at any slope position. At harvest the aboveground perennial grass averaged 1.94 g $\pm$ 0.24 g DW 0.25 m^{-2} (mean $\pm$ SE) at their highest density (8 plants 0.25 m^{-2}) compared to an average of 28.07 g $\pm$ 3.48 g DW 0.25 m^{-2} for annual grasses.

		Log (*Austrodanthonia* deaths quadrat^{-1})				*Enneapogon* deaths quadrat^{-1}			
Source	DF	SS	F	P-value	r^2	SS	F	P-value	r^2
Model	29	8.79	1.19	0.30	0.45	11.38	0.43	0.99	0.23
Slope position (S)	2	1.61	3.17	0.05		0.25	0.14	0.87	
Block (B) [S]	21	4.39	0.82	0.68		7.63	0.40	0.99	
Competition (C)	2	0.62	1.23	0.30		2.08	1.14	0.33	
C × S	4	2.16	2.13	0.09		1.42	0.39	0.82	
Error	42	10.68				38.50			
Total	71	19.47				49.88			

Table 6.1: Effects of slope position and competition by annual grasses on mortality of perennial grass transplants over the experimental period (ANOVAs).

Austrodanthonia, on the other hand, was not affected by slope position, but by competition interacting with time (Table 6.2b). During late spring in the first season, and autumn, winter and spring in the second season, growth rates were reduced by more than 50% by the presence of annual grasses, independent of whether their density was at half or full ambient levels (Figure 6.4b). The impact of annual grasses on *Austrodanthonia* growth rates appeared stronger during the second, drier season, despite the lower biomass of annual grasses. *Enneapogon* performed very poorly. Initially it did significantly better in the lowest slope position (Table 6.2c; Figure 6.4c), but later experienced considerable mortality in all treatments.

	Source	Test	Value	F	Numerator DF	Denominator DF	P-value
(a) Annual grasses	All Between	F	28.50	49.33	26	45	<0.0001
	Slope position (S)	F	20.52	461.66	2	45	<0.0001
	Block (B) [S]	F	7.98	17.10	21	45	<0.0001
	Competition (C)	F	0.0003	0.01	1	45	0.91
	S × C	F	0.002	0.04	2	45	0.96
	All Within	G-G ε	0.67	9.29	88.2	152.6	<0.0001
	Time (T)	G-G ε	0.67	46.20	3.4	152.6	<0.0001
	T × S	G-G ε	0.67	68.48	6.8	152.6	<0.0001
	T × B [S]	G-G ε	0.67	4.88	71.2	152.6	<0.0001
	T × C	G-G ε	0.67	1.12	3.4	152.6	0.35
	T × S × C	G-G ε	0.67	0.41	6.8	152.6	0.89
(b) Austrodanthonia	All Between	F	1.30	1.30	24	24	0.26
	S	F	0.003	0.04	2	24	0.96
	B [S]	F	0.59	0.75	19	24	0.74
	C	F	0.60	14.33	1	24	0.001
	S × C	F	0.07	0.86	2	24	0.43
	All Within	G-G ε	0.32	0.79	75.8	75.8	0.84
	T	G-G ε	0.32	4.94	3.2	75.8	0.003
	T × S	G-G ε	0.32	1.08	6.3	75.8	0.38
	T × B [S]	G-G ε	0.32	0.54	60.0	75.8	0.99
	T × C	G-G ε	0.32	3.68	3.2	75.8	0.01
	T × S × C	G-G ε	0.32	1.14	6.3	75.8	0.35
(c) Enneapogon	All Between	F	0.38	0.58	26	40	0.93
	S	F	0.09	1.72	2	40	0.19
	B [S]	F	0.31	0.58	21	40	0.91
	C	F	0.001	0.05	1	40	0.83
	S × C	F	0.01	0.22	2	40	0.80
	All Within	G-G ε	0.31	1.01	32.5	50.0	0.48
	T	G-G ε	0.31	0.22	1.3	50.0	0.70
	T × S	G-G ε	0.31	4.56	2.5	50.0	0.01
	T × B [S]	G-G ε	0.31	0.77	26.3	50.0	0.76
	T × C	G-G ε	0.31	0.05	1.3	50.0	0.87
	T × S × C	G-G ε	0.31	0.89	2.5	50.0	0.44

Table 6.2: Effects of slope position and interspecific competition on the growth rate of (a) annual grasses, (b) *Austrodanthonia* and (c) *Enneapogon* between measurement dates (Repeated-measures MANOVA).

With growth rate per DW competitor as response variable, slope position still had an overall positive effect on annual grasses and initially on *Enneapogon* (Table 6.3a, c; Figure 6.5a, c), but not on *Austrodanthonia* (Table 6.3b; Figure 6.5b), indicating that its competitive response per annual

grass DW did not change along the slope. *Austrodanthonia* growth rate per annual grass DW was highly variable, which was partially due to the grazing damage, but measurement error or other factors that control growth rates cannot be ruled out.

	Source	Test	Value	F	Numerator DF	Denominator DF	P-value
(a) Annual grasses	All Between	F	5.39	4.22	23	18	< 0.01
	Slope position (S)	F	1.67	14.99	2	18	< 0.01
	Block (B) [S]	F	3.46	2.97	21	18	0.01
	All Within	G-G ε	0.39	1.38	44.5	34.8	0.17
	Time (T)	G-G ε	0.39	8.27	1.9	34.8	< 0.01
	T × S	G-G ε	0.39	2.16	3.9	34.8	0.10
	T × B [S]	G-G ε	0.39	1.22	40.6	34.8	0.28
(b) *Austrodanthonia*	All Between	F	0.31	0.39	21	27	0.98
	S	F	0.02	0.33	2	27	0.72
	B [S]	F	0.28	0.40	19	27	0.98
	All Within	G-G ε	0.34	0.65	72.1	92.7	0.97
	T	G-G ε	0.34	2.06	3.4	92.7	0.10
	T × S	G-G ε	0.34	0.84	6.9	92.7	0.56
	T × B [S]	G-G ε	0.34	0.59	65.3	92.7	0.99
(c) *Enneapogon*	All Between	F	0.36	0.67	23	43	0.85
	S	F	0.03	0.71	2	43	0.50
	B [S]	F	0.33	0.68	21	43	0.83
	All Within	G-G ε	0.40	1.43	37.1	69.4	0.10
	T	G-G ε	0.40	0.58	1.6	69.4	0.53
	T × S	G-G ε	0.40	3.36	3.2	69.4	0.02
	T × B [S]	G-G ε	0.40	1.30	33.9	69.4	0.18

Table 6.3: Effects of slope position on growth rate/DW competitor of (a) annual grasses, (b) *Austrodanthonia* and (c) *Enneapogon* between measurement dates (Repeated-measures MANOVA).

At the measurement dates, where more than one but not all replicates of a target taxa had inflorescences present, the annual grasses were more likely to flower in the lowest slope position, while *Austrodanthonia* was more likely to flower at the highest slope position (Table 6.4). There was no apparent effect of *Austrodanthonia* on the presence of inflorescences in annual grasses, while there appeared to be a negative effect of annual grasses on the presence of inflorescences in *Austrodanthonia* in 2002. While the χ^2 cannot be seen as reliable due to low counts, the differences between some treatment levels are fairly large.

| Target species | Date | Slope position | Competition Level | | | | | |
			0	0.5	1	Σ	χ^2	P-value
Annual grasses	24-25/9/01	Base	5	5	5	15	20.57	0.008
		Middle	0	1	1	2		
		Top	1	1	2	4		
		Σ	6	7	8	21		
Austrodanthonia	24-25/9/01	Base	2	0	2	4	16.88	0.03
		Middle	2	1	2	5		
		Top	4	5	6	15		
		Σ	8	6	10	24		
Austrodanthonia	20-22/11/01	Base	6	5	4	15	9.00	0.34
		Middle	6	3	4	13		
		Top	7	6	7	20		
		Σ	19	14	15	48		
Austrodanthonia	14-15/10/02	Base	3	0	1	4	22.67	0.004
		Middle	1	1	1	3		
		Top	7	2	2	11		
		Σ	11	3	4	18		

Table 6.4: Effects of competition & slope position on the number of replicates flowering at measurement dates when >1 but less than all experimental plants flowered (Pearson χ^2 for all treatment combinations; χ^2 suspect, since 20% of cells have expected counts < 5).

Glasshouse Experiment

Interspecific competition along the soil moisture gradient affected most growth parameters of *Austrodanthonia* and *Avena*. Growth rates increased with soil moisture in all cases, however, the rate of change differed depending on species identity and interspecific competition (Table 6.5; Figure 6.6a). Growth rates were equally low for *Austrodanthonia* and *Avena* at the lowest soil moisture but three times higher in *Avena* than in *Austrodanthonia* at the highest soil moisture. Interspecific competition had little effect at the lower soil moistures, but at 60% gravimetric soil moisture it decreased the growth rate of *Avena* to 69% or by 0.05 g day^{-1}, and of *Austrodanthonia* to 47% or by 0.03 g day^{-1}. Thus, the growth rate of *Avena* decreased most in absolute terms, while the growth rate of *Austrodanthonia* decreased most in relative terms.

Changes in root/shoot ratios along the soil moisture gradient also interacted with species identity and interspecific competition (Table 6.5; Figure 6.6b). The root/shoot ratio of *Avena* was not affected by competition but decreased from 0.84 at 5% gravimetric soil moisture to 0.38 at 60% gravimetric soil moisture. In *Austrodanthonia* root/shoot ratios of plants without competitors decreased with increasing soil moisture. Interspecific competition further decreased root/shoot

ratios at 5% gravimetric soil moisture but had no effects at the other moisture levels. Thus, the drop in root/shoot ratios from plants without competitors to plants with competitors at 5% gravimetric soil moisture was both relatively and absolutely larger in *Austrodanthonia*.

The amount of water use per pot depended on the combination of the treatment factors (Table 6.5; Figure 6.6c). Water use increased exponentially from 5% to 60% soil moisture. There was no difference in water use between species and competition levels at the two lowest soil moisture levels. At 60% soil moisture, however, interspecific competition doubled the water use of *Austrodanthonia* pots but did not affect the water use of *Avena* pots.

Growth rate per DW competitor increased with soil moisture but there was a large variability within some treatment levels and the ANOVA model had a low fit (Table 6.5; Figure 6.6d). On average *Avena* had a higher growth rate per DW competitor than *Austrodanthonia*, especially at 60% soil moisture.

Source	DF	Growth rates (r^2 = 0.83) SS	F	P-value	Root/shoot (r^2 = 0.68) SS	F	P-value	Water use (r^2 = 0.91) SS	F	P-value	Growth rates/competitor (r^2 = 0.16) DF	SS	F	P-value
Model	7	0.21	63.24	< 0.0001	3.37	26.47	< 0.0001	263.74	134.78	< 0.0001	3	0.2	2.72	0.06
Moisture (M)	1	0.13	273.96	< 0.0001	1.33	73.11	< 0.0001	241.75	864.77	< 0.0001	1	0.1	4.42	0.04
Species (S)	1	0.04	80.42	< 0.0001	1.49	81.90	< 0.0001	0.75	2.69	0.10	1	0.1	2.83	0.10
Competition (C)	1	< 0.01	7.79	0.01	0.18	9.83	0.002	4.24	15.16	0.0002				
S × M	1	0.03	63.75	< 0.0001	0.26	14.46	0.0003	1.21	4.32	0.04	1	< 0.01	0.92	0.34
S × C	1	< 0.01	1.66	0.20	0.02	1.04	0.31	5.52	19.75	< 0.0001				
M × C	1	< 0.01	14.69	0.0002	0.08	4.22	0.04	5.77	20.65	< 0.0001				
M × S × C	1	< 0.01	0.44	0.51	0.01	0.72	0.40	4.50	16.10	0.0001				
Error	88	0.04			1.60			24.60			44	0.08		
Total	95	0.25			4.98			288.34			47	0.10		

Table 6.5: Effects of gravimetric soil moisture (5, 30, 60%), species (*Austrodanthonia; Avena*) and interspecific competition (no or two competitors) on growth parameters (ANOVAs).

The competitive response within each treatment also depended on soil moisture. Both species showed little change in competitive response to increasing interspecific competitor biomass within the two lowest soil moistures. At 60% soil moisture both showed an increasing competitive response, *i.e.* lower growth rates, with increasing interspecific competitor biomass (Table 6.6; Figure 6.7). The slope was steeper in *Austrodanthonia*, suggesting that the response to the same increase in biomass by an interspecific competitor was much stronger in *Austrodanthonia* than in *Avena*.

Soil moisture	Species	Regression	F	P-value	r^2
5%	Austrodanthonia	GR = -0.018 + 0.061 × competitor DW	6.20	0.44	0.10
	Avena	GR = 0.009 -0.001 × competitor DW	0.70	0.05	0.51
30%	Austrodanthonia	GR = 0.023 -0.008 × competitor DW	3.74	0.10	0.38
	Avena	GR = 0.025 -0.001 × competitor DW	0.48	0.52	0.07
60%	Austrodanthonia	GR = 0.179 -0.020 × competitor DW	19.02	< 0.01	0.76
	Avena	GR = 0.155 -0.006 × competitor DW	9.20	0.02	0.61

Table 6.6: Effect of average competitor dry weight on growth rates at different soil moistures (Regressions).

Although *Avena* gained more weight overall, it had also higher mortality rates at 5% gravimetric soil moisture, where only two *Avena* plants survived with *Austrodanthonia* competitors and five without competitors (Table 6.7). The number of *Avena* individuals flowering also increased sharply with soil moisture and competition appeared to have a small negative effect on these numbers. The survival of *Austrodanthonia*, on the other hand, was independent of competition and soil moisture (Table 6.7). Also, a much lower proportion of *Austrodanthonia* flowered and they appeared to be more likely to flower at 60% soil moisture.

		% Survival					% Flowering				
	Competitor	5%	30%	60%	χ^2	P-value	5%	30%	60%	χ^2	P-value
Austrodanthonia	0	8	8	8	50.5	<0.0001	1	0	2	48.6	<0.0001
	2	7	8	8			0	0	2		
Avena	0	5	8	8			1	6	8		
	2	2	8	8			0	6	7		

Table 6.7: Effects of gravimetric soil moisture (5, 30, 60%), species (*Avena, Austrodanthonia*) & competition (no competitor, two interspecific competitors) on survival (n = 8) and presence of an inflorescence (of surviving replicates). Pearson χ^2 for all treatment combinations; χ^2 suspect, since 20% of cells have expected counts < 5.

Discussion

Interspecific competition and soil moisture gradients had different effects on the survival, growth rates and likelihood of flowering of the annual grasses and the two perennial grass species. As expected, annual grasses had the highest growth rates and a higher likelihood of flowering at the highest soil moisture availability, both in the field and in the glasshouse. Overall, competition by *Austrodanthonia* had no effect on annual grass growth rates in the field, independent of soil moisture and whether absolute or relative levels of competition were considered. In the glasshouse *Austrodanthonia* had a negative effect on *Avena* growth rate at the highest soil moisture and on *Avena* survival at the lowest soil moisture.

In contrast, the survival of *Austrodanthonia* was relatively independent of competition or soil moisture in the field and the glasshouse. Its growth rate was less affected by soil moisture than by competition. Increasing annual grass biomass strongly reduced *Austrodanthonia* growth rates both in the field and glasshouse. In the field *Austrodanthonia* was most likely to flower without competitors. There was no evidence that *Austrodanthonia* is able to out-compete annual grasses at any moisture level, although its rate of survival at low soil moisture was higher than that of *Avena*. Lastly, *Enneapogon* did not appear to be strongly affected by competition or slope position. It occurs at the site naturally in low abundance, mostly in lower slope positions. No obvious cause was apparent for its high mortality. As a C_4 species *Enneapogon* may only establish successfully during seasons with high summer rain, which did not occur during the experimental period.

These results agree with the initial predictions of the competitive advantage of annual grasses at higher levels of soil moisture availability and with other studies (Melgoza *et al.* 1990; Dyer & Rice 1999). They also concur with studies that propose a correlation between relative performance in monoculture and relative performance in competition at particular resource levels (Austin 1982; Navas *et al.* 2002; Groves *et al.* 2003). Furthermore, they provide details of competitive interactions time and competitor level and in different environmental conditions and thus allow predictions of competitive outcomes over a wide spatiotemporal scale.

The effect of competition depended strongly on resource supply and resource uptake rates, as proposed by Huston (1994). Whether in competition or not, *Avena* took up significantly more water and has significantly higher growth rates than *Austrodanthonia* at high soil moisture, while at lower soil moistures there are little differences in growth rates and water use for both species. Thus, the effects of the presence of competitors were largest when the differences between growth rates and/or resource uptake of the competing species were largest, *i.e.* at the highest resource availability level in the glasshouse and the winter/spring seasons in the field.

However, at low resource availability this trend did not continue. The data suggest that *Austrodanthonia* has a competitive advantage over *Avena* in terms of survival at low resource availability, as found in other perennial/annual grass comparisons (Hamilton *et al.* 1999). This, however, is not reflected by relative higher growth rates or lower water use of *Austrodanthonia* compared to *Avena* in the glasshouse. Similarly, in the drier year (2002) in the field *Austrodanthonia* did not have higher growth rates per DW competitor than in the wetter year. Its higher survival rate may be due to physiological characters other than growth rate or water use. This requires further investigation of other physiological characters important in competitive interactions in addition to resource uptake and use.

Overall, the interannual variability in soil moisture (Figure 6.1)and the spatial soil moisture variability had similar effects on competitive interactions. *Austrodanthonia* growth rates and growth rates per DW competitor were similar in the drought year 2002 and the average rainfall year 2001, while the growth rate of *Avena* in the lowest slope position was twice as high in 2001 than 2002. The glasshouse results suggest that the drier conditions in 2002 should have led to a decrease in the competitive effect of *Avena* on *Austrodanthonia*. However, there are no clear differences between the years in the growth rate of *Austrodanthonia* (Figure 6.4b; Figure 6.5b). If anything, the competitive effect on the growth rate was actually stronger during July to September of 2002 than of 2001 (Figure 6.4b). This unexpected result may be due to experimental conditions (newly established plants after a disturbance in 2001 versus well established plants in 2002) or other processes or resources that affected the competitive interactions, such as changes in nutrient dynamics.

The overall outcome of any competitive interactions between the annual and perennial grasses investigated here will depend not only on soil moisture, but also on the initial density of the two groups and on the time spent in competition. At high soil moisture levels in the glasshouse the highest density ratio of 2:1 *Austrodanthonia: Avena* resulted in *Austrodanthonia* and *Avena* gaining an average of 3.6 g and 10.7 g respectively over a shared growing season. Thus, the overall *Austrodanthonia: Avena* ratio will have to be considerably higher before an *Austrodanthonia* population can outgrow an *Avena* population during a shared growing season experiencing high rainfall. These high ratios of perennial to annual grasses tend to be found at sites receiving the least soil moisture after rainfall (Chapter 3). At these sites *Avena* does poorly, independent of competition, and *Austrodanthonia* or other perennial grasses are more likely to remain dominant. In sites with high ratios of annual to perennial grasses *Austrodanthonia* is unlikely to outgrow *Avena* at any soil moisture level during a shared growing season. Even half the ambient density of annual grasses still had more or less the same competitive effect on *Austrodanthonia* than the total ambient density of annual grasses.

Conclusion

The results of this study are consistent with the mechanistic and stochastic theories of competition and invasion, in which the intensity and importance of competitive interactions or the occurrence of invasion are related to resource dynamics and species-specific physiological factors such as resource uptake and use (Austin 1982; Huston & DeAngelis 1994; Davis *et al.* 2000; Navas *et al.* 2002; Groves *et al.* 2003). While the results indicate an increase in absolute competitive intensity at higher productivity as suggested by Grime (1979), the relative competitive effect on *Austrodanthonia* per unit competitor of annual grasses is similar across seasons and areas with different resource dynamics. I suggest that the increasing competitive

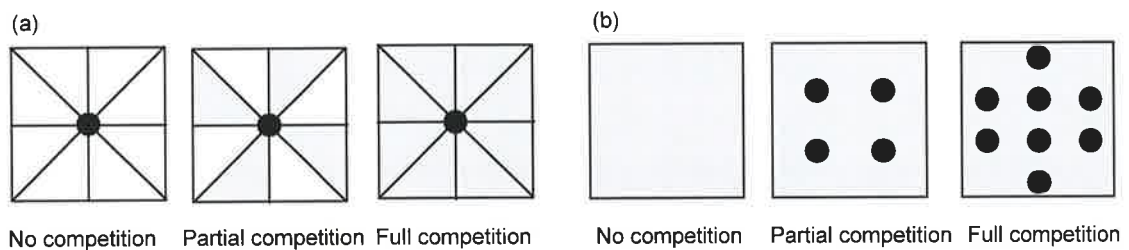effect of *Avena* on *Austrodanthonia* at higher productivity is due to the larger difference in resource uptake rates and growth rates between the species rather than any difference in productivity. Compared to the performance of *Austrodanthonia* the performance of *Avena* strongly increases in areas receiving/retaining the most soil moisture after rainfall. Thus, even though the competitive effect per unit annual grass is similar in all areas, the absolute amount of annual grasses and thus their absolute competitive effect on *Austrodanthonia* is higher in areas receiving/retaining the most soil moisture after rainfall than in areas receiving/retaining the least soil moisture after rainfall.

While the factors that controlled the initial invasion of annual grasses into perennial grasslands in the mid-north are unknown, any future invasions in now ungrazed systems are likely to be driven by these competitive interactions and by resource dynamics, as suggested by Davis (2000). The relatively low water uptake and growth rates by the dominant perennial grass species in this system (Chapter 5) could result in surplus soil moisture during periods of high rainfall, especially in areas receiving run-on, and thus provide opportunities for annual grasses to invade without other factors, such as disturbance or nutrient addition.

Figures
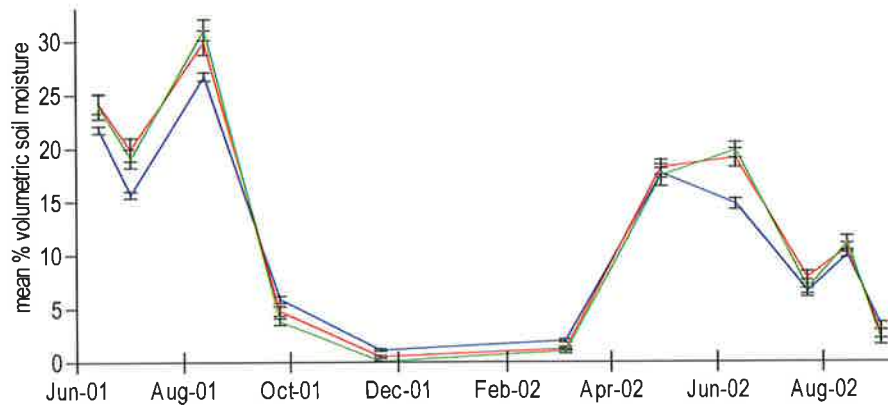
Figure 6.1: Mean volumetric soil moisture ± SE (n = 8) at different slope positions (base; middle; top) during the experimental period. Data summarised from Chapter 3.

No competition   Partial competition   Full competition   No competition   Partial competition   Full competition

Figure 6.2: Experimental design to determine (a) the competitive effects of annual grasses (□ = unclipped, □ = clipped fortnightly during growing season) on perennial grass (•) and (b) competitive effects of perennial grass (•) on annual grasses. Quadrats 0.5 m × 0.5 m.
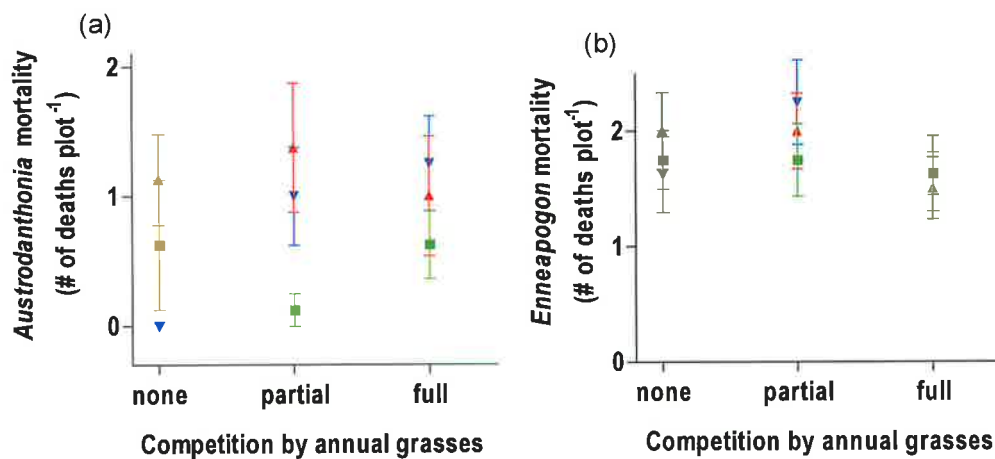
Figure 6.3: Effect of slope position (base; middle; top) and competition by annual grasses on mortality of (a) *Austrodanthonia* and (b) *Enneapogon* June 2001- October 2002 at a remnant grassland in the mid-north of South Australia. Error bars represent ± 1 SE.
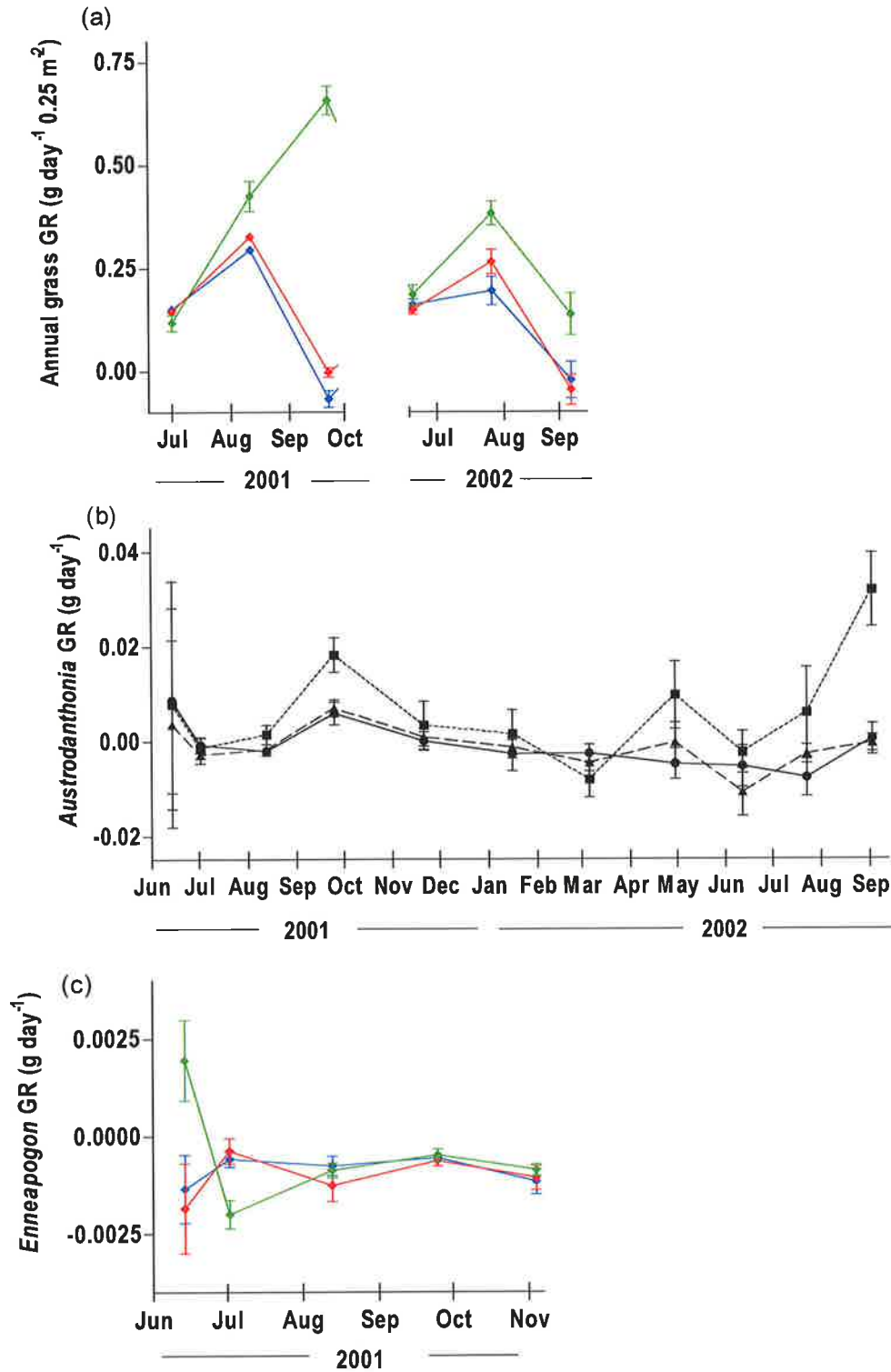
Figure 6.4: Effects of slope position (base; middle; top) and interspecific competition (— full; --- partial; ··· no ambient competitor density) on growth rate of (a) annual grasses (competition levels pooled), (b) *Austrodanthonia* (slope positions pooled) and (c) *Enneapogon* (competition levels pooled) between the date plotted on the x-axis and next measurement date at a grassland in the South Australian mid-north between June 2001 - October 2002. Significant time × treatment interactions at $\alpha = 0.05$ for (a) - (c) (MANOVA, Table 6.2). Error bars represent ± 1 SE.
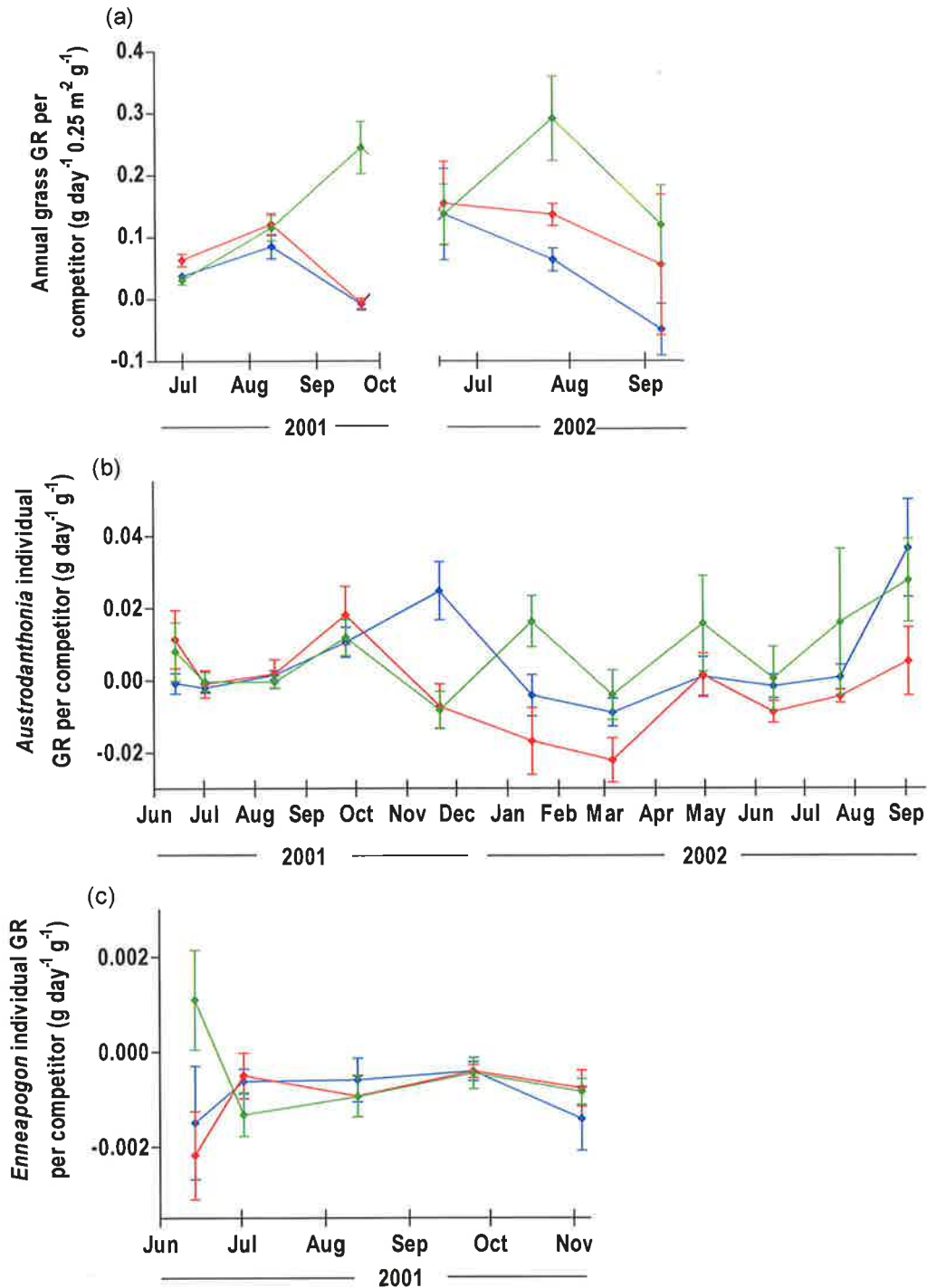
Figure 6.5 Effects of slope position (bottom; middle; top) on the growth rate per unit competitor during the period between the date plotted on the x-axis and next measurement date of (a) annual grasses, (b) *Austrodanthonia* and (c) *Enneapogon* at a grassland in the South Australian mid-north between June 2001- October 2002. Significant time × treatment interactions at $\alpha = 0.05$ in (a) and (c) (MANOVA, Table 6.3). Error bars represent $\pm$ 1 SE.
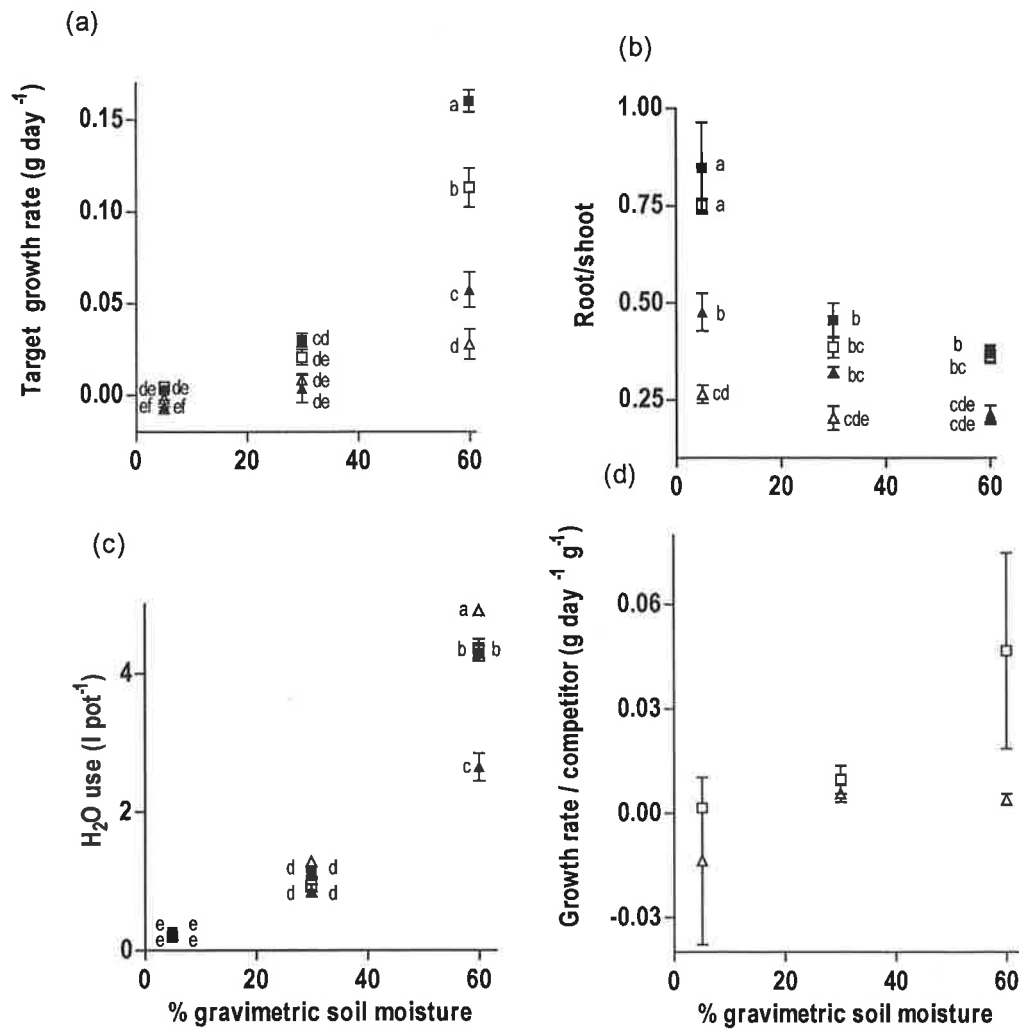
Figure 6.6: Effects of gravimetric soil moisture on (a) growth rate; (b) root/shoot ratio; (c) water use and (d) growth rate/competitor of *Avena* (■); *Avena* + 2 *Austrodanthonia* (□); *Austrodanthonia* (▲); *Austrodanthonia* + 2 *Avena* (△). Different letters indicate significant differences at $\alpha = 0.05$ in (a) – (c) (ANOVA, Table 6.5, Tukey-Kramer HSD tests). Significant positive effect of soil moisture at $\alpha = 0.05$ in (d) (ANOVA, Table 6.5). Error bars represent ± 1 SE.
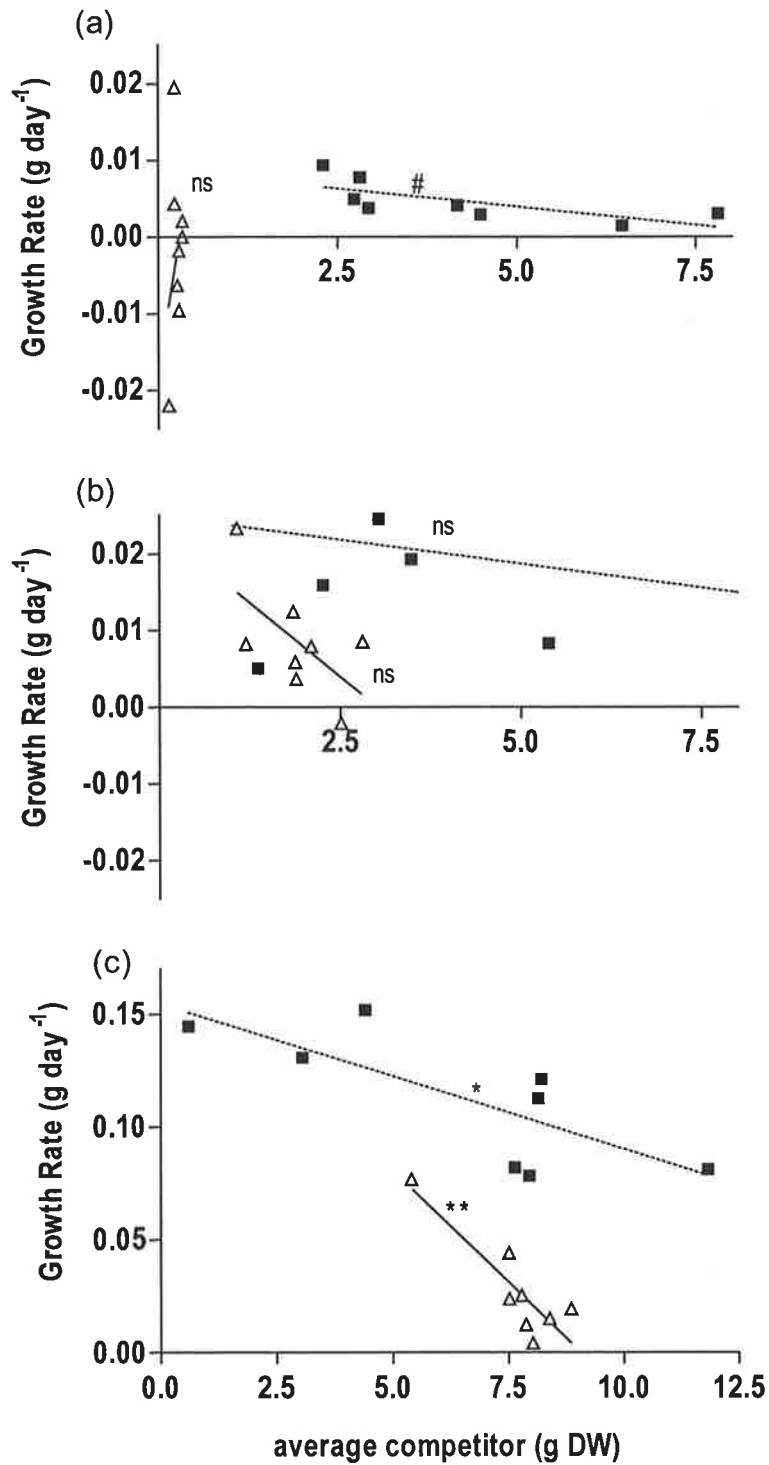
Figure 6.7: Effects of competitor weight on growth rates of *Avena* (··■··) and *Austrodanthonia* (—△—) at (a) 5 % gravimetric soil moisture; (b) 30 % gravimetric soil moisture and (c) 60 % gravimetric soil moisture.
# P < 0.06; * P < 0.05; ** P < 0.01 (Linear regressions, Table 6.6).

7. Summary and Conclusions

Grasslands in the mid-north of South Australia

The species composition of remnant grassland in the mid-north of South Australia ranges from areas dominated by native perennial grasses, graminoids and some herbaceous species to areas consisting entirely of exotic annual grasses and some exotic annual dicots. Large differences in species composition and abundances occur within and between remnants. My results confirm that underlying large-scale and small-scale heterogeneity in belowground resource availability is an important factor associated with this patchiness in plant species composition. The recruitment and growth of invasive annual grasses respond strongly to soil moisture availability and my results suggest that rainfall on a large scale and soil moisture distribution on a small scale are the main driving variables of annual grass recruitment, growth and competitive interactions with perennial grasses. I found no clear environmental variables that drive the recruitment and growth of perennial grasses. They are negatively associated with annual grasses and experience strong competition by annual grasses.

Soil moisture - a driving variable of annual and perennial grass abundance?

Surveys showed the abundance of annual grasses was strongly positively correlated with rainfall and soil moisture received/retained after rainfall, while the abundance of perennial grasses, on the other hand, tended to be negatively correlated with soil moisture, rainfall or other factors denoting lower productivity. Several experiments indicated the processes underlying these results. Firstly, the recruitment of annual exotics in the field is limited by soil moisture or by propagules, while recruitment of perennial grasses in the field appears uncommon. Under controlled conditions the common perennial grass *Austrodanthonia caespitosa* required high soil moisture to germinate and establish in high numbers. Secondly, the growth rates, long-term water uptake and water use efficiency of the dominant annual grass *Avena barbata* exceeded those of common perennial grasses at high soil moisture. At low soil moisture *Avena* had similar growth rates to perennial grasses. No clear differences in water use were evident at low soil moisture between *Avena* and *Austrodanthonia*, except for a higher rate of survival at low soil moisture in *Austrodanthonia* than *Avena*.

Overall, there was little evidence of any combination of factors at which *Austrodanthonia* or other perennial grasses have an absolute competitive advantage over *Avena* or other annual grasses, with the exception of higher survivorship at low resource availability in the glasshouse. Consequently, exotic annual grasses had a strong competitive effect on *Austrodanthonia* in terms of survival, growth and possibly recruitment, as found in other grasslands (Harris 1967; Harris &

Wilson 1970; Melgoza *et al.* 1990; Claassen & Marler 1998; Dyer & Rice 1999; Hamilton *et al.* 1999; Kolb *et al.* 2002). *Austrodanthonia* appeared particularly vulnerable to competition by *Avena* at the seedling stage, since competitive effects were apparent at both low and high water availability and prior to and after an imposed drought. Established *Austrodanthonia* plants were less vulnerable in terms of survival at any water availability. However, when growth rate was measured as a response variable, the competitive effect of *Avena* on *Austrodanthonia* increased with soil moisture. This increase was due to the increased biomass of annual grasses not changes in the competitive effect per unit biomass of annual grasses.

Overall, while soil moisture may drive annual grass abundance, annual grass abundance appears to drive perennial grass abundance. It is thus unlikely that unstocked grasslands in the mid-north of South Australia would return to a dominance by native perennial grasses in average climatic conditions and without active management of annual grasses. Whether annual grass abundances in remnant sites stabilise or further increase will depend on climatic conditions as well as the demographic dynamics of the perennial grasses. The lack of knowledge of perennial grass demography in this system thwarts long-term predictions.

Assumptions and caveats

In addition to the strong effect of soil moisture on annual grasses there were a variety of site-specific and species-specific responses in the survey and the monitoring study. While it would have been preferable to run experimental trials at several sites, the survey and monitoring results of several sites agree with the experimental results of the strong response of annual grasses to below-ground resource availability and their strong competitive effect on perennial grasses. Due to the lack of knowledge of the vegetation prior to European settlement and site-specific management, the causes for most of the site-specific responses are unlikely to be resolved. Thus, when extrapolating these results to other species, sites or past and future processes in grasslands, the following three issues need to be considered: Firstly, the conclusion that below-ground resource availability for annual grass invasion is more important than biotic factors such as grazing and other changes introduced since European settlement relies on the assumption that moisture and nutrient dynamics have not been altered by long-term grazing or by annual grasses themselves. It is possible, for example, that grazing may have change belowground resource availability through changes in cryptogams. Visually, cryptogam communities differ between areas, with lichen dominating perennial grass areas, and mosses dominating annual grass areas. Grazing by hard-hoofed animals can destroy, change or create cryptogamic crusts (Andrew & Lange 1986; Hiernaux *et al.* 1999; Eldridge *et al.* 2000). In other systems these crusts affect soil moisture dynamics; either decreasing or increasing infiltration rates depending on crust type and system (DeFalco *et al.* 2001; Maestre *et al.* 2002) or increasing nutrient availability (DeFalco *et al.*

2001). Changes in crusts produced by grazing could thus affect soil moisture or nutrient availability and thus annual grass invasion. To my knowledge no published information exists on lichen crusts in the mid-north of South Australia. Experimental irrigation indicated that lichen-dominated areas had lower infiltration rates than moss-dominated areas (pers. obs., 2000-2002), however experimental evidence is needed to establish further cause-effect relationships or feedbacks.

Secondly, only few species were studied in detail and interactions only between two taxa, as opposed a variety of species interacting. Care needs to be taken when extrapolating to other species. While *Avena* is the dominant exotic annual grass at this site and in other grasslands in the area (Robertson 1998, Chapter 3), there is a wide range of other native perennial grasses in the area as well as other graminoids and dicots. I chose to study mainly *Austrodanthonia* due to its high abundance (Robertson 1998, Chapter 3) and comparatively high growth rate (Chapter 5). While there may be differences in the relative competitive effect of other annual grasses on other native perennial grasses, there is no evidence to suggest that other native perennial grasses in this area are able to outcompete annual grasses at high resource availability. Only annual grass abundance tends to be positively associated with high rainfall and soil moisture, independent of previous management history (Chapter 3). Furthermore, perennial grass abundance was strongly negatively correlated with annual grass abundance within and between most other sites. This suggests that competitive effects of annual grasses on perennial grasses occur between several species and at most sites.

Thirdly, while soil moisture availability is clearly an important variable driving the invasion of annual grasses in this system the results do not indicate whether the resource responsible is moisture or nutrients. Soil moisture and nutrient availability are often positively related (Marschner 1995) and the two factors cannot be readily separated in the field. Even the glasshouse experiments may have confounded soil moisture with nutrient availability, since nutrient release in slow-release fertiliser depends on soil moisture (Dawson & Akratanakul (1973) in King & Balogh 2000). Nutrient availability alone can drive competitive interactions between annual and perennial grasses (Muller & Garnier 1990; Claassen & Marler 1998; Hoopes & Hall 2002; Kolb *et al.* 2002; Groves *et al.* 2003) and lowering nutrient availability can reverse the invasion of annual grasses in unstocked grassland (Paschke *et al.* 2000). I chose to monitor soil moisture in this project since it could be monitored at a larger scale and at a much lower cost than nutrient availability. Which resource is more important in the initial stages of invasion or in the potential re-invasion of perennial grasses remains to be investigated. For the purpose of the remaining discussion I will refer to belowground resource availability.

The ability of invasion theories to explain the invasion of the mid-north grasslands of South Australia by annual grasses

The worldwide invasion of perennial grasslands by annual grasses and the inherent spatiotemporal resource availability of grasslands make them an perfect candidate for testing predictions of invasion theories. While this thesis did not set out to test various invasion theories in one system or one invasion theory in several systems, it aimed to explore the overall predictions of invasion theories in the grasslands of the mid-north of South Australia. Equilibrium theories predict that plant invaders share certain characters such as high growth rates and reproductive output, or that invaded systems share characters such as low diversity, high productivity and high frequency or intensity of disturbance. The non-equilibrium theories, on the other hand, stress the importance of environmental fluctuations and stochastic events. The fluctuating resource availability theory (Davis *et al.* 2000) broadly predicts that when propagules of a species are present and the habitat is suitable, (1) systems that experience resource fluctuations are more likely to be invaded than systems with stable resource levels; (2) systems are more likely to be invaded after an abrupt change (due to, for example, disturbance, disease or pest outbreak) in the rate of supply of a limiting resource due to increased influx or decreased uptake by present vegetation; (3) invasibility increases with the interval between an increase in resource supply and capture of resources by present vegetation.

The predictions of the latter theory worked well for the introduced annual grasses. Assuming that increased recruitment, growth, biomass, likelihood of flowering and survival all contribute to a large-scale invasion (significant increase in abundance of a species previously at low abundance or absent), then higher annual grass biomass and growth was associated with areas that experienced both higher soil moisture fluctuations (even though the average was the same in most cases) and higher resource supply (more soil moisture after rainfall). The third prediction was not tested for directly. However, competition by perennial grasses (removing perennial grasses by clipping in the recruitment experiment or adding a perennial grass in the field competition experiment) had no effect on annual grass recruitment or biomass. In addition, the perennial grasses tested had relative low water uptake and growth rates. This suggests that immediate water uptake by perennial plants is low and slow, increasing the interval between soil moisture supply and water depletion.

However, the results are also consistent with equilibrium-theories. Annual grasses share some of Baker's characters of invaders (Baker 1965) such as quick growth, early flowering and high competitive ability. In addition annual grasses recruited better when resource availability was increased by irrigation, although clipping (a disturbance) did not affect their recruitment.

All predictions worked less well for the native perennial grasses. *Austrodanthonia* also shares several characters of invasive plants, such as being a plastic perennial, being able to reproduce vegetatively and being able to germinate in a wide range of conditions. In addition, the area I attempted to invade with perennial grasses was of higher productivity than other areas and it contained adult perennial grasses, suggesting it was suitable for recruitment in the past. Moreover, I increased resource availability by decreasing resource use (clipping) and increasing resource supply (irrigation) as well as added viable seed. Nevertheless I was not able to trigger an invasion in areas dominated by annual grasses. Two explanations are possible. Firstly, the environment dominated by annual grasses may not be suitable to perennial grasses anymore. Annual grasses in the system modify aboveground and belowground resource availability and conditions through growth and litter production (Lenz *et al.* 2003). This may potentially limit sexual recruitment of perennial grasses, independent of the biotic effects of annual grasses. In general, if an introduced species limits future recruitment of native species by irreversible habitat modification, the fluctuating resource availability theory would predict a low likelihood of re-invasion by native species. Whether recruitment of perennial grasses is naturally rare or only rare in areas dominated by annual grasses remains to be investigated. Over several field seasons I did not observe any significant recruitment by perennial grasses at any field site. Secondly, it is possible that the addition of resources and the decrease in resource uptake were not sufficient to allow perennial grass recruitment during the 6-month experimental period. However, if the invading species requires extreme resource and habitat modification for a long time, its likelihood of recruitment decreases sharply. Even though the habitat may still be suitable for adult plants and seeds are present, the recruitment of the species is not promoted by resource fluctuations or additional supply. This suggests that species identity is still an important factor in the invasion process, regardless of whether a particular habitat is suitable for a species. A species with a demography driven by high recruitment and fast growth (*i.e.* ruderal strategy) will react differently to resource availability than a species with a demography driven by low growth rates, longevity and high stress tolerance (*i.e.* stress tolerating strategy). While species of both extremes of these strategies can become invaders (Newsome & Noble 1986), the mechanisms of these invasions may be quite different. I am not aware of any studies that have set out to compare different mechanisms of invasion for plants with different life history strategies. This maybe a fruitful area for further research for both ecological theory and management/risk assessment applications.

Implications for management of temperate grasslands in the mid-north

Overall, there was no evidence of any combination of factors at which *Austrodanthonia* or other perennial grasses have an absolute competitive advantage over *Avena* or other annual grasses. Thus, it is unlikely that grasslands in this system would return to a dominance by

perennial grasses in average climatic conditions and without active management of annual grasses. Whether annual grass abundances stabilise or further increase will depend on climatic conditions as well as the demographic dynamics of the perennial grasses. Active management is necessary to stop further competitive exclusion of established perennial grasses and presumably other natives in unstocked systems. Annual grasses must be managed, using selective herbicides, slashing, or pulse grazing (Davies 1997), not only to reduce their competitive effect on perennial grasses but also to decrease their effect on overall diversity and to decrease the positive feedback they appear to have on their own abundance (Lenz *et al.* 2003).

The management system must be opportunistic in order to be able to adapt to local climatic conditions, events and particularly current plant species composition. At one extreme it would be necessary to increase the performance of established perennial grasses in areas where annual grasses are already highly abundant, and on the other extreme to prevent large increases in annual grass abundance in areas where annual grass abundance is still low. Years where soil moisture during the shared growing season (April to October) is often at field capacity are high priority years for actively decreasing annual grass abundance in all areas. In years where soil moisture is rarely at field capacity during the shared growing season, areas high in annual grass abundance remain a priority, while areas that have low annual grass abundance are unlikely to be invaded further. The rare years where soil moisture is high during the perennial-grass-only growing season (November –March) may be especially advantageous to perennial grasses. A management system that is based on a flow-chart type progress would be more suitable than the fixed management plan currently in place at most sites (set stocking for grazing/destocking for conservation).

Conclusions

The results suggest that belowground resource availability is the main factor controlling the invasion of annual grasses, but less important to perennial grasses in unstocked grasslands with the exception of its interaction with the strong competitive effects by annual grasses on perennial grasses. Similarly, various predictions of non-equilibrium and equilibrium based invasion theories fitted the behaviour of annual grasses, but to a lesser degree the perennial grasses.

Out of necessity these conclusions are based on studies and experiments of two growing seasons or less and hence are tentative. While this approach is suitable for annual grasses, it proved highly unsatisfactorily for the perennial grasses. The population dynamics of perennial grasses are presumably based on longer periods, although to what degree is unknown. For example, it may be possible that significant sexual recruitment only occurs in the rare years of high summer rainfall. On the other hand, changes in mycorrhizal activity and lichen crusts may have led to long-term or even irreversible changes in resource dynamics. The perennial grasses

present may simply be persisting in an environment that has changed dramatically and thus no obvious correlations between environmental factors and perennial grass abundance exist.

Wide fluctuation in resources that control dominant species will result in similar fluctuations in the abundance of these species and their interactions with other species. Similarly, the abundance of species it is not always controlled by the average resource levels, but in this case, by the maximum resource levels. Knowledge of resource dynamics and how different species respond to these dynamics is vital for an understanding of a system where resources fluctuate widely or a system in which variables other than average levels regulate abundances. Resource dynamics are also particularly important in understanding plant invasions. It will only be possible to formulate targeted management plans that are suitable to dynamic systems if we understand the mechanisms of an invasion and the dynamics behind the factors regulating the mechanisms.

8. Appendix I: Pilot study of correlations between environmental factors and grass abundances

Introduction

Casual observations suggest that grasslands in the South Australian mid-north with high native perennial grass abundance tend to be restricted to steep hill slopes and poor soils. These patterns suggest that native grasses perform relatively better or invasive grasses worse in these environments. However, these sites are simply not suited to agricultural cultivation. In addition, the past and current management of the sites such as grazing, fertiliser addition and deliberate and species introduction further confounds species-environment correlations.

The invasion of exotic annual grasses in temperate grasslands of South Australia, on the other hand, is ubiquitous. *Avena barbata* is present at most, if not all sites and various *Bromus* spp. and *Vulpia* spp. are frequently found (Robertson 1998, Chapter 3). Hyde (1995) suggests that annual grass invasion is more frequent on sites with higher rainfall (p.33), deeper soils (p.33, 42) or alkaline, dry soils (p. 20). Also, sheep camps at higher elevation and ridges, where soils are generally shallow may be associated with high abundance of annual grasses and other exotic weeds (Hyde *et al.* 2000, p. 26).

While various surveys have studied the floristic composition of grassland remnants in the mid-North of South Australia (Hyde 1995; Robertson 1998), to my knowledge no quantified published information exists on the correlation of native perennial grasses and exotic annual grasses with abiotic factors such as rainfall, texture and nutrient availability. However, the observations suggested correlations of grass abundance with factors involved in soil productivity. The following study was a pilot study for the study in Chapter 3. I aimed to establish whether correlations between environmental factors determining soil moisture and nutrient availability existed and to assess the method I had planned to use for measuring the abundance of the different grass types.

Methods

I carried out the study at the Burra site (see Chapter 4 for a description) 24-27 July 2000. I read five plots on the first afternoon. It rained heavily that night confounding the soil moisture readings for the remaining quadrats 2 days later. In total I selected ten 0.5 m × 0.5 m quadrats at a random direction and distance from the centre of four areas along the slope (low, mid-low, mid-high and high slope position). In each quadrat I recorded the percentage frequency of perennial and annual grasses by subdividing the quadrat into 25 0.1 m × 0.1 m subquadrats and recording

the percentage of subquadrats the species was rooted in. Because no inflorescences were present, perennial grasses could only be identified to genus and annual grasses not at all (mainly *Avena barbata* at this site, Chapter 3). If the quadrat was located on a slope, I recorded its slope (maximum difference in elevation within the quadrat) and noted its microtopography in comparison to its surroundings within 1 m (lower or higher than surroundings). I also collected up to three soil samples in each quadrat using a 6 cm diameter auger, one at 0-5 cm depth, and if possible one at 15-20 cm and one at 30-35 cm depth, each in a different randomly selected subquadrat. To estimate soil depth I continued augering in the deepest of these until the auger hit a large solid rock surface or reached a depth of 40 cm. Soil depth more than 40 cm was arbitrarily assigned as 45 cm.

I determined gravimetric soil moisture content of soil samples (drying at 80 °C to constant weight) and estimated soil texture by sieving the soil samples from 0-5 cm and of 30-35 cm depth through sieves of varying diameter (2000, 1000, 500, 250, 125, 63 μm) and recording the fraction left in each sieve. For statistical analysis, texture was divided into fractions larger than 250 μm, representing coarser particles, and smaller than 250 μm, representing finer or clay particles.

For the MANOVAs and ANOVAs on % frequencies and gravimetric soil moisture I tested all data distributions for normality (Shapiro-Wilk W, JMP 3.1.4) and homoscedasticity (Brown-Forsythe, JMP 3.1.4) at $P \leq 0.05$. The % frequency data conformed to assumptions of normality in the majority of distributions and to the assumption of homoscedasticity. The soil moisture data did not conform to the assumption of homoscedasticity and I used a Welch ANOVA, followed by non-parametric Tukey-type multiple comparison tests (Zar 1984).

Results and Discussion

Survey design

Most environmental and vegetation variables measured showed significant correlations with each other (Table 8.1). Results confirmed a negative correlation between annual grass abundance and the abundance of the most common perennial grasses, *Austrostipa* spp. at a 0.5 m × 0.5 m scale, which was the minimum scale I subsequently used in all other surveys and experiments. The strongest correlations were negative correlations between annual grass % frequency and *Austrostipa* spp. % frequency (Figure 8.1a), a negative correlation of annual grasses with soil particles larger than 250 μm and a positive correlation of *Austrostipa* with soil particles larger than 250 μm (Figure 8.1b) *Austrodanthonia* spp. were recorded only in low numbers and did not show any correlations with other variables.

The lack of significant correlations between variables that appeared visually obviously correlated (such as annual grass abundance and slope position) indicated that percentage frequency was not a suitable measure for annual grasses and their correlations to environmental variables. The presence of annual grass in a 10 cm × 10 cm subquadrat can indicate both a high and a low density, and there were visually large density and biomass differences within a 100% frequency. I thus decided to harvest annual grass aboveground biomass for any further surveys. However, even with improved resolution of estimating annual grass abundance, there is also clearly a need for increased replication to include further species and to determine relationships across ranges of abundances and variables.

For perennial grasses, on the other hand, % frequency on this scale appeared to be an appropriate measure of abundance, since their observed range in density at this site was much lower. In addition, landholders or stakeholders were averse to the destructive sampling of perennial grasses.

	Slope position	Quadrat slope	Soil depth	Annual grass	Austrodanthonia	Austrostipa	Coarse textures 0-5 cm	Coarse textures 30-35 cm	% Soil moisture 0-5 cm	% Soil moisture 15-20 cm	% Soil moisture 30-35 cm
Slope position	1.00	-0.62#	-0.74*	-0.28ns	0.33ns	0.19ns	0.08ns	-0.69*	-0.11ns	0.50ns	0.61#
Quadrat slope		1.00	0.40ns	-0.06ns	-0.20ns	0.15ns	0.19ns	0.51ns	0.43ns	-0.01ns	-0.18ns
Soil depth			1.00	0.55ns	-0.51ns	-0.33ns	-0.35ns	0.59#	-0.21ns	-0.69*	-0.75*
Annual grass				1.00	-0.23ns	-0.74*	-0.66*	0.62#	-0.18ns	-0.75*	-0.55ns
Austrodanthonia					1.00	0.11ns	0.40ns	-0.20ns	0.12ns	0.10ns	0.20ns
Austrostipa						1.00	0.79**	-0.37ns	-0.19ns	0.44ns	0.25ns
Coarse textures 0-5 cm							1.00	-0.33ns	-0.09ns	0.32ns	0.15ns
Coarse textures 30-35 cm								1.00	-0.08ns	-0.76*	-0.73*
% Soil moisture 0-5 cm									1.00	0.56#	0.47ns
% Soil moisture 15-20 cm										1.00	0.89***
% Soil moisture 30-35 cm											1.00

Table 8.1: Correlations between environmental factors and species abundances at the Burra site in July 2000 (Spearman's ρ; fine textures = coarse textures x (−1)). ns $P > 0.10$; # $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

Grass abundance and soil moisture

While the soil moisture at 15-20 cm depth showed a significant correlation with annual grass frequency, this was due to the confounding effect of rain between the first and second half of the readings. Initially, soil moisture was highest in the top soil layer than further down, but on the second survey day heavy rain had wetted all layers measured equally (Table 8.2). To take into account the confounding effect of rain, I included survey day into the MANOVA and the

subsequent ANOVAs of the correlation of soil moisture with annual grasses and *Austrostipa* at different depths (Table 8.3). Day, but not soil moisture at 0-5 cm had a significant correlation with both annual grasses and *Austrostipa* spp.. This suggests that the correlations between moisture and grass frequency resulted from different grass abundance being recorded on days with different soil moisture. I thus decided to exclude soil moisture as a response variable in the larger survey, but include further variables that drive soil moisture, such as topographical variables, rainfall and other edaphic variables. A regular and longer-term monitoring of soil moisture was required to determine the correlations between this variable and grass abundance.

Day	0-5 cm	15-20 cm	30-35 cm
1	20.94 ± 1.80^a	11.88 ± 0.98^b	11.53 ± 10.63^b
2	21.51 ± 0.53^a	18.69 ± 1.54^a	17.20 ± 12.22^{ab}

Table 8.2: % gravimetric soil moisture (mean $\pm$ SE, n = 5) with depth and day in July 2000 at the Burra site. Different letters denote significant differences at α = 0.05 (Welch ANOVA, Tukey-type multiple comparison test).

		Source	Test	Approx. F	Numerator DF	Denominator DF	P-value
(a)	0-5 cm depth	Whole Model	Wilks' λ	1.80	6	10	0.20
		Soil moisture	F Test	1.49	2	5	0.31
		Day	F Test	6.41	2	5	0.04
		Day $\times$ soil moisture	F Test	1.64	2	5	0.28
	15-20 cm depth	Whole Model	Wilks' λ	1.03	6	10	0.46
		Soil moisture	F Test	0.30	2	5	0.75
		Day	F Test	0.81	2	5	0.50
		Day $\times$ soil moisture	F Test	0.14	2	5	0.87
	30-35 cm depth	Whole Model	Wilks' λ	1.07	6	10	0.44
		Soil moisture	F Test	1.23	2	5	0.37
		Day	F Test	0.39	2	5	0.69
		Day $\times$ soil moisture	F Test	0.44	2	5	0.67
(b)	Annual grasses	Whole Model	F Test	4.98	3	6	0.046
		Soil moisture	F Test	2.30	1	6	0.18
		Day	F Test	13.81	1	6	0.01
		Day $\times$ soil moisture	F Test	3.43	1	6	0.11
	Austrostipa spp.	Whole Model	F Test	2.17	3	6	0.19
		Soil moisture	F Test	2.51	1	6	0.16
		Day	F Test	6.02	1	6	0.0495
		Day $\times$ soil moisture	F Test	1.69	1	6	0.24

Table 8.3: (a) Correlation of soil moisture at different depths and measuring day (Identity MANOVAs); (b) corelations of soil moisture at 0-5 cm and measuring day on the frequency of annual grasses and *Austrostipa* spp. (ANOVAs).

Figures
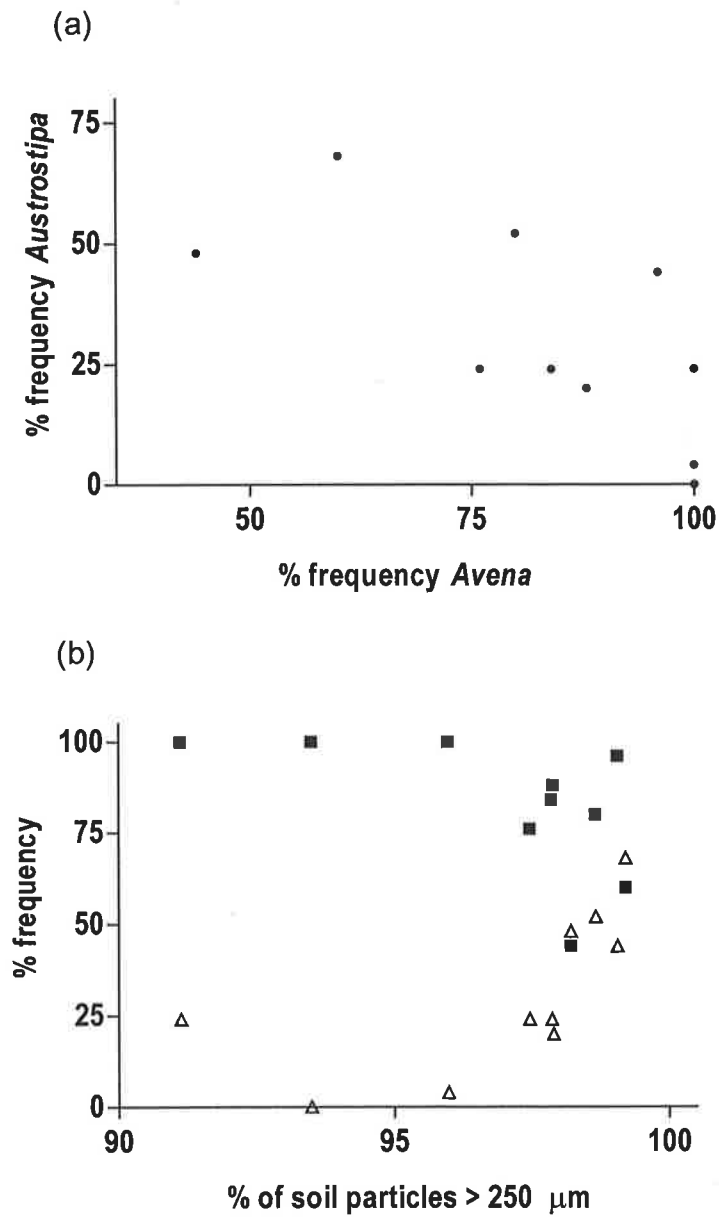
(a)

(b)

Figure 8.1: Correlation between (a) % frequency of *Austrostipa* spp. (△) and annual grasses (··■··) and (b) soil particle size and *Austrostipa* spp. and annual grasses in 0.5 m × 0.5 m quadrats at the Burra site in July 2000.

9. Appendix II: Pilot study on the existence of resource islands at a grassland in the South Australian mid-north

Introduction

Research in arid, semi-arid grasslands and sub-tropical grassland has indicated that perennial tussock grasses often form so called 'resource islands' by accumulating total and mineralizable soil N and total and respirable organic C, resulting in higher resource levels than the soils in adjacent openings (Hook *et al.* 1991; Vinton & Burke 1995; Bennett & Adams 1999). The presence of these resource islands often has facilitative effects on other species, especially in the case of resource islands under shrubs and trees in arid systems (Pugnaire *et al.* 1996; Facelli & Brock 2000). Grasses may perform a similar facilitative role (Maestre *et al.* 2001). Thus, both in terms of understanding resource heterogeneity and species interactions, it is vital to determine whether resource islands are present in grasslands that have not previously been investigated for resource levels. Results of such a study will aid in directing research into the appropriate avenues. This pilot study aimed to assess levels soil organic carbon and moisture in a grassland in the mid-north of South Australia and to determine sees whether heterogeneity in these levels correlates with types of vegetation.

Methods

The study was carried out in a grassland 1 km north of Burra, South Australia (see Chapter 4 for description). In May 2000 I placed three transects in each of two slope positions, one at the very base of the slope in an area dominated by exotic annuals, and one towards the top of the slope in an area dominated by native perennial grasses with open interstitial spaces. The transects were placed along the slope 5 m apart. Along each transect I located five points every 30 cm, starting from a random point along the transect. At each point I noted the type of vegetation present (annual, none, perennial) and took a soil sample at 0–5 cm depth. I removed litter, rocks and vegetation from each sample, stored them in airtight sealed containers for transport and analysed them for organic carbon using the Walkley & Black titration method (Allison 1965) and gravimetric soil moisture.

I tested the data distributions of soil organic carbon and soil moisture by vegetation type for normality (Shapiro-Wilk W, JMP 3.1.4) and homoscedasticity (Brown-Forsythe, JMP 3.1.4) at $P \leq 0.05$. All data distributions conformed to the assumptions of normality, however the organic carbon distributions did not conform to assumptions of homoscedasticity. I thus analysed the

organic carbon distribution using a Welch ANOVA and a Tukey-type multiple comparison test with unequal sample sizes (Zar 1984, p. 200).

Results

Results confirmed that the slope positions clearly differed in vegetation types, with annual grasses dominating all of the sample sites in the lower slope position and perennial grasses with interstitial spaces in various combinations dominating the upper slope position (Table 9.1).

Vegetation type	Bottom of slope			Top of slope		
	Transect 1	Transect 2	Transect 3	Transect 1	Transect 2	Transect 3
Annual weeds	100	100	100	0	0	0
Perennial grasses	0	0	0	40	60	20
Open space	0	0	0	60	40	80

Table 9.1: Vegetation types (%, n =5) by slope position and transect at the field site.

Organic carbon levels varied between 1.5-2.5 % and gravimetric soil moisture levels varied between 8-10%. While there was no significant difference between soil moisture with vegetation (Figure 9.1a; Table 9.2a), organic carbon levels showed high variation, both between the vegetation types and within annual vegetation itself (Figure 9.1b; Table 9.2b). Average organic carbon levels were 2% in the annual vegetation (or lower slope position) compared to 1.6% under perennial grasses and 1.8% in areas where no vegetation was present.

		Source	DF	SS	F	P-value	r^2
(a)	Soil moisture (%)	Model	2	1.17	0.52	0.60	0.04
		Error	27	30.33			
		Total	29	31.50			

		Numerator DF	Denominator DF	F	P-value
(b)	Organic carbon (%)	2	13.06	6.40	0.01

Table 9.2: (a) Correlations of vegetation type with (a) % gravimetric soil moisture (ANOVA) and (b) % organic carbon at 0-5 cm depth (Welch ANOVA) in May 2002 at a grassland in the South Australian mid-north.

Resource islands under perennial grasses in other systems have around 20-25% more carbon (total or organic) than adjacent open areas (Vinton & Burke 1995; Bennett & Adams 1999). When just comparing the organic carbon levels under perennial grasses and in the open using a standard ANOVA with the standard errors and numbers of the data distribution here, there would have been sufficient power (Power > 0.95) to detect a minimum effect size (difference between the means) of 0.19% organic carbon or more at $\alpha = 0.05$ (Table 9.3). This corresponds to a difference of circa 13% between organic carbon levels under perennial grasses and in the

open. This suggests that the sampling procedure should have resulted in sufficient power to find a difference of 20-25% easily.

α	σ	Effect size	n	Power
0.05	0.174	0.09	15	0.44
0.05	0.174	0.19	15	0.97
0.05	0.174	0.29	15	1.00

Table 9.3: Power of ANOVAs between means of organic carbon levels underneath perennial grasses and in the open, given different effect sizes (differences between the means).

Discussion

There was no evidence that perennial grasses at the Burra field site are associated with resource islands. While the survey does not establish any cause-effect relationships, there is a clear association of annual grasses with higher organic carbon levels on one hand, and perennial grasses with lower organic carbon levels on the other. Furthermore the variances of the distributions of soil organic carbon under the different vegetation types were unequal. The data suggest that there is actually more variation among soil organic carbon under annual grasses than under perennial grasses.

There are several explanations for the lack of evidence for resource islands. Firstly, resource islands may exist for other resources than organic carbon or soil moisture or for their more labile fractions (Vinton & Burke 1995). Secondly, resource islands may have existed over the whole site prior to European settlement, but have since disappeared with management and not re-established since grazing ceased. Resource islands may take decades to establish (Burke *et al.* 1998), but can disintegrate within 36 months after the death of the individual plant (Kelly & Burke 1997). Moreover resource islands can be reduced or eliminated by the invasion of annual grasses (Vinton & Burke 1995). Thirdly, substantial resource islands may never have existed in this system in the first place or may only be very small and of little difference to the surrounding vegetation. The grasses in this system may be too short lived to create resource islands.

While experimental manipulations are necessary to establish clear cause-effect relationships, a more extensive survey in further areas (Chapter 3) has confirmed that perennial grasses are generally associated with lower resource levels than annual grasses and there was no indication (such as increased variation in resources) that resource islands exist in perennial grass dominated sites for any of the measured variables, regardless of time since grazing or other management.

On the other hand, I had not expected to see a higher variation in resource levels in the area dominated by annual grasses since the aboveground vegetation in this area is fairly homogenous. A further possible explanation for this result is that native perennial grasses may create

substantial resource islands only when they are able to grow to a large size. This requires higher levels of productivity than currently found at sites where perennial grasses still dominate as well as long life spans. Sites with higher productivity tend to be associated with high levels of annual grass invasion. It is possible that prior to European settlement, productive perennial grasses may have dominated these more productive areas and that the higher variation in organic carbon levels in these areas is a relict from perennial vegetation in the past.

Clearly, further surveys and experiments are necessary to confirm or reject any of the above explanations. However, since none of my research carried out during this project has indicated a possibility of resource islands, I believe that in this system under the current management regime, resources are indeed highly heterogenous in both time and space, but not necessarily on the scale of resource islands found around perennial grasses in other systems.

Figures

(a)

(b)
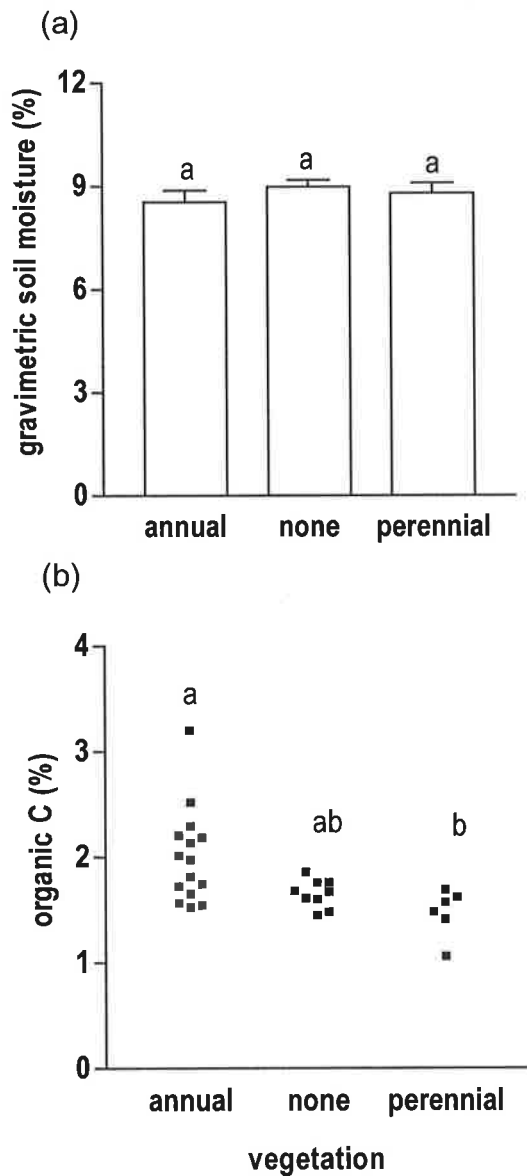
vegetation

Figure 9.1: (a) % gravimetric soil moisture (mean + SE) and (b) % soil organic carbon (raw data) at 0-5 cm depth in different vegetation in May 2002 at a grassland in the South Australian mid-north. Error bars denote 1 SE. Letters denote significant differences at α = 0.05 ((a) ANOVA; (b) Welch ANOVA, Tukey-type multiple comparison test with unequal sample sizes).

10. References

Aerts R., Boot R. G. A. & van der Aart P. J. M. (1991). The relation between aboveground and belowground biomass allocation patterns and competitive ability. *Oecologia* **81**, 551-559.

Afzal M. & Adams W. A. (1992). Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. *Soil Science Society of America Journal* **56**, 1160-1166.

Agrawal B. & Tiwari S. C. (1987). Standing state and cycling of nitrogen in a Garhwal Himalayan (India) grassland under grazing, burning and protection against herbage removal regimes. *Proceedings of the Indian Academy of Sciences. Plant Sciences* **97**, 433-442.

Allison L. (1965). Organic carbon. In: *Methods of soil analysis. Part 2. Chemical and microbiological properties.* (eds. D. D. Evans, L. E. Ensminger, F. E. Clark & J. White) pp. 1367-1378. American Society of Agronomy, Madison, Wisconsin.

Andrew M. H. & Lange R. T. (1986). Development of a new piosphere in arid chenopod shrubland grazed by sheep: 1. Changes to the soil surface. *Australian Journal of Ecology* **11**, 395-410.

Andrew M. H., Noble I. R. & Lange R. T. (1979). A non-destructive method for estimating the weight of forage on shrubs. *Australian Rangelands Journal* **1**, 225-231.

Archer N. A. L., Quinton J. N. & Hess T. M. (2002). Below-ground relationships of soil texture, roots and hydraulic conductivity in two-phase mosaic vegetation in South-east Spain. *Journal of Arid Environments* **52**, 535-553.

Arii K. & Turkington R. (2001). Assessing competition intensity along productivity gradients using a simple model. *Canadian Journal of Botany* **79**, 1486-1491.

Austin A. T. & Sala O. E. (2002). Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *Journal of Vegetation Science* **13**, 351-360.

Austin M. P. (1982). Use of a relative physiological performance value in the prediction of performance in multispecies mixtures from monoculture performance. *Journal of Ecology* **70**, 559-570.

Austin M. P., Williams O. B. & Belbin L. (1981). Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. *Vegetatio* **47**, 201-211.

Ayyad M. A. G. & Dix R. L. (1964). An analysis of a vegetation-microenvironmental complex on prairie slopes in Saskatchewan. *Ecological Monographs* **34**, 421-442.

Baker H. G. (1965). Characteristics and modes of origin of weeds. In: *The Genetics of Colonising Species.* (eds. H. G. Baker & G. L. Stebbins) pp. 147-169. Academic Press, New York.

Bakker J. & Wilson S. D. (2001). Competitive abilities of introduced and native grasses. *Plant Ecology* **157**, 117-125.

Bakker J. P. & Berendse F. (1999). Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution* **14**, 63-68.

Barrett J. E., McCulley R. L., Lane D. R., Burke I. C. & Lauenroth W. K. (2002). Influence of climate variability on plant production and N-mineralization in Central US grasslands. *Journal of Vegetation Science* **13**, 383-394.

Bartolome J. W., Stroud M. C. & Heady H. F. (1980). Influence of natural mulch on forage production on differening California range sites. *Journal of Range Management* **33**, 4-8.

Bazzaz F. A. (1986). Life Histories of Colonizing Plants: some demographic, genetic and physiological features. In: *Ecology of Biological Invasions of North America and Hawaii.* (eds. H. A. Mooney & J. A. Drake) pp. 96-110. Springer-Verlag, New York.

Bennett L. T. & Adams M. A. (1999). Indices for characterising spatial variability of soil nitrogen semi-arid grasslands of northwestern Australia. *Soil Biology and Biochemistry* **31**, 735-746.

Benson J. S. & Redpath P. A. (1997). The nature of pre-European native vegetation in south-eastern Australia: A critique of Ryan, D.G., Ryan, J.R., and Starr, B.J. (1995) The Australian Landscape - Observations of Explorers and Early Settlers. *Cunninghamia* **5**, 285-328.

Bischoff A. (2002). Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biological Conservation* **104**, 25-33.

Blicker P. S., Olson B. E. & Engel R. (2002). Traits of the invasive *Centaurea maculosa* and two native grasses: effect of N supply. *Plant and Soil* **247**, 261-269.

Brooks M. L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* **40**, 344-353.

Buckland S. M., Thompson K., Hodgson J. G. & Grime J. P. (2001). Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology* **38**, 301-309.

Burke I. C., Lauenroth W. K., Vinton M. A., Hook P. B., Kelly R. H., Epstein H. E., Aguiar M. R., Robles M. D., Aguilera M. O., Murphy K. L. & Gill R. A. (1998). Plant-soil interactions in temperate grasslands. *Biogeochemistry* **42**, 121-143.

Burke M. J. W. & Grime J. P. (1996). An experimental study of plant community invasibility. *Ecology* **77**, 776-790.

Cahill J. F., Jr. (1999). Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology* **80**, 466-480.

Cahill J. F., Jr. (2002). What evidence is necessary in studies which separate root and shoot competition along productivity gradients? *Journal of Ecology* **90**, 201-204.

Cahill J. F., Jr. & Casper B. B. (1999). Growth consequences of soil nutrient heterogeneity for two old-field herbs, *Ambrosia artemisiifolia* and *Phytolacca americana*, grown individually and in combination. *Annals of Botany* **83**, 471-478.

Callaway R. M. & Aschehoug E. T. (2000). Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science* **290**, 521-523.

Callaway R. M., Mahall B. E., Wicks C., Pankey J. & Zabinski C. (2003). Soil fungi and the effects of an invasive forb on grasses: Neighbor identity matters. *Ecology* **84**, 129-135.

Capon M. H. & O'Connor T. G. (1990). The predation of perennial grass seeds in Transvaal (South Africa) savanna grasslands. *South African Journal of Botany* **56**, 11-15.

Carson W. P. & Peterson C. J. (1990). The role of litter in an old-field community: Impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia* **85**, 8-13.

Carson W. P. & Pickett S. T. A. (1990). Role of resources and disturbance in the organization of an old-field plant community. *Ecology* **71**, 226-238.

Chanasyk D. S. & Naeth M. A. (1995). Grazing impacts on bulk density and soil strength in the foothills fescue grasslands of Alberta, Canada. *Canadian Journal of Soil Science* **75**, 551-557.

Chapin F. S. I. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology & Systematics* **11**, 233-260.

Chiarucci A., Maccherini S., Bonini I. & De Dominicis V. (1999). Effects of nutrient addition on community productivity and structure of serpentine vegetation. *Plant Biology* **1**, 121-126.

Claassen V. P. & Marler M. J. (1998). Annual and perennial grass growth on nitrogen-depleted decomposed granite. *Restoration Ecology* **6**, 175-180.

Clewett J. F., Clarkson N. M., George D. A., Ooi S. H., Owens D. T., Partridge I. J. & Simpson G. B. (2003). Rainman StreamFlow version 4.3: a comprehensive climate and streamflow analysis package on CD to assess seasonal forecasts and manage climate risk. Queensland Government, Department of Primary Industries, Brisbane.

Collins S. L., Bradford J. A. & Sims P. L. (1988). Succession and fluctuation in *Artemisia* dominated grassland. *Vegetatio* **73**, 89-100.

Connolly J., Wayne P. & Bazzaz F. A. (2001). Interspecific competition in plants: How well do current methods answer fundamental questions? *American Naturalist* **157**, 107-125.

Connolly J., Wayne P. & Murray R. (1990). Time course of plant-plant interactions in experimental mixtures of annuals: Density, frequency, and nutrient effects. *Oecologia* **82**, 513-526.

Coronato F. R. & Bertiller M. B. (1996). Precipitation and landscape related effects on soil moisture in semi-arid rangelands of Patagonia. *Journal of Arid Environments* **34**, 1-9.

Coupland R. T. (1992). Mixed Prairie. In: *Natural grasslands: Introduction and western hemisphere* (ed. R. T. Coupland) pp. 151-182. Elsevier, Amsterdam.

Cronk Q. C. B. & Fuller J. L. (1995). *Plant Invaders.* Chapman & Hall, London.

Crooks J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* **97**, 153-166.

Crosthwait J., Madden B. & O'Connor K. F. (1996). Native pasture and the farmer's choice: Evaluation of management and sowing options. *New Zealand Journal of Agricultural Research* **39**, 541-557.

Cui M. & Caldwell M. M. (1997). A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* **191**, 291-299.

D'Antonio C. M. & Vitousek P. M. (1992). Biological Invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology & Systematics* **23**, 63-87.

Daubenmire R. (1992). Palouse Prairie. In: *Natural grasslands: Introduction and western hemisphere* (ed. R. T. Coupland) pp. 297-312. Elsevier, Amsterdam.

Davies R. (1982). *The conservation of major plant associations in South Australia.* Conservation Council of South Australia Inc., Adelaide.

Davies R. (1997). *Weed management in temperate native grasslands and box grassy woodlands in South Australia.* Black Hill Flora Centre, Botanic Gardens of South Australia, Athelstone, South Australia.

Davies R. (2000). Description, distribution, conservation status and weed management of box and buloke grassy woodlands in South Australia. In: *Temperate Eucalypt Woodlands in Australia* (eds. R. J. Hobbs & C. J. Yates) pp. 167-189. Surrey Beatty & Sons, Chipping Norton, NSW.

Davis M. A., Grime J. P. & Thompson K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**, 528-534.

Davis M. A. & Pelsor M. (2001). Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* **4**, 421-428.

Davis M. A., Wrage K. J., Reich P. B., Tjoelker M. G., Schaeffer T. & Muermann C. (1999). Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecology* **145**, 341-350.

Day P. R. (1965). Particle fractionation and particle size analysis. In: *Methods of soil analysis* (eds. C. A. Black & *e. al.*) pp. 545-567, Madison, Wisconsin.

DeFalco L. A., Detling J. K., Tracy C. R. & Warren S. D. (2001). Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. *Plant and Soil* **234**, 1-14.

Defosse G. E., Bertiller M. B. & Robberecht R. (1997). Effects of topography, soil moisture, wind and grazing on *Festuca* seedlings in a Patagonian grassland. *Journal of Vegetation Science* **8**, 677-684.

Descroix L., Barrios J. L. G., Vandervaere J. P., Viramontes D. & Bollery A. (2002). An experimental analysis of hydrodynamic behaviour on soils and hillslopes in a subtropical mountainous environment (Western Sierra Madre, Mexico). *Journal of Hydrology* **266**, 1-14.

Dickson J. H., Rodriguez J. C. & Machado A. (1987). Invading plants at high altitudes on Teneriffe (Canary Islands) especially in the Teide National Park. *Botanical Journal of the Linnean Society* **95**, 155-180.

Diemer M. & Schmid B. (2001). Effects of biodiversity loss and disturbance on the survival and performance of two *Ranunculus* species with differing clonal architectures. *Ecography* **24**, 59-67.

Dietz H., Steinlein T. & Ullmann I. (1998). The role of growth form and correlated traits in competitive ranking of six perennial ruderal plant species grown in unbalanced mixtures. *Acta Oecologica* **19**, 25-36.

Dodd M. B., Lauenroth W. K. & Burke I. C. (2002). Associations between vegetation patterns and soil texture in the shortgrass steppe. *Plant Ecology* **158**, 127-137.

Dormaar J. F., Smoliak S. & Willms W. D. (1989). Vegetation and soil responses to short-duration grazing on fescue grasslands. *Journal of Range Management* **42**, 252-256.

Dowling P. M., Garden D. L., Eddy D. A. & Pickering D. I. (1996). Effect of soil pH on the distribution of *Danthonia* species on the tablelands of central and southern New South Wales. *New Zealand Journal of Agricultural Research* **39**, 619-621.

Dukes J. S. (2001). Biodiversity and invasibility in grassland microcosms. *Oecologia* **126**, 563-568.

Dyer A. R. & Rice K. J. (1997). Intraspecific and diffuse competition: The response of *Nassella pulchra* in a California grassland. *Ecological Applications* **7**, 484-492.

Dyer A. R. & Rice K. J. (1999). Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* **80**, 2697-2710.

Eldridge D. J., Semple W. S. & Koen T. B. (2000). Dynamics of cryptogamic soil crusts in a derived grassland in south-eastern Australia. *Austral Ecology* **25**, 232-240.

Enoki T., Kawaguchi H. & Iwatsubo G. (1996). Topographic variations of soil properties and stand structure in a *Pinus thunbergii* plantation. *Ecological Research* **11**, 299-309.

Ernst W. H. O. & Tolsma D. J. (1992). Growth of annual and perennial grasses in a savanna of Botswana under experimental conditions. *Flora* **186**, 287-300.

Ewing A. L. & Menke J. W. (1983). Response of soft chess (*Bromus mollis*) and slender oat (*Avena barbata*) to simulated drought cycles. *Journal of Range Management* **36**, 415-418.

Facelli J. M. (1994). Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* **75**, 1727-1735.

Facelli J. M. & Brock D. J. (2000). Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of South Australia. *Ecography* **23**, 479-491.

Facelli J. M. & Facelli E. (1993). Interactions after death: Plant litter controls priority effects in a successional plant community. *Oecologia* **95**, 277-282.

Facelli J. M., Leon R. J. C. & Deregibus V. A. (1989). Community structure in grazed and ungrazed grassland sites in the Flooding Pampa, Argentina. *American Midland Naturalist* **121**, 125-133.

Facelli J. M., Montero C. M. & Leon R. J. C. (1988). Effect of different disturbance regimen on seminatural grasslands from the subhumid Pampa. *Flora* **180**, 241-249.

Facelli J. M. & Pickett S. T. A. (1991). Plant litter: Its dynamics and effects on plant community structure. *Botanical Review* **57**, 1-32.

Facelli J. M., Williams R. G., Fricker S. & Ladd B. (1999). Establishment and growth of seedlings of *Eucalyptus obliqua*: Interactive effects of litter, water, and pathogens. *Australian Journal of Ecology* **24**, 484-494.

Famiglietti J. S., Rudnicki J. W. & Rodell M. (1998). Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas. *Journal of Hydrology* **210**, 259-281.

Farley R. A. & Fitter A. H. (1999). Temporal and spatial variation in soil resources in a deciduous woodland. *Journal of Ecology* **87**, 688-696.

Feral C. J. W., Epstein H. E., Otter L., Aranibar J. N., Shugart H. H., Macko S. A. & Ramontsho J. (2003). Carbon and nitrogen in the soil-plant system along rainfall and land-use gradients in southern Africa. *Journal of Arid Environments* **54**, 327-343.

Fernández R. J. & Reynolds J. F. (2000). Potential growth and drought tolerance of eight desert grasses: Lack of a trade-off? *Oecologia* **123**, 90-98.

Flannery T. (1994). *The future eaters: an ecological history of the Australasian lands and people*. Reed Books, Chatswood, N.S.W.

Flores-Martínez A., Ezcurra E. & Sánchez-Colón S. (1998). Water availability and the competitive effect of a columnar cactus on its nurse plant. *Acta Oecologica* **19**, 1-8.

Forkner R. E. & Hunter M. D. (2000). What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* **81**, 1588-1600.

Foster B. L. (1999). Establishment, competition and the distribution of native grasses among Michigan old-fields. *Journal of Ecology* **87**, 476-489.

Foster B. L. (2000). Competition at the population level along a standing crop gradient: a field experiment in successional grassland. *Plant Ecology* **151**, 171-180.

Foster B. L. (2002). Competition, facilitation, and the distribution of *Schizachyrium scoparium* along a topographic-productivity gradient. *Écoscience* **9**, 355-363.

Foster B. L. & Gross K. L. (1998). Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *Ecology* **79**, 2593-2602.

Foster B. L., Smith V. H., Dickson T. L. & Hildebrand T. (2002). Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* **99**, 300-307.

Fowler N. L. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology & Systematics* **17**, 89-110.

Fowler N. L. (1988). What is a safe site?: Neighbor, litter, germination date, and patch effects. *Ecology* **69**, 947-961.

Fox M. D. & Fox B. J. (1986). The susceptibility of natural communities to invasion. In: *Ecology of Biological Invasions.* (eds. R. H. Groves & J. J. Burdon) pp. 57-66. Cambridge University Press, Cambridge.

Frank D. A., Groffman P. M., Evans R. D. & Tracy B. F. (2000). Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia* **123**, 116-121.

Freckleton R. P. & Watkinson A. R. (1997a). Measuring and modelling plant neighbour effects - response. *Functional Ecology* **11**, 536.

Freckleton R. P. & Watkinson A. R. (1997b). Measuring plant neighbour effects. *Functional Ecology* **11**, 532-534.

Fretwell S. D. (1977). The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine* **20**, 169-185.

Garden D. L., Dowling P. M., Eddy D. A. & Nicol H. I. (2001). The influence of climate, soil, and management on the composition of native grass pastures on the central, southern, and Monaro tablelands of New South Wales. *Australian Journal of Agricultural Research* **52**, 925-936.

Garrett K. A. & Dixon P. M. (1997). Environmental pseudointeraction: The effects of ignoring the scale of environmental heterogeneity in competition studies. *Theoretical Population Biology* **51**, 37-48.

Geoscience Australia (2003). Natmap Raster Mosaic. Geoscience Australia, Canberra.

Gibson D. J., Connolly J., Hartnett D. C. & Weidenhamer J. D. (1999). Designs for greenhouse studies of interactions between plants. *Journal of Ecology* **87**, 1-16.

Gibson R., Hewitt A., Sparling G. P. & Bosch O. (2000). Vegetation change and soil quality in Central Otago Tussock Grasslands, New Zealand. *The Rangeland Journal* **22**, 190-204.

Goldberg D. E. (1990). Components of resource competition in plant communities. In: *Perspectives on Plant Competition* (eds. J. B. Grace & G. D. Tilman). Academic Press, San Diego.

Goldberg D. E. (1994). Influence of competition at the community level: An Experimental version of the null models approach. *Ecology* **75**, 1503-1506.

Goldberg D. E. (1996). Competitive ability: Definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **351**, 1377-1385.

Goldberg D. E. & Fleetwood L. (1987). Competitive effect and response in four annual plants. *Journal of Ecology* **75**, 1131-1144.

Goldberg D. E. & Landa K. (1991). Competitive effect and response: Hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* **79**, 1013-1030.

Goldberg D. E. & Novoplansky A. (1997). On the relative importance of competition in unproductive environments. *Journal of Ecology* **85**, 409-418.

Goldberg D. E., Rajaniemi T. K., Gurevitch J. & Stewart-Oaten A. (1999). Empirical approaches to quantifying interaction intensity: Competition and facilitation along productivity gradients. *Ecology* **80**, 1118-1131.

Greenwood K. L., MacLeod D. A. & Hutchinson K. J. (1997). Long-term stocking rate effects on soil physical properties. *Australian Journal of Experimental Agriculture* **37**, 413-419.

Grime J. P. (1979). *Plant strategies and vegetation processes.* John Wiley & Son, New York.

Grove P. B., Mark A. F. & Dickinson K. J. M. (2002). Vegetation monitoring of recently protected tussock grasslands in the southern South Island, New Zealand. *Journal of the Royal Society of New Zealand* **32**, 379-414.

Groves R. H., Austin M. P. & Kaye P. E. (2003). Competition between Australian native and introduced grasses along a nutrient gradient. *Austral Ecology* **28**, 491-498.

Gurevitch J. (1986a). Competition and the local distribution of the grass *Stipa neomexicana. Ecology* **67**, 46-57.

Gurevitch J. (1986b). Restriction of a 3-carbon photosynthetic pathway grass to dry ridges in a semiarid grassland. *Canadian Journal of Botany* **64**, 1006-1011.

Gurevitch J., Wilson P., Stone J. L., Teese P. & Stoutenburgh R. J. (1990). Competition among old-field perennials at different levels of soil fertility and available space. *Journal of Ecology* **78**, 727-744.

Haase P., Pugnaire F. I. & Incoll L. D. (1995). Seed production and dispersal in the semi-arid tussock grass *Stipa tenacissima* L. during masting. *Journal of Arid Environments* **31**, 55-65.

Hamilton J. G., Holzapfel C. & Mahall B. E. (1999). Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* **121**, 518-526.

Harrington G. N. (1991). Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* **72**, 1138-1149.

Harris G. A. (1967). Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum. Ecological Monographs* **37**, 89-110.

Harris G. A. & Wilson A. M. (1970). Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* **51**, 530-534.

Harrison S. (1999). Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* **121**, 99-106.

Hartnett D. C. & Wilson G. W. T. (1999). Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* **80**, 1187-1195.

Heady H. F. (1956). Changes in the central California annual plant community induced by the manipulation of natural mulch. *Ecology* **37**, 798-811.

Heady H. F., Bartolome J. W., Pitt M. D., Savelle G. D. & Stroud M. C. (1992). California prairie. In: *Natural grasslands: Introduction and western hemisphere* (ed. R. T. Coupland) pp. 313-335. Elsevier, Amsterdam.

Hector A., Dobson K., Minns A., Bazeley-White E. & Lawton J. H. (2001). Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research* **16**, 819-831.

Heidinga L. & Wilson S. D. (2002). The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. *Diversity & Distributions* **8**, 249-258.

Hengeveld R. (1988). Mechanisms of Biological Invasions. *Journal of Biogeography* **15**, 819-828.

Hewitt A. E. (1996). Estimating Surface Erosion Using Cs-137 At a Semi-Arid Site in Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* **26**, 107-118.

Hiernaux P., Bielders C. L., Valentin C., Bationo A. & Fernandez R. S. (1999). Effects of livestock grazing on physical and chemical properties of sandy soils in Sahelian rangelands. *Journal of Arid Environments* **41**, 231-245.

Hobbs R. J. (1989). The nature and effects of disturbance relative to invasions. In: *Biological Invasions: A Global Perspective* (eds. J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmánek & M. Williamson) pp. 389-405. John Wiley and Sons, New York.

Hobbs R. J. & Mooney H. A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* **72**, 59-68.

Hodgkinson K. C. & Quinn J. A. (1976). Adaptive variability in the growth of *Danthonia caespitosa* Gaud. populations at different temperatures. *Australian Journal of Botany* **24**, 381-396.

Hook P. B. & Burke I. C. (2000). Biogeochemistry in a shortgrass landscape: Control by topography, soil texture, and microclimate. *Ecology* **81**, 2686-2703.

Hook P. B., Burke I. C. & Lauenroth W. K. (1991). Heterogeneity of soil and plant nitrogen and carbon associated with individual plants and openings in North American shortgrass steppe. *Plant and Soil* **138**, 247-256.

Hoopes M. F. & Hall L. M. (2002). Edaphic factors and competition affect pattern formation and invasion in a California grassland. *Ecological Applications* **12**, 24-39.

Huenneke L. F. (1989). Distribution and regional patterns of California grasslands. In: *Grassland structure and function: California annual grassland* (eds. L. F. Huenneke & H. A. Mooney) pp. 1-12. Kluwer Academic Publishers, Dordrecht.

Huenneke L. F., Hamburg S. P., Koide R. T., Mooney H. A. & Vitousek P. M. (1990). Effects of soil resources on plant invasion and community structure in Californian (USA) serpentine grassland. *Ecology* **71**, 478-491.

Huenneke L. F. & Vitousek P. M. (1990). Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: Implications for management of native Hawaiian forests. *Biological Conservation* **53**, 199-212.

Huston M. A. & DeAngelis D. L. (1994). Competition and coexistence: The effects of resource transport and supply rates. *American Naturalist* **144**, 954-977.

Huxtable C. H. A. & Whalley R. D. B. (1999). Emergence and survival of three native grass species sown on roadsides on the Northern Tablelands, New South Wales, Australia. *Australian Journal of Botany* **47**, 221-235.

Hyde M. K. (1995). The temperate grasslands of South Australia: their composition and conservation status pp. 399. World Wide Fund for Nature Australia, Sydney.

Hyde M. K., Davies R., Steed Y. & Reynolds T. (2000). Mokota Conservation Park, Burra Hills, South Australia: A Baseline Biodiversity Study pp. 92. Nature Conservation Society of South Australia, Threatened Plant Action Group, Adelaide.

Inouye B. D. (2001). Response surface experimental designs for investigating interspecific competition. *Ecology* **82**, 2696-2706.

Jackson L. E. (1985). Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* **12**, 349-361.

Jackson L. E. & Roy J. (1986). Growth patterns of Mediterranean annual and perennial grasses under simulated rainfall regimes of southern France and California (USA). *Acta Oecologica Oecologia Plantarum* **7**, 191-212.

Jain S. K. (1982). Variation and adaptive role of seed dormancy in some annual grassland species. *Botanical Gazette* **143**, 101-106.

Jain S. K. & Rai K. N. (1980). Population biology of *Avena barbata*. 8. Colonization experiments as a test of the role of natural selection in population divergence. *American Journal of Botany* **67**, 1342-1346.

Jaramillo V. J. & Detling J. K. (1992). Small-scale heterogeneity in semi-arid North American grassland: II. Cattle grazing of simulated urine patches. *Journal of Applied Ecology* **29**, 9-13.

Jessop J. P. & Toelken H. R. eds. (1986). *Flora of South Australia*. South Australian Government, Adelaide.

Joffre R. (1990). Plant and soil nitrogen dynamics in Mediterranean grasslands: A comparison of annual and perennial grasses. *Oecologia* **85**, 142-149.

Johnstone I. M. (1986). Plant invasion windows: a time-based classification of invasion potential. *Biological Review* **61**, 369-394.

Jones C. E. (1996). Pastoral value and production from native pastures. *New Zealand Journal of Agricultural Research* **39**, 449-456.

Jurjavcic N. L., Harrison S. & Wolf A. T. (2002). Abiotic stress, competition, and the distribution of the native annual grass *Vulpia microstachys* in a mosaic environment. *Oecologia* **130**, 555-562.

Kalamees R. & Zobel M. (1998). Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, western Estonia. *Acta Oecologica* **19**, 175-180.

Kalamees R. & Zobel M. (2002). The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology* **83**, 1017-1025.

Kammer P. M. (2002). Developmental responses of subdominant grassland species to current weather conditions and their relevance for annual vegetation changes. *Folia Geobotanica & Phytotaxonomica* **37**, 185-204.

Keane R. M. & Crawley M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* **17**, 164-170.

Kelly R. H. & Burke I. C. (1997). Heterogeneity of soil organic matter following death of individual plants in shortgrass steppe. *Ecology* **78**, 1256-1261.

Kemp D. R. & Dowling P. M. (1991). Species distribution within improved pastures over central New South Wales (Australia) in relation to rainfall and altitude. *Australian Journal of Agricultural Research* **42**, 647-660.

Kennedy T. A., Naeem S., Howe K. M., Knops J. M. H., Tilman G. D. & Reich P. B. (2002). Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636-638.

King K. W. & Balogh J. C. (2000). Development of a Nitrogen-Release Algorithm for Slow Release Fertilizers. *Transactions Of The American Society Of Agricultural Engineers* **43**, 661-664.

Kirkpatrick J., McDougall K. & Hyde M. K. (1995). *Australia's most threatened ecosystem*. Surrey Beatty and Sons, in association with The World Wide Fund for Nature, Chipping Norton, NSW.

Kloot P. M. (1980). Dr. Richard Schomburgk's "Naturalised Weeds" (1879). *Journal of Adelaide Botanic Gardens* **2**, 195-220.

Knapp A. K. (1984). Water relations and growth of 3 grasses during wet and drought years in a tallgrass prairie. *Oecologia* **65**, 35-43.

Knapp A. K., Fahnestock J. T., Hamburg S. P., Statland L. B., Seastedt T. R. & Schimel D. S. (1993). Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. *Ecology* **74**, 549-560.

Kolar C. S. & Lodge D. M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**, 199-204.

Kolb A., Alpert P., Enters D. & Holzapfel C. (2002). Patterns of invasion within a grassland community. *Journal of Ecology* **90**, 871-881.

Kotanen P. M. (1997). Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. *Journal of Applied Ecology* **34**, 631-644.

Lauenroth W. K. & Dodd J. L. (1978). The effects of water and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* **36**, 211-222.

Lauenroth W. K. & Milchunas D. G. (1992). Short-Grass Steppe. In: *Natural grasslands: Introduction and western hemisphere* (ed. R. T. Coupland) pp. 183-226. Elsevier, Amsterdam.

Leishman M. R. (1999). How well do plant traits correlate with establishment ability? Evidence from a study of 16 calcareous grassland species. *New Phytologist* **141**, 487-496.

Lenz T. I., Moyle-Croft J. L. & Facelli J. M. (2003). Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. *Austral Ecology* **28**, 23-32.

Levang-Brilz N. & Biondini M. E. (2002). Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains Grasslands, USA. *Plant Ecology* **165**, 117-144.

Levine J. M. (2000). Species diversity and biological invasions: Relating local process to community pattern. *Science* **288**, 852-854.

Levine J. M. & D'Antonio C. M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15-26.

Li L., Chen Z., Wang Q., Liu X. & Li Y. (1997). Changes in soil carbon storage due to over-grazing in *Leymus chinensis* steppe in the Xilin River Basin of Inner Mongolia. *Journal of Environmental Sciences China* **9**, 486-490.

Li Sheng G., Harazono Y., Oikawa T., Zhao Ha L., He Zong Y. & Chang Xue L. (2000). Grassland desertification by grazing and the resulting micrometeorological changes in Inner Mongolia. *Agricultural and Forest Meteorology* **102**, 125-137.

Lodge G. M. (1994). The role and future use of perennial native grasses for temperate pastures in Australia. *New Zealand Journal of Agricultural Research* **37**, 419-426.

Lonsdale W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522-1536.

Lunt, I.D., Barlow, T. & Ross, J.(1998). Plains Wandering: Exploring the grassy plains of south-eastern Australia. Victorian National Parks Association and the Trust for Nature (Victoria), Melbourne.

Lutge B. U., Hardy M. B. & Hatch G. P. (1998). Soil and sward characteristics of patches and non-patches in the Highland Sourveld of South Africa. *Tropical Grasslands* **32**, 64-71.

Mack R. N. (1981). Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. *Agro-Ecosystems* **7**, 145-165.

Mack R. N. (1989). Temperate grasslands vulnerable to plant invasions: Characteristics and consequences. In: *Biological Invasions: A Global Perspective* (eds. J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek & M. Williamson) pp. 155-179. John Wiley and Sons, New York.

Maestre F. T., Bautista S., Cortina J. & Bellot J. (2001). Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* **11**, 1641-1655.

Maestre F. T., Huesca M., Zaady E., Bautista S. & Cortina J. (2002). Infiltration, penetration resistance and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe. *Soil Biology & Biochemistry* **34**, 895-898,.

Markham J. H. & Chanway C. P. (1996). Measuring plant neighbour effects. *Functional Ecology* **10**, 548-549.

Maron J. L. & Connors P. G. (1996). A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* **105**, 302-312.

Maron, J.L. & Jeffries, R.L. (2001) Restoring enriched grasslands: Effects of mowing on species richness, productivity, and nitrogen retention. *Ecological Applications* 11, 1088-1100.

Marschner H. (1995). *Mineral nutrition of higher plants*. Academic Press, London.

Marshall D. R. & Jain S. K. (1969). Interference in pure and mixed populations of *Avena fatua* and *Avena barbata*. *Journal of Ecology* **57**, 251-270.

Materechera S. A., Mandiringana O. T., Mbokodi P. M. & Nyamapfene K. (1998). Organic matter, pH and nutrient distribution in soil layers of a savanna Thornveld subjected to different burning frequencies at Alice in the Eastern Cape. *South African Journal of Plant and Soil* **15**, 109-115.

Maxwell S. E. (2003). Changes to plant community structure by invasive species: influence on arthropod communities in natural temperate grasslands. Unpublished Honours Thesis pp. 60, Environmental Biology, University of Adelaide, Adelaide.

Mayor M. D., Boo R. M., Pelaez D. V. & Elia O. R. (2003). Seasonal variation of the soil seed bank of grasses in central Argentina as related to grazing and shrub cover. *Journal of Arid Environments* **53**, 467-477.

Maze K. M., Koen T. B. & Watt L. A. (1993). Factors influencing the germination of six perennial grasses of central New South Wales. *Australian Journal of Botany* **41**, 79-90.

McCune B. & Grace J. B. (2002). *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.

McCune B. & Keon D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* **13**, 603-606.

McCune B. & Mefford M. J. (1999). PC-ORD. MjM Software, Gleneden Beach, Oregon.

McGraw J. B. & Chapin F. S. I. (1989). Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* spp. *Ecology* **70**, 736-749.

McIntosh P. D. & Allen R. B. (1998). Effect of exclosure on soils, biomass, plant nutrients, and vegetation, on unfertilised steeplands, Upper Waitaki District, South Island, New Zealand. *New Zealand Journal of Ecology* **22**, 209-217.

McIntosh P. D., Allen R. B. & Scott N. (1997). Effects of exclosure and management on biomass and soil nutrient pools in seasonally dry high country, New Zealand. *Journal of Environmental Management* **51**, 169-186.

McIntyre S. & Lavorel S. (1994). How environmental and disturbance factors influence species composition in temperature Australian grasslands. *Journal of Vegetation Science* **5**, 373-384.

Melgoza G., Nowak R. S. & Tausch R. J. (1990). Soil water exploitation after fire: Competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**, 7-13.

Milbau A., Nijs I., Van Peer L., Reheul D. & De Cauwer B. (2003). Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. *New Phytologist* **159**, 657-667.

Milchunas D. G., Lauenroth W. K. & Chapman P. L. (1992). Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia* **92**, 520-531.

Milchunas D. G., Lauenroth W. K., Chapman P. L. & Kazempour M. K. (1989). Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* **80**, 11-24.

Milchunas D. G., Sala O. E. & Lauenroth W. K. (1988). A generalised model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**, 87-106.

Miller T. E. & Werner P. A. (1987). Competitive effects and responses between plant species in a first-year old-field community. *Ecology* **68**, 1201-1210.

Moore C. W. E. (1964). Distribution of grasslands. In: *Grasses & Grasslands* (ed. C. Barnard) pp. 182-205. MacMillan & Co Ltd, London.

Moore J. L., Mouquet N., Lawton J. H. & Loreau M. (2001). Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos* **94**, 303-314.

Morgan J. W. (1998a). Importance of canopy gaps for recruitment of some forbs in *Themeda triandra*-dominated grasslands in south-eastern Australia. *Australian Journal of Botany* **46**, 609-627.

Morgan J. W. (1998b). Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *Journal of Vegetation Science* **9**, 181-190.

Morgan J. W. (1998c). Small-scale plant dynamics in temperate *Themeda triandra* grasslands of southeastern Australia. *Journal of Vegetation Science* **9**, 347-360.

Morgan J. W. (2001). Seedling recruitment patterns over 4 years in an Australian perennial grassland community with different fire histories. *Journal of Ecology* **89**, 908-919.

Morrow L. A. & Stahlman P. W. (1984). The history and distribution of downy brome (*Bromus tectorum*) in North America. *Weed Science* **32**, 2-6.

Muller B. & Garnier E. (1990). Components of relative growth rate and sensitivity to nitrogen availability in annual and perennial species of *Bromus*. *Oecologia* **84**, 513-518.

Mwendera E. J., Saleem M. A. M. & Dibabe A. (1997). The effect of livestock grazing on surface runoff and soil erosion from sloping pasture lands in the Ethiopian highlands. *Australian Journal of Experimental Agriculture* **37**, 421-430.

Myers J. H. & Bazely D. (2003). *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge.

Naeem S., Knops J. M. H., Tilman G. D., Howe K. M., Kennedy T. A. & Gale S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**, 97-108.

Naeth M. A., Chanasyk D. S., Rothwell R. L. & Bailey A. W. (1991). Grazing impacts on soil water in mixed prairie and fescue grassland ecosystems of Alberta (Canada). *Canadian Journal of Soil Science* **71**, 313-326.

Naeth M. A., Pluth D. J., Chanasyk D. S., Bailey A. W. & Fedkenheuer A. W. (1990). Soil compacting impacts of grazing in mixed prairie and fescue grassland ecosystems of Alberta (Canada). *Canadian Journal of Soil Science* **70**, 157-168.

Navas M.-L., Garnier E., Austin M. P., Viaud A. & Gifford R. M. (2002). Seeking a sound index of competitive intensity: Application to the study of biomass production under elevated CO_2 along a nitrogen gradient. *Austral Ecology* **27**, 463-473.

Nernberg D. & Dale M. R. T. (1997). Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. *Canadian Journal of Botany* **75**, 2140-2145.

Newsome A. E. & Noble I. R. (1986). Ecological and physiological characteristics of invasive species. In: *Ecology of Biological Invasions* (eds. R. H. Groves & J. J. Burdon) pp. 1-20. Cambridge University Press, Cambridge.

Nicholson P. H. (1981). Fire and the Australian Aborigine - an enigma. In: *Fire and the Australian biota* (eds. A. M. Gill, R. H. Groves & I. R. Noble) pp. 55-76. Australian Academy of Science, Canberra.

Nicholson R. A. & Hui C. (1993). Growth and survival of Japanese brome on limestone soils in western Kansas. *Prairie Naturalist* **25**, 185-195.

Northcote K. H. (1960). Atlas of Australian Soils: Sheet 1: Port Augusta - Adelaide - Hamilton area. Commonwealth Scientific and Industrial Research Organization, in association with Melbourne University Press, Canberra, A.C.T.

O'Connor T. G. (1991). Local extinction in perennial grasslands: A life-history approach. *American Naturalist* **137**, 753-773.

O'Connor T. G. & Roux P. W. (1995). Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: Influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology* **32**, 612-626.

Ogle S. M., Reiners W. A. & Gerow K. G. (2003). Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist* **149**, 46-58.

Oksanen L., Fretwell S. D., Arruda J. & Niemela P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**, 240-261.

Orians G. H. (1986). Site characteristics favouring invasions. In: *Ecology of Biological Invasions of North America and Hawaii.* (eds. H. A. Mooney & J. A. Drake) pp. 133-148. Springer-Verlag, New York.

Osem Y., Perevolotsky A. & Kigel J. (2002). Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology* **90**, 936-946.

Paschke M. W., McLendon T. & Redente E. F. (2000). Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* **3**, 144-158.

Peart D. R. (1989). Species interactions in a successional grassland: II. Colonization of vegetated sites. *Journal of Ecology* **77**, 252-266.

Peco B., Ortega M. & Levassor C. (1998). Similarity between seed bank and vegetation in Mediterranean grassland: A predictive model. *Journal of Vegetation Science* **9**, 815-828.

Pérez-Fernández M. A., Lamont B. B., Marwick A. L. & Lamont W. G. (2000). Germination of seven exotic weeds and seven native species in south-western Australia under steady and fluctuating water supply. *Acta Oecologica* **21**, 323-336.

Pettit N. E., Ladd P. G. & Froend R. H. (1998). Passive clearing of native vegetation: Livestock damage to remnant jarrah (*Eucalyptus marginata*) woodlands in western Australia. *Journal of the Royal Society of Western Australia* **81**, 95-106.

Poorter H. & Nagel O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* **27**, 595-607.

Prober S. M., Thiele K. R. & Lunt I. D. (2002). Identifying ecological barriers to restoration in temperate grassy woodlands: soil changes associated with different degradation states. *Australian Journal of Botany* **50**, 699-712.

Pugnaire F. I., Haase P. & Puigdefabregas J. (1996). Facilitation between higher plant species in a semiarid environment. *Ecology* **77**, 1420-1426.

Pywell R. F., Bullock J. M., Roy D. B., Warman L., Walker K. J. & Rothery P. (2003). Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* **40**, 65-77.

Quilchano C., Egido J. A. & Gonzalez M. I. (1995). Climate sequence of soils developed on granites in the Sierra de Gata, Salamanca, Spain. *Arid Soil Research and Rehabilitation* **9**, 385-397.

Quinn J. A. & Hodgkinson K. C. (1983). Population variability in *Danthonia caespitosa* (Gramineae) in responses to increasing density under 3 temperature regimes. *American Journal of Botany* **70**, 1425-1431.

Quinn J. A. & Hodgkinson K. C. (1984). Plasticity and population differences in reproductive characters and resource allocation in *Danthonia caespitosa* (Graminae). *Bulletin of the Torrey Botanical Club* **111**, 19-27.

Rayment G. E. & Higginson F. R. (1992). *Australian laboratory handbook of soil and water chemical methods*. Inkata Press, Melbourne.

Rejmánek M. (1989). Invasibility of plant communities. In: *Biological Invasions: A Global Perspective* (eds. J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek & M. Williamson) pp. 369-388. John Wiley and Sons, New York.

Renzhong W. & Ripley E. A. (1997). Effects of grazing on a *Leymus chinensis* grassland on the Songnen plain of north-eastern China. *Journal of Arid Environments* **36**, 307-318.

Reynolds H. L. & D'Antonio C. M. (1996). The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. *Plant and Soil* **185**, 75-97.

Reynolds H. L., Hungate B. A., Chapin F. S. I. & D'Antonio C. M. (1997). Soil heterogeneity and plant competition in an annual grassland. *Ecology* **78**, 2076-2090.

Reynolds S. A., Corbin J. D. & D'Antonio C. M. (2001). The effects of litter and temperature on the germination of native and exotic grasses in a coastal California grassland. *Madroño* **48**, 230-235.

Ripley E. A. (1992). Grassland climate. In: *Natural grasslands: introduction and Western hemisphere* (ed. R. T. Coupland) pp. 7-24. Elsevier, Amsterdam.

Robertson M. A. (1998). A biological survey of grasslands and grassy woodlands of the Lofty Block Bioregion South Australia 1995-1996. Department of Environment, Heritage and Aboriginal Affairs, Adelaide.

Romo J. T. & Eddleman L. E. (1987). Effects of Japanese brome on growth of bluebunch wheatgrass, junegrass and squirreltail seedlings. *Reclamation & Revegetation Research* **6**, 207-218.

Ross D. J., Speir T. W., Tate K. R. & Feltham C. W. (1997). Burning in a New Zealand snow-tussock grassland: Effects on soil microbial biomass and nitrogen and phosphorus availability. *New Zealand Journal of Ecology* **21**, 63-71.

Ross J. (1999). Guide to best practice conservation of temperate native grasslands pp. 75 pages. World Wide Fund for Nature (Australia), Environment Australia.

Roush M. L. & Radosevich S. R. (1985). Relationships between growth and competitiveness of four annual weeds. *Journal of Applied Ecology* **22**, 895-906.

Schlesinger W. H., Raikes J. A., Hartley A. E. & Cross A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**, 364-374.

Scott A. W. & Whalley R. D. B. (1982). The distribution and abundance of species of *Danthonia* on the New England tablelands (Australia). *Australian Journal of Ecology* **7**, 239-248.

Seabloom E. W., Harpole W. S., Reichman O. J. & Tilman G. D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 13384-13389.

Semmartin M. & Oesterheld M. (1996). Effect of grazing pattern and nitrogen availability on primary productivity. *Oikos* **75**, 431-436.

Shea K. & Chesson P. L. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**, 170-176.

Sheppard A. W., Smyth M. J. & Swirepik A. (2001). The impact of a root-crown weevil and pasture competition on the winter annual *Echium plantagineum*. *Journal of Applied Ecology* **38**, 291-300.

Silvertown J., Dodd M. E., McConway K. J., Potts J. & Crawley M. J. (1994). Rainfall, biomass variation, and community composition in the Park Grass Experiment. *Ecology* **75**, 2430-2437.

Singh J. S., Bourgeron P. S. & Lauenroth W. K. (1996). Plant species richness and species-area relations in a shortgrass steppe in Colorado. *Journal of Vegetation Science* **7**, 645-650.

Singh J. S., Milchunas D. G. & Lauenroth W. K. (1998). Soil water dynamics and vegetation patterns in a semiarid grassland. *Plant Ecology* **134**, 77-89.

Smeins F. E., Diamond D. D. & Hanselka C. W. (1992). Coastal Prairie. In: *Natural grasslands: Introduction and western hemisphere* (ed. R. T. Coupland) pp. 269-290. Elsevier, Amsterdam.

Smith M. D. & Knapp A. K. (2001). Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *International Journal of Plant Sciences* **162**, 785-792.

Stachowicz J. J., Fried H., Osman R. W. & Whitlatch R. B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology* **83**, 2575-2590.

Stohlgren T. J., Schell L. D. & Vanden Heuvel B. (1999). How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* **9**, 45-64.

Stromberg M. R. & Griffin J. R. (1996). Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* **6**, 1189-1211.

Stuwe J. & Parsons R. F. (1977). *Themeda triandra* grassland on the basalt plains, Victoria: floristics and management effects. *Australian Journal of Ecology* **2**, 467-476.

Suding K. N. & Goldberg D. E. (2001). Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* **82**, 2133-2149.

Svejcar T. & Sheley R. (2001). Nitrogen dynamics in perennial- and annual-dominated arid rangeland. *Journal of Arid Environments* **47**, 33-46.

Theodose T. A., Jaegeri C. H. I., Bowman W. D. & Schardt J. C. (1996). Uptake and allocation of 15N in alpine plants: Implications for the importance of competitive ability in predicting community structure in a stressful environment. *Oikos* **75**, 59-66.

Thompson K., Hodgson J. G., Grime J. P. & Burke M. J. W. (2001). Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *Journal of Ecology* **89**, 1054-1060.

Thompson L. M. & Troeh F. R. (1973). *Soils and soil fertility*. McGraw-Hill, New York.

Tilman G. D. (1977). Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* **58**, 338-348.

Tilman G. D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton.

Tilman G. D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81-92.

Tilman G. D. & El Haddi A. (1992). Drought and biodiversity in grasslands. *Oecologia* **89**, 257-264.

Troumbis A. Y., Galanidis A. & Kokkoris G. D. (2002). Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos* **98**, 239-250.

Underwood A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology Annual Review* **19**, 513-605.

Underwood A. J. (1997). *Experiments in ecology*. Cambridge University Press, Cambridge.

Van der Putten W. H., Mortimer S. R., Hedlund K., Van Dijk C., Brown V. K., Leps J., Rodriguez-Barrueco C., Roy J., Diaz Len T. A., Gormsen D., Korthals G. W., Lavorel S., Santa Regina I. & Smilauer P. (2000). Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. *Oecologia* **124**, 91-99.

Veenendaal E. M., Ernst W. H. O. & Modise G. S. (1996). Reproductive effort and phenology of seed production of savanna grasses with different growth form and life history. *Vegetatio* **123**, 91-100.

Vila M. & Lloret F. (2000). Seed dynamics of the mast seeding tussock grass *Ampelodesmos mauritanica* in Mediterranean shrublands. *Journal of Ecology* **88**, 479-491.

Vinton M. A. & Burke I. C. (1995). Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology* **76**, 1116-1133.

Vitousek P. M., Walker L. R., Whiteaker L. D., Mueller-Dombois D. & Matson P. A. (1987). Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* **238**, 802-804.

von Ende C. N. (1993). Repeated-measures analysis: Growth and other time-dependent measures. In: *Design and Analysis of Ecological Experiments*. (eds. S. M. Scheiner & J. Gurevitch) pp. 113-137. Chapman & Hall, New York.

Walsh N. G. & Entwistle T. J. (1994). *Flora of Victoria*. Inkata Press, Melbourne.

Wardle D. A., Bonner K. I., Barker G. M., Yeates G. W., Nicholson K. S., Bardgett R. D., Watson R. N. & Ghani A. (1999). Plant removals in perennial grassland: Vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* **69**, 535-568.

Warren J., Christal A. & Wilson F. (2002). Effects of sowing and management on vegetation succession during grassland habitat restoration. *Agriculture Ecosystems & Environment* **93**, 393-402.

Watson L. & Dallwitz M. J. (1980). *Australian grass genera: Anatomy, morphology and keys*. The Australian National University Research School of Biological Sciences, Canberra.

Welden C. W. & Slauson W. L. (1986). The intensity of competition versus its importance: an overlooked distinction and some implications. *The Quarterly Review of Biology* **61**, 23-44.

Whisenant S. G. (1990). Postfire population dynamics of *Bromus japonicus*. *American Midland Naturalist* **123**, 301-308.

Whitford W. G., Steinberger Y., MacKay W. P., Parker L. W., Freckman D., Wallwork J. A. & Weems D. (1986). Rainfall and decomposition in the chihuahuan desert. *Oecologia* **68**, 512-515.

Willatt S. T. & Pullar D. M. (1984). Changes in soil physical properties under grazed pastures. *Australian Journal of Soil Research* **22**, 343-348.

Williams J., Prebble R. E., Williams W. T. & Hignett C. T. (1983). The influence of texture, structure and clay mineralogy on the soil moisture characteristic. *Australian Journal of Soil Research* **21**, 15-32.

Williams O. B. (1961). Studies in the ecology of the riverine plain. III. Phenology of a *Danthonia caespitosa* Gaudich. grassland. *Australian Journal of Agricultural Research* **12**, 247-259.

Williams R. G. (2003). The effects of grazing by sheep (and kangaroos) on plant diversity in a Lomandra Tussock grassland community in South Australia (Draft). In: *Environmental Biology, School of Earth & Environmental Sciences.* University of Adelaide, Adelaide.

Williamson G. J. (2002). The effects of temporal water heterogeneity on competition and coexistence in arid ephemeral plants. Honours Thesis. In: *Environmental Biology* pp. 70. University of Adelaide, Adelaide.

Wilson S. D. & Tilman G. D. (1995). Competitive responses of eight old-field plant species in four environments. *Ecology* **76**, 1169-1180.

Young J. A. & Evans R. A. (1989). Seed production and germination dynamics in California annual grasslands. In: *Grassland structure and function: California annual grassland* (eds. L. F. Huenneke & H. A. Mooney) pp. 39-45. Kluwer, Dordrecht.

Zar J. H. (1984). *Biostatistical analysis.* Prentice-Hall International, Englewood Cliffs, New Jersey, USA.

Zhou G., Wang Y. & Wang S. (2002). Responses of grassland ecosystems to precipitation and land use along the Northeast China Transect. *Journal of Vegetation Science* **13**, 361-368.

Zobel M., Otsus M., Liira J., Moora M. & Mols T. (2000). Is small-scale species richness limited by seed availability or microsite availability? *Ecology* **81**, 3274-3282.